# Competition Dynamics in Invertebrates Across Geographical Gradients

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## Abstract

Studying competition dynamics of invertebrate species is essential to understanding species distribution, how species become invasive, and dealing with pests and pollinators. However, there is a gap in the literature when it comes to what geographical factors influence invertebrate competition. This study investigates competition dynamics of terrestrial invertebrates across various ecosystems and geographical areas, as well potential predictors for the patterns observed. I used food lures across sites in multiple countries, and recorded the number of visitors and level of consumption to attribute a competition score to each lure. Three different food types were used to account for dietary preferences (Fat, Protein, and Sugar). The results show that there is a significant variation of competition scores across sites. In addition, I identified a significant statistical interaction between sites and food types in relation to competition scores, which suggests that competition is different between the sites, but the pattern of variation differs per food type. A regression was conducted to see if Net Primary Productivity or the geological age of an ecosystem were predictors of the variation in competition scores. Geological age came out statistically significant for the scores in the Fat food type, suggesting that it may be an important driver for invertebrate competition. Idiosyncrasies of the sites are discussed with the aim to identify other factors that may affect competition levels and their patterns. This research contributes to the study of competition dynamics in terrestrial invertebrates and could inspire an approach to predicting interactions and effects of new or introduced species.

## Introduction

Studying interactions between species is at the core of ecology, and research on competition dynamics is important as dominant species can influence the distribution of other organisms, such as pests, pathogens, and invasive species (Ribas, 2002). There have been several studies that investigate how invertebrate diversity is affected by geographical characteristics (Kaspari et al., 2004, Guilherme et al., 2019), yet there is little in the literature on the magnitude of competition in terrestrial invertebrates across these gradients. Thus, in this study I aim to investigate the competition dynamics of invertebrate species from varying locations and characteristics. To do so, I analyze competition levels and mechanisms at each site and then evaluate if Net Primary Productivity (NPP) and geological age are predictors for these competition levels.

Net Primary Productivity (NPP) is defined as the result of the gross amount of energy fixed by plants through photosynthesis minus the energy they use for respiration (Woodwell & Whittaker, 1968). This net energy is then available to the plant to grow in biomass, so NPP relates to a measure of energy available for creating an amount of biomass in an area or ecosystem. Since the NPP of a location is affected by its environmental factors (Guilherme et al., 2021), NPP could serve as a proxy for the effect of climate and resources on invertebrate communities. Previous studies show that some environmental variables can be essential in shaping insect distribution at large scales (Kaspari et al., 2000, 2004). For example, precipitation is correlated with ant species turnover (Vasconcelos et al., 2010), and vegetation density is strongly associated with both functional and taxonomic composition of ants (Guilherme et al., 2019). In addition, the energy limitation hypothesis directly links the species richness (number of species in a community) of consumer taxa to NPP as it conveys that NPP limits a taxon's density in an area, and it has been demonstrated on ant abundances (Kaspari et al., 2000). This tells us that as climatic conditions limit NPP, NPP in turn limits the abundance of resources, which then affects the abundance of consumers the ecosystem can sustain, and so forth with higher trophic levels (Guilherme et al., 2021). Thus, the factors that drive NPP of an ecosystem can affect the abundance and richness of its invertebrates. When investigating competition, such information is valuable since larger invertebrate communities could facilitate the development of numerous interactions and of diverse nature. These make NPP an important variable to test as a predictor of competition, so I will use it as one of the two proposed factors of competition in this study.

The second variable is geological age. The geological age of the ecosystem is an important factor to study because it can be a driver at the regional level of the interaction networks between and within species (Trøjelsgaard, 2013). According to Trøjelsgaard (2013), 1) at young islands most organisms are generalists and interactions between them are weak, 2) at mid aged sites there is a peak of speciation, so niches are filled, and 3) at old areas, there is a decline in speciation and species are becoming more of generalists because the fauna are at a point where they cannot survive solely from individual niches so they have to adapt to a wider set of conditions. Furthermore, old islands have unique interactions that have evolved through time and everything is highly connected (Trøjelsgaard, 2013). In relation to and often due to speciation, species richness is also affected by the age of the land. The geographical age hypothesis says that the species richness of organisms increases with the geological age of the ecosystem, and it has been proven applicable in several locations, including Azores islands (Borges, 1999). Furthermore, this hypothesis is also supported by the 'species-pool hypothesis' (Taylor et al., 1990) which predicts that "all else being equal, the larger the local and/or global area of a habitat type and the older its geological age, the greater the past opportunity for speciation and hence, the greater the number of available species that are adapted to that particular type of habitat". So geological age will be a proposed driver of competition in this study.

The purpose of this research is to learn about competition dynamics of terrestrial invertebrates and by doing so, shed light into how species interact in several ecosystems and what forces affect competition. Knowledge of these mechanisms can enhance conservation planning and species distribution modelling by helping scientists see patterns and do predictions more accurately. The big picture goal is to provide information to better protect important species, control pests, and manage invasive species. Thus, this study holds value in the advancement of knowledge of competition dynamics that is needed for solving real world issues.

The objectives of my research are to 1) understand site-based differences in invertebrate competition dynamics and the factors in their differences, and 2) analyze if and how invertebrate competition correlates with NPP and geological age of a site. My hypothesis is that NPP and geological age are significant factors of and positively correlated to invertebrate competition in terrestrial ecosystems, based on the theories and literature above. More specifically, I hypothesize that a site with high NPP and great geological age will experience high competition as it supports many species that have adapted and coevolved to compete for resources in filled niches. In contrast, I think that a low NPP in a young land will lead to low competition as there are still open niches and there are few interactions due to the low invertebrate abundance in the site. On the other hand, a low NPP and large age may lead to moderately high competition because interactions have developed through time but there is low species abundance so less interactions seen. Finally, a high NPP with a young age may generate moderately low competition as open niches may still be available, but the population is growing fast so many interactions are developed.

# Methods

## Study Sites

This experiment was conducted in person in these five geographical locations: San Cristobal, Galapagos; Tiputini, Ecuadorian Amazon Forest; Appledore, ME USA; Craigieburn, South Island, New Zealand; and Whakatīwai, North Island, New Zealand (coordinates in Appendix B). I tested two different areas (high (H) and low (L) elevation within the ecosystem) in each place, so in total this study had ten sample areas (from here on referred to as "Sites" (Table 1)). The choice of these study Sites was constrained by lack of travel funding for this study, and therefore Sites had to be accessible during my time at Cornell and my studies abroad. Within that constraint, I chose Sites that encompassed a wide range of latitudes, geographic characteristics, and varying ecosystem types, to have as ample representation as could be available. This is important for this study because it allows for better analysis in if the proposed drivers of competition are indeed factors that affect interactions of terrestrial invertebrates in general, instead of being only significant regionally. This is supported by how some studies suggest differences in invertebrate abundance and competition with changing latitudes (Procter, 1984; Schemske et al., 2009).

The Galapagos Islands are located 972km west off the Ecuadorian Coast (Wauters, 2014), and the experiment was conducted on San Cristobal island, one of the oldest in the archipelago with estimated emergence of 2.4 Ma (Percy, 2020). Due to the highly variable weather, there is a climosequence strongly dependent on elevation, ranging from very arid at the coastline to humid at the summit (Percy, 2020). This work was conducted on the arid lowlands in Puerto Baquerizo Moreno vs humid highlands around Hacienda Tranquila. The humid highlands have luscious green vegetation, and its main land use is for agriculture (such as banana and sugarcane plantations) (Hamann, 1979). The lowlands are in the Dry Zone (Schofield, 1989) and are arid with fewer plants. The data from the lowlands was collected within the town of San Cristobal.

The Amazon Sites are located in the Tiputini Biodiversity Station within the Parque Nacional Yasuní in the Ecuadorian Amazon. The area of the station is one of the closest to being pristine in the tropical forest of this country and is situated next to the Tiputini River. The Amazon H Site is referred by locals as "Terra Firme" as it is an area farther from and more elevated than the river so the water from precipitation that is not absorbed by the soil and plants is usually flushed out down to the river (Myster, 2014; Nigel et. al., 1999). The Amazon L Site on the other hand, is in the "Flooded Forest", which is an area next to the river that frequently floods from precipitation and water level rise (Myster, 2014). The weather during collection was hot and humid, was generally sunny, but had brief strong precipitation.

Appledore Island is located 10 km off the coast of Portsmouth, Maine in the Gulf of Maine. The data collection Sites were on the Shoals Marine Laboratory housing grounds (Appledore H), and down near the docks (Appledore L). The vegetation in Appledore is mostly herbs, shrubs, and grassy areas (Nichols, 2008). The weather during collection was usually sunny and temperate.

Whakatīwai is a coastal region on the shore of the Firth of Thames, in the Hauraki Gulf, North Island, New Zealand. It is an inhabited area with a low population and its land use mostly going to cattle and sheep pastures. The data collection Sites were within a small grassy program campus

Finally, Craigieburn is a range of mountains south of Arthur's Pass in the Canterbury Region, South Island, New Zealand. The vegetation in the data collection area of this Site was predominantly a pure forest of mountain beech (*Nothofagus solandri* var. *cliffortioides*), and some grasses. This is an alpine zone, so the weather was cool and dry.

## Study Species

The species studied were land invertebrates of any species. The most common organisms that were observed were ants and flies, but at times the lures would attract other insects like very small arthropods, wasps, and crickets. A list of the orders of species seen per Site can be found in Appendix C.

## Experimental Design and Field Methods

As per Wauters et al. 2014's methodology, baits contained 1/2 teaspoon of peanut butter (fat), canned tuna (protein), and granulated sugar or fruit (sugar). These foods were chosen due to their accessibility in all Sites which allows for consistency. The three foods (referred as "Food Types", see Table 1) were placed on a fourth of a 12 cm x 12 cm napkin or toilet paper square. Each bait is treated as one replica as the different food items are used to account for different diet preferences between species (Figure 1). As an observational study, after 15, 30, 45, 60, and 120 minutes of bait placement, the species present and their identity were recorded, and a picture was taken. A group of four baits were placed at four specific Locations (Table 1): 2-10 meters from a building (House), at dense vegetation, on an open area, and on the side of a road. Each bait was placed about 3-10 meters away from the other three baits in the group. There are 2 or 4 groups of four baits per Site, which translates in a total of 4 or 16 baits per Site. The groups were placed as far as possible from each other within the ecosystem borders of the Site. This was done for the ten Sites.

**Figure 1.** Layout of experiment: pieces of a protein (canned tuna, right), a fat (peanut butter, left), and a sugar (orange, bottom) are placed in different small pieces of paper on the ground. These are the three Food Types (Table 1).

## Analytical Methods

A score for competition was given to each food type per experiment:

Competition score = total # of visits during the first 60 minutes x consumption score

For the number of visits, each individual counts as one visit, but if one ant brought its colony, then the pioneer ant and the colony is one unit and thus they count as just one visit. The consumption score was taken by observing how much of the food was consumed or touched during the first 60 minutes (regardless of how much each species ate, and selecting only the highest level of involvement): 1– untouched, 2– touched (an invertebrate was seen eating some of the food, not barely walking over it), 3– food moved around napkin, 4– parts of the food moved off napkin, 5– everything taken.

ANOVA was used in R (R Core Team, 2022) from the package **car** (Fox & Weisberg, 2019) to compare overall competition scores between each Site, Location, and Food Type, as well as a combination of them. The log (score +1) or sqrt(score) were used to account for the zeros (a 0 score means no competition because replica had no visits) and most importantly to make the data be closer to Gaussian distribution. The results are reported based on this form of analysis. The jarque.test function from the package **moments** (Komsta & Novomestky, 2022) was used to determine which of the above transformations were preferred statistically. The preferred transformation is the one that allows a closer approximation of Gaussian residuals, indicated by a lower test statistic in jarque.test, to better satisfy the assumption of having Gaussian residuals for ANOVA. The function emmeans from the package **emmeans** (Lenth, 2023) indicated which pairs of data had significantly different competition scores (i.e. between Sites, Food Types, or Locations). A multiple linear regression also was run for evaluating the joint effects of the two predictors (NPP and geological age) for corresponding competition levels. For the regression analysis, I used the lm function in the **stats** package (R Core Team, 2022) to perform a multiple linear regression of the relationship between NPP, geological age, and Competition Scores (see glossary in Table 1).

**Table 1.** Glossary of terms specific to this paper

| Term | Definition |
|---|---|
| Site | With capital "S". The geographical locations where experiments (lures) were laid out. If written as "site" with lower case "s", then it refers to any location on the world, not specific to this study, when making generalizations |
| Food Type | The kind of food that a lure had to attract invertebrates. There were three food lures placed at each experiment replica: one with a Protein (canned tuna), a Fat (peanut butter), and a Sugar (orange) (Figure 1) |
| Location | With capital "L". The characteristic of the place where a lure was laid out. There were four variations, so four location types for the lures: dense vegetation, open land, on a road, and near a house/building. |
| Geological Age | The age of the ecosystem of each Site, based on when ecosystem as it is known today began to form. |
| NPP | The resulting value of the gross amount of energy fixed by plants through photosynthesis minus the energy they use for respiration (Woodwell & Whittaker, 1968). This net energy is then available to the plant to grow in biomass. |
| Experiment | The placing of three napkins, each with either the protein, fat, or sugar. These three foods are observed and photographed during the period of 60 minutes. The number of invertebrate visitors are counted and the level of consumption assessed. One experiment means one replica. A zone is an area where the foods are placed at four specific Locations. There are 2 or 4 zones per Site, which translates in a total of 4 or 16 experiments per Site. This is done for the ten Sites. |
| Competition Score | Competition score = total # of visits during the first 60 minutes x consumption score. See Analytical Methods for details. |

**Table 2.** NPP values from NASA Data as well as different sources of data across several sites

| Site | Month | Lateral Coordinates Used | Longitudinal Coordinates Used | 2012 | 2013 | 2014 | 2015 | 2016 | NPP of similar locations from different datasets | Author | Year | Location | Average NPP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Galapagos H | February | 0.902 S | 89.611 W | 3.3 | 3.6 | 6.5 | 5.38 | 6.5 | 3.5 (in 2016) | Garcia et. al., 2014 | 2014 | Guayas Providence, Ecuador | 4.80 (in 2016) |
| Galapagos L | February | 0.902 S | 89.611 W | 1.6 | 1.2 | 2.25 | 1.42 | 2.34 | 1.9 | Garcia et. al., 2014 | 2014 | Manabi providence, Ecuador | 1.80 |
| Amazon H | April | 0.638 S | 76.15 W | 1.5 | 3.9 | 1.3 | 2.25 | 3.55 | 2.9 | *Metcalfe et al., 2010 | 2010 | The Caxiuana National Forest, Brazil | 2.57 |
| Amazon L | April | 0.638 S | 76.15 W | 1.5 | 3.9 | 1.3 | 2.25 | 3.55 | 2.9 | *Metcalfe et al., 2010 | 2010 | The Caxiuana National Forest, Brazil | 2.57 |
| Appledore H | July | 42.99 N | 70.615 W | 4.1 | 5.5 | 6.5 | 6.5 | 6.5 | 5.67 | *Magill et al., 1996, Hoeppner& Dukes, 2012 | 2010 | **North East, USA | 5.79 |
| Appledore L | July | 42.99 N | 70.615 W | 4.1 | 5.5 | 6.5 | 6.5 | 6.5 | 5.67 | *Magill et al., 1996, Hoeppner & Dukes, 2012 | 2010 | **North East, USA | 5.79 |
| Whakatiwai H | October | 37.088 S | 175.302 E | 6.5 | 6.5 | 6.47 | 5.38 | 6.5 | 5.56 | *Volder et al., 2007 | 2003 | Grassfield Canberra, ACT, Australia | 6.15 |
| Whakatiwai L | October | 37.088 S | 175.302 E | 6.5 | 6.5 | 6.47 | 5.38 | 6.5 | 5.56 | *Volder et al., 2007 | 2003 | Grassfield Canberra, ACT, Australia | 6.15 |
| Craigieburn H | October | 43.127 S | 171.728 E | 1.2 | 1.6 | 1.89 | 1.81 | 1.51 | 1.29 | Graeme, 2001 | 2001 | Cristchurch hardwood forest, New Zealand | 1.55 |
| Craigieburn L | October | 43.127 S | 171.728 E | 1.2 | 1.6 | 1.89 | 1.81 | 1.51 | 1.29 | Graeme, 2001 | 2001 | Cristchurch hardwood forest, New Zealand | 1.55 |

* From the dataset compiled by Song et. al., 2020
g C / m^2 per day
** Average of northern Maine (Forest) and 2x Waltham, MA, USA (Suburban)

The NPP data are taken from the NASA Earth Observations data set (NASA, 2012-2016), as well as in situ NPP data by individual projects in the areas or similar ecosystems found in the literature (Table 2). The NASA data are averaged over the last 5 years of available data (2012-2016) on the month this study's data was located per Site (Table 3). The geological age of each Site for this study is based on when the present ecosystem began to form (Table 3).

**Table 3.** The Average NPP (NASA data) and geological age of each site

| Site | Average NPP | Ecosystem Age (Myears) |
|---|---|---|
| Galapagos H | 5.06 | 3 |
| Galapagos L | 1.78 | 3 |
| Amazon H | 2.51 | 10 |
| Amazon L | 2.51 | 10 |
| Appledore H | 5.82 | 0.018 |
| Appledore L | 5.82 | 0.018 |
| Whakatiwai H | 6.27 | 80 |
| Whakatiwai L | 6.27 | 80 |
| Craigieburn H | 1.6 | 80 |
| Craigieburn L | 1.6 | 80 |

# Results

Overall, the levels of competition in invertebrates vary by Site, which means there are characteristics of each place that shape its competition dynamics. However, it appears that NPP and geological age are not strong factors for competition. To analyse the data, I compared different variables of the study versus competition scores through two-way ANOVAs and a summary of results can be found in Table 4.

## Competition Scores Versus Sites

There is a significant difference between the Sites when they are analysed against competition scores without a Site-Food Type interaction in a two-way ANOVA (Two-way ANOVA, $F(9,218) = 5.4547$, $p < 0.0001$; Figure 2). The list of which Sites are statistically different can be found in Table 4. In general, it seems that the Amazon (particularly Amazon H) and Appledore Island have higher competition scores than the other Sites (Figure 2). Meanwhile, the Galapagos, Whakatiwai, and Craigieburn L appear to have very similar ranges of competition in invertebrates. Amazon H has three data points that are much larger than most of its scores (Appendix A1), but statistically only one is considered an outlier, so this Site has a higher mean than the others (Figure 2).

It is important to note that this analysis included all scores from all three food types. Hence, I conducted another two-way ANOVA to analyse if there exists an interaction between Site and Food Type, which would indicate that the impact one variable has on competition depends on a second variable. This analysis appeared non-significant ($F(18,198) = 1{,}5642$, $p_{\text{interaction}} = 0.072323$, $p_{\text{Site}} = 1.455e-07$, $p_{\text{Food Type}} = 0.003206$). However, when the three high scores in Amazon H were removed, the result of the interaction of Site:Food Type was significant ($F(18,195) = 1.7966$, $p_{\text{interaction}} = 0.027863$, $p_{\text{Site}} = 3.836e-06$, $p_{\text{Food Type}} = 0.005191$). This tells us that when there are no particular anomalous high scores (Appendix A3), competition between invertebrates is different between Sites but the pattern of variation is not the same for all food types. The discussion section explores the nature of these three high scores.

Since Site and Food Type are interacting, I analysed competition scores versus Site for each separate Food Type. As predicted, we get slightly varying patterns in each Food Type across Sites. For Protein (Figure 3a), the Sites had statistically different scores (Two-way ANOVA, $F(9,66) = 3.1439$, $p < 0.001$). However, this time Appledore (H and L) and Craigieburn L seem to have the highest competition scores while the Amazon, Galapagos, and Whakatiwai had low mean scores. For Fat trials (Figure 3b), statistically significant differences also exist but are fewer (Twoway ANOVA, $F(9,66) = 2.2337$, $p < 0.05$). Here, most noticeably is how Amazon H has a very wide spread compared to the other Sites due to the three trials anomalous high scores, which bring the mean and median up. Apart from the Amazon, Appledore seems to have the highest competition scores, and Craigieburn has the lowest. Finally, sugar lures (Figure 3c) also had a significant difference between the Sites (Two-way ANOVA, $F(9,66) = 4.1778$, $p < 0.0001$). The sugar competition scores are less uniform since Amazon H and Appledore have high medians, while Amazon L, Galapagos H, and Craigieburn have very low medians (close to 0).

## Competition Scores Versus Food Type, and Versus Location

Additional comparisons were conducted with competition versus Food Type and competition scores versus Location. The Food Type comparison was significant (Two-way ANOVA, $F(2,225) = 4.5747$, $p < 0.0001$), and it appears that each type has similar spreads with a few outliers (Figure 4, Appendix A4). Protein has the highest median. On the other hand, the comparison with Location type did not have significant differences (Two-way ANOVA, $F(3,60) = 2.4329$, $p = 0.07$; Figure 5).

## Linear Regression

The results of the previous section show that the scores are different for each Site. Thus, a multiple linear regression was used to test if NPP and geological age (Age) significantly predicted Competition Scores. The fitted regression model was log(`Competition Scores`+1) ~ NPP + log(`Age (years)`) + `Food Type`. The transformation of taking the log of Competition Scores helps brings the data closer to Gaussian, while the log of Age reduces the leverage of extreme values. Because the geological age of Appledore is very small compared to other Sites, the data for Appledore was removed from the analysis to prevent the skew from affecting significance. In the regression equation, Food Type is used to account for the interaction between Site:Food Type previously determined, which suggested predicted competition scores may likely be shaped by Food Type as well. Because the interaction of Site:Location was not significant (Two-way ANOVA, $F(21) = 1.2836$, $p = 0.1933$), Location was excluded from regression analyses.

The overall regression was not statistically significant ($R^2 = 0.02293$, $F(4,175) = 2.05$, $p = 0.08943$), so NPP and Age may not individually predict competition scores. Another identical regression was run but now removing the three anomalous scores in Amazon H by selecting for only the scores below 23. The overall regression for this version was also not statistically significant ($R^2 = 0.01786$ , $F(4,172) = 1.8$, $p = 0.131$) This means that there is not enough statistical evidence that NPP and Age are predictors of all of the competition scores.

However, different results were produced when the linear regression was done for competition scores from each Food Type separately (Table 5). Each of these regressions were conducted with and without selecting for values less than 23. All food regressions except Fat had a nonsignificant overall p value, so again there is not enough evidence that the proposed variables are factors of competition. Only in the regression with Fat competition scores (with score values <23 analysed), there was an overall statistically significant regression value, and here Age was statistically significant ($R^2 = 0.07766$, $F(2,55) = 3.4$, $p = 0.04055$, $\beta_{NPP} = 0.13525$, $p_{NPP} = 0.12275$, $\beta_{Age} = -0.23639$, $p_{Age} = 0.02687$). This means that for competition scores coming from the Fat food type in this study, the geological age of the Site was a significant factor in shaping the competition of its terrestrial invertebrates. Because the estimate is negative, the regression suggests that with higher Age there is less competition seen. Comparing with the box plot, this estimate is unexpected as Galapagos is the youngest Site (when excluding Appledore) and Whakatiwai is the oldest, yet they both show similar ranges in their Fat competition scores.

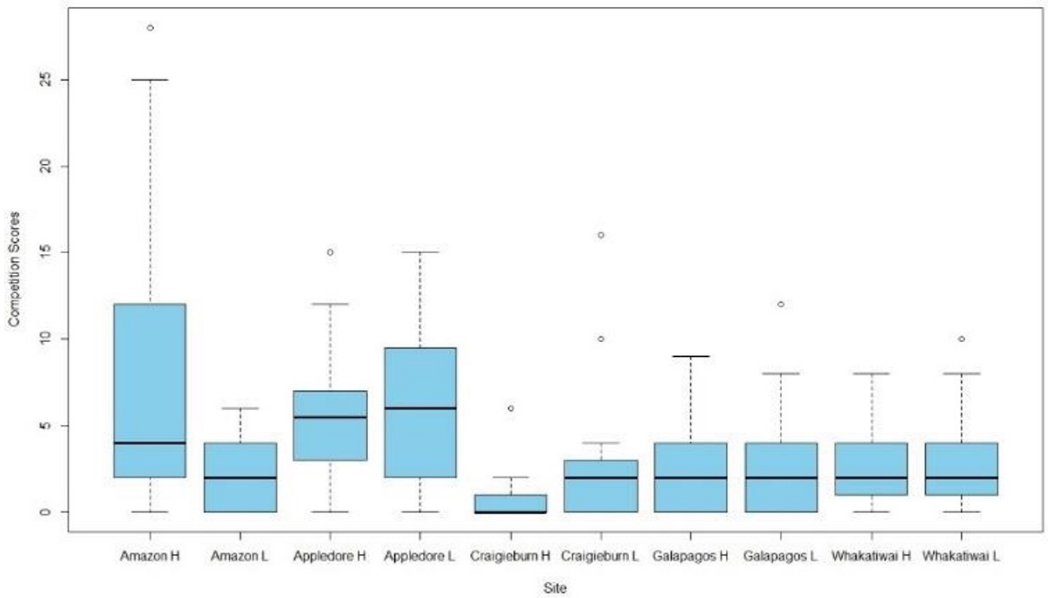
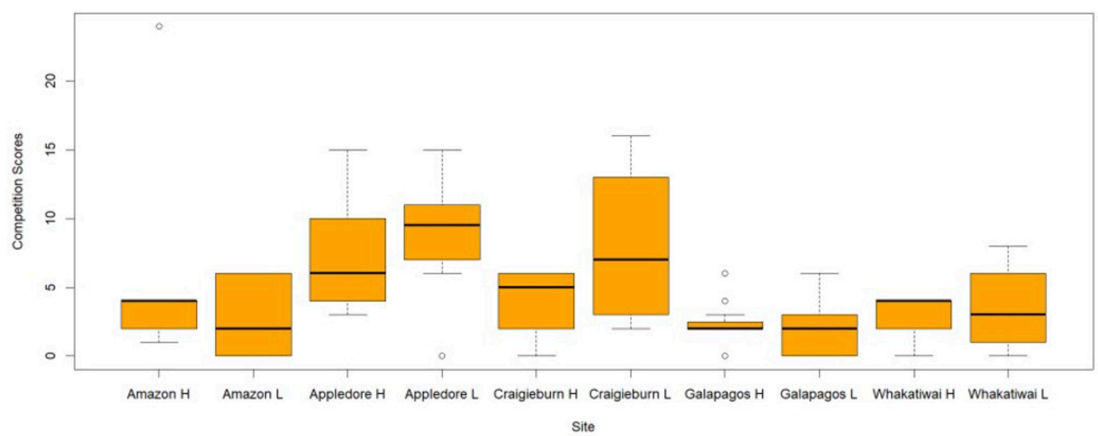
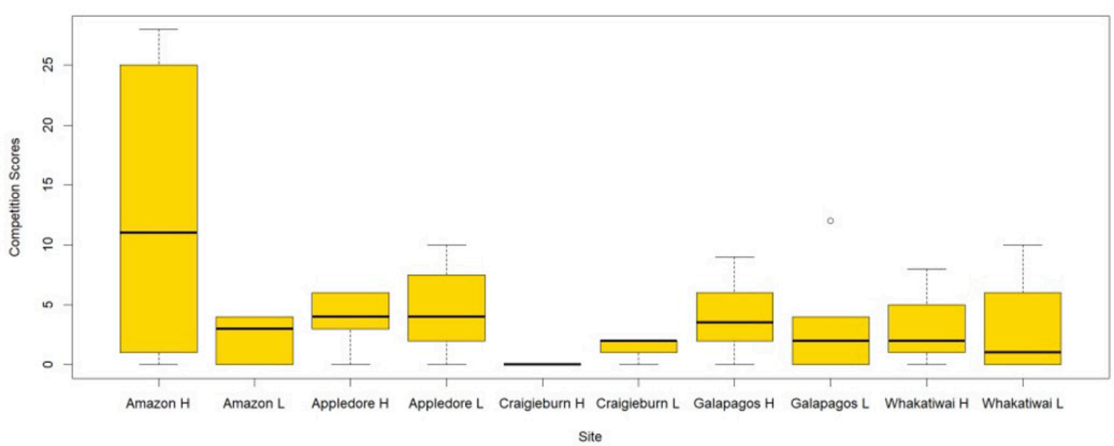



**Figure 2.** Boxplot of Competition Scores versus Sites. There is a significant difference (Two-way ANOVA, $F(9,218) = 5.4547$, $p < 0.0001$) between the Sites. The following Sites were significantly different to each other: Amazon H / Amazon L, Amazon H / Galapagos H, Amazon H / Galapagos L, Amazon H / Craigieburn H, Amazon L / Appledore H, Amazon L / Appledore L, Appledore H / Galapagos H, Appledore H / Galapagos L, Appledore H / Craigieburn H, Appledore H / Craigieburn L, Appledore L / Galapagos L, Appledore L / Craigieburn H

a)




b)



c)

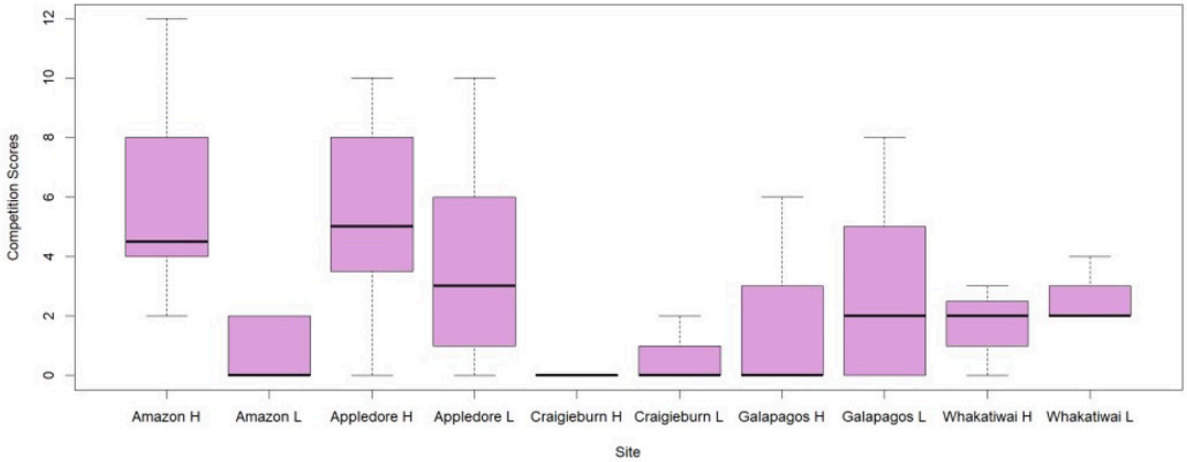



**Figure 3.** The Boxplots show the competition scores for Sites per Food Type. **a.** For Protein the Sites had statistically different scores (Two-way ANOVA, F(9,66) = 3.1439, $p < 0.001$). The following were significantly different to each other: Appledore H / Galapagos L, Appledore L / Galapagos L **b.** For Fat trials there were statistically significant differences (Two-way ANOVA, F(9,66) = 2.2337, $p < 0.05$) in only the following: Amazon H - Craigieburn H **c.** Finally, for the sugar lures there was also a significant difference (Two-way ANOVA, F(9,66) = 4.1778, $p < 0.0001$) between these Sites: Amazon H - Amazon L, Amazon H - Galapagos H, Amazon H - Craigieburn H, Amazon H - Craigieburn L, Amazon L - Appledore H, Appledore H - Galapagos H, Appledore H - Craigieburn H, Appledore H - Craigieburn L.

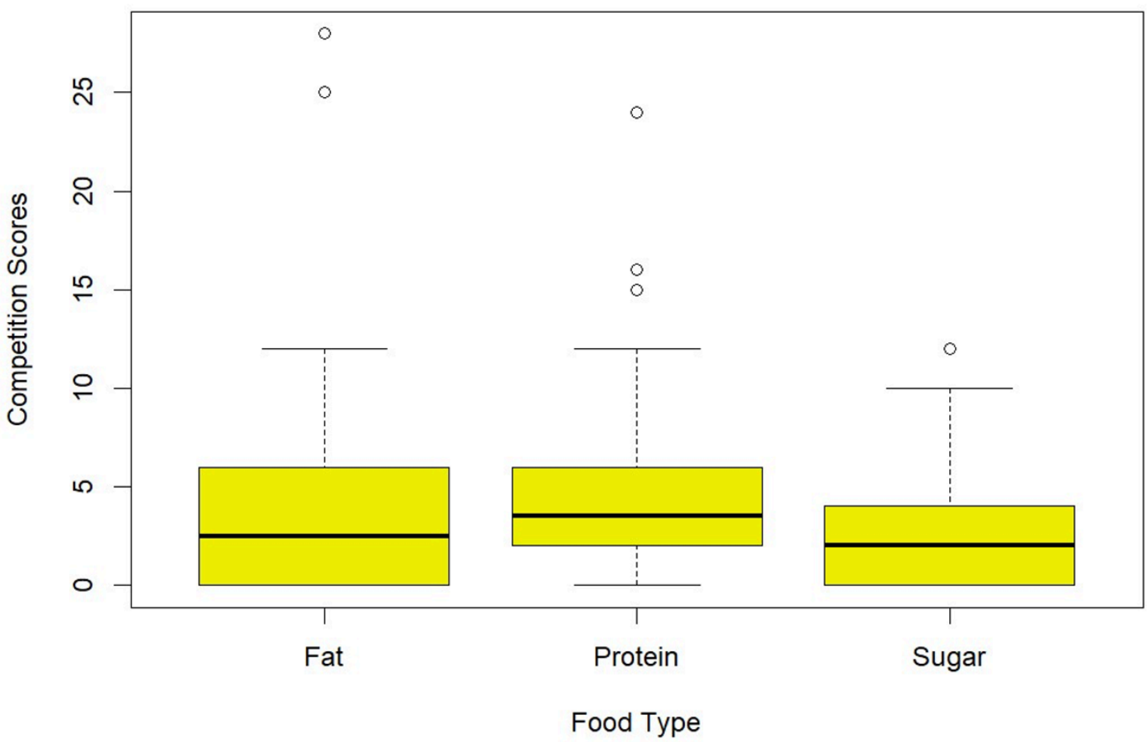



**Figure 4.** Boxplot of Competition Scores versus Food Type. There was a significant difference (Two-way ANOVA, F(2,225) = 4.57›47, $p < 0.0001$) between Protein and Sugar.

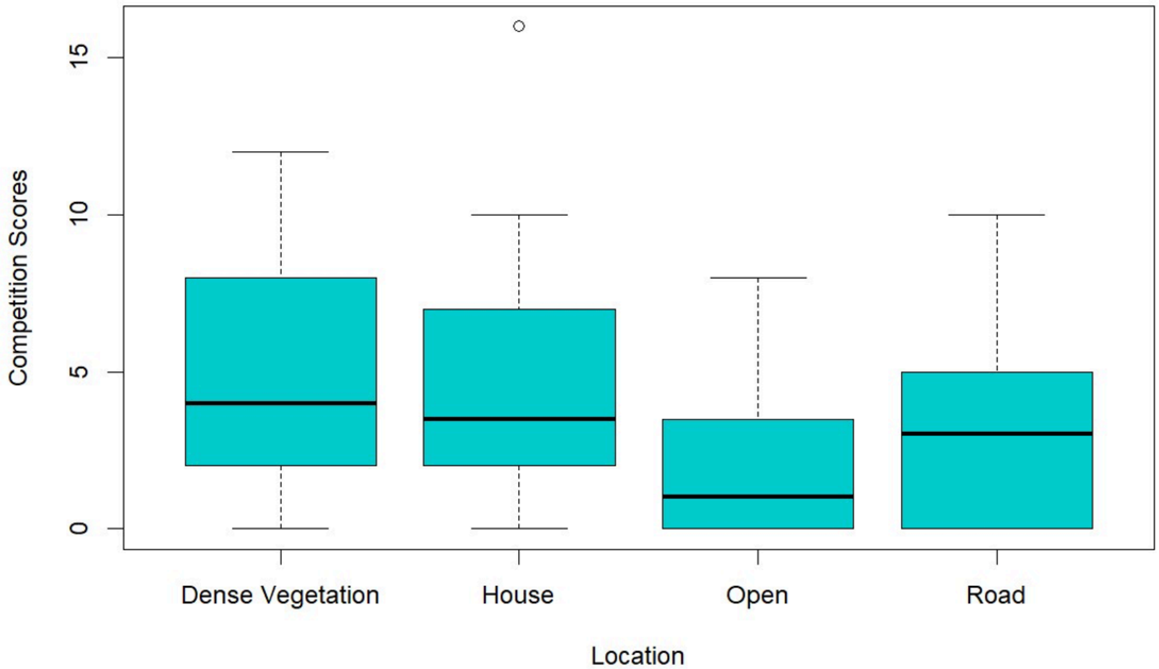



**Figure 5.** Boxplot of Competition Scores versus Location. There was no significant differences between the Locations (Two-way ANOVA, $F(3,60) = 2.4329$, $p = 0.07$)

**Table 4.** Summary of tests with a Two-way ANOVA. The conversion of competition scores (x) to Sqrt x or Log (x+1) was determined based on which one allowed the data to be closer to a Gaussian distribution. The alpha level to determine significance is defined as 0.05.

| Testing | Anova Competition Scores | p value | Significant? | Differences |
|---|---|---|---|---|
| **Competition Scores vs Site * Food Type (All scores)** | Sqrt x | • Site: 1.455e-07<br>• Food Type: 0.003206<br>• Site:`Food Type`: 0.072323 | • Site: Y<br>• Food Type: Y<br>• Site:`Food Type`: N | |
| **Competition Scores vs Site * Food Type (Competition Scores <23)** | Sqrt x | • Site: 3.836e-06<br>• Food Type: 0.005191<br>• Site:`Food Type`: 0.027863 | • Site: Y<br>• Food Type: Y<br>• Site:`Food Type`: Y | |
| **Competition Scores vs Site** | Log (x+1) | 5.00E-07 | Y | Amazon H / Amazon L, Amazon H / Galapagos H, Amazon H / Galapagos L, Amazon H / Craigieburn H, Amazon L / Appledore H, Amazon L / Appledore L, Appledore H / Galapagos H, Appledore H / Galapagos L, Appledore H / Craigieburn H, Appledore H / Craigieburn L, Appledore L / Galapagos L, Appledore L / Craigieburn H |
| **Competition Scores vs Food Type** | Log (x+1) | 0.01129 | Y | Protein / Sugar |
| **Protein Competition Scores vs Site** | Log (x+1) | 0.00327 | Y | Appledore H / Galapagos L, Appledore L / Galapagos L |
| **Fat Competition Scores vs Site** | Sqrt x | 0.03033 | Y | Amazon H - Craigieburn H |
| **Sugar Competition Scores vs Site** | Sqrt x | 0.0002675 | Y | Amazon H - Amazon L, Amazon H - Galapagos H, Amazon H - Craigieburn H, Amazon H - Craigieburn L, Amazon L - Appledore H, Appledore H - Galapagos H, Appledore H - Craigieburn H, Appledore H - Craigieburn L |
| **Protein Competition Scores vs Location** | Log (x+1) | 0.98 | N | NA |
| **Fat Competition Scores vs Location** | Log (x+1) | 0.73 | N | NA |

**Table 4.** Continued

| Testing | Anova Competition Scores | p value | Significant? | Differences |
|---|---|---|---|---|
| **Competition Scores vs Site * Location** | Log (x+1) | • Site: 6.982e-05<br>• Food Type: 0.4383<br>• Site: Location: 0.1933 | • Site: Y<br>• Location: N<br>• Site:Location: N | |
| **Competition Scores vs Location** | Sqrt x | 0.06984 | N | NA |
| **Dense Vegetation Competition Scores vs Site** | Log (x+1) | 0.07684 | N | NA |
| **House Competition Scores vs Site** | Sqrt x | 0.3341 | N | NA |
| **Open Competition Scores vs Site** | Sqrt x | 0.00341 | Y | Appledore H - Galapagos L, Appledore H - Whakatiwai H, Appledore L - Whakatiwai H |
| **Road Competition Scores vs Site** | Log (x+1) | 0.09393 | N | NA |
| **Dense Vegetation Competition Scores vs Food Type** | Log (x+1) | 0.9146 | N | NA |
| **House Competition Scores vs Food Type** | Log (x+1) | 0.1173 | N | NA |
| **Open Competition Scores vs Food Type** | Log (x+1) | 0.1793 | N | NA |
| **Road Competition Scores vs Food Type** | Log (x+1) | 0.3874 | N | NA |

**Table 5.** Summary of linear regression analyses and their outputs.

| Regression Equation | p value | Overall p value | $R^2$ |
|---|---|---|---|
| **All** sqrt(Competition Scores) ~ NPP + log (Age + 1) + Food Type | • (Intercept): 8.75e-07 ***<br>• NPP: 0.2782<br>• log(`Ecological Environment Age (years)`): 0.0015 **<br>• `Food Type`Protein: 0.4623<br>• `Food Type`Sugar: 0.0231 * | 1.939e-05 *** | 0.09787 |
| **W/o Appledore** log (Competition Scores + 1) ~ NPP + log (Age + 1) + Food Type | • (Intercept): 0.0419 *<br>• NPP: 0.4761<br>• log(`Ecological Environment Age (years)`): 0.5404<br>• `Food Type`Protein: 0.9466<br>• `Food Type`Sugar: 0.0179 * | 0.08943 | 0.02293 |
| **(<23) w/o Appledore** sqrt(Competition Scores) ~ NPP + log (Age + 1) + Food Type | • (Intercept): 0.0460 *<br>• NPP: 0.3585<br>• log(`Ecological Environment Age (years)`): 0.5239<br>• `Food Type`Protein: 0.8951<br>• `Food Type`Sugar 0.0417 * | 0.131 | 0.01786 |

**Table 5.** Continued

| Regression Equation | p value | Overall p value | $R^2$ |
|---|---|---|---|
| **Protein** log (Competition Scores + 1) ~ NPP + log (Age + 1) | • (Intercept): 0.3329<br>• NPP: 0.6451<br>• log(`Ecological Environment Age (years)`): 0.0452 * | 0.13 | 0.03642 |
| **(<23) Protein** sqrt(Competition Scores) ~ NPP + log (Age + 1) | • (Intercept): 0.2748<br>• NPP: 0.6761<br>• log(`Ecological Environment Age (years)`): 0.0329 * | 0.09977 | 0.04613 |
| **Fat** log (Competition Scores + 1) ~ NPP + log (Age + 1) | • (Intercept): 0.00936 **<br>• NPP: 0.22704<br>• log(`Ecological Environment Age (years)`): 0.04402 * | 0.08464 | 0.05082 |
| **(<23) Fat** sqrt(Competition Scores) ~ NPP + log (Age + 1) | • (Intercept): 0.00603 **<br>• NPP: 0.12275<br>• log(`Ecological Environment Age (years)`): 0.02687 * | 0.04055 * | 0.07766 |
| **Sugar** sqrt(Competition Scores) ~ NPP + log (Age + 1) | • (Intercept): 0.218<br>• NPP: 0.752<br>• log(`Ecological Environment Age (years)`): 0.517 | 0.7874 | -0.02644 |

# Discussion

This study demonstrates that levels of competition in invertebrate species vary by Site and Food Type. This variation is not strongly linked to NPP, though perhaps to the geological age of the Site.

Because a significant variation of competition scores between Sites exists (Figure 2), we can assume that there are regional factors that shape the competition of terrestrial invertebrates. This assumption is possible because I used competition scores in this study, which serve as a standard measurement that can be compared throughout Sites and experiments. By having statistical proof that these differences exist, we can move onto the first objective of this study, which is identifying what factors could be significant drivers of competition. First, we will do a qualitative analysis of the Site characteristics.

In general, the Amazon and Appledore Sites had higher medians than the other Sites, which in comparison appeared to have lower scores and similar spreads. When talking about the Amazon in the discussion I refer to Amazon H mainly, since Amazon L is a small percentage of land in the region and works differently as it gets frequent floods (high insect turnover from disturbance). When characterizing Amazon H and Appledore, we see a relatively large amount of biomass in both which relates to abundant food resources for invertebrates. Even though Appledore does not have large trees, its vegetation consists of dense shrubs, herbs, and green grasses (Nichols, 2008). With plentiful resources, these sites may support larger populations of invertebrates which allow for frequent and complex interactions.

In addition, these two Sites have access to high dispersal from outside the system. The Amazon is thousands of years old and it is connected to neighboring ecosystems, so it experiences high dispersal from visitor animals and people that inadvertently carry insects. A study found that dispersal rates affect the diversity patterns of ants in the Amazon (Guilherme et. al., 2021), and this might also play a role in competition. For Appledore island, the Shoals Marine Laboratory located runs several classes and research all the time outside wintertime, so the island receives many people that come and go in boats from mainland Maine (10km away). Further, Appledore and neighbor islands are nesting grounds for several populations of marine birds (Shoals Marine Lab, 2023) who visit the mainland frequently. Strong dispersal rates allow for the creation of diverse communities and in consequence, create diverse interactions.

High plant biomass plus high dispersal may create a rising invertebrate population until it reaches the carrying capacity (Wisniewski, 1980). Carrying capacity is a term referring to the maximum population level that an environment can support based on its finite resources (Verhulst, 1838). At this level, the resources available will be low and competition could be high as communities engage in intra and inter species competition for food (Wisniewski, 1980). The other Sites in the study did not have this combination of high biomass and dispersal, so this qualitative assessment suggests that levels of dispersal and biomass may be important variables affecting competition in an ecosystem.

On the other hand, the Sites with the lowest competition scores tended to be in Craigieburn. This could be because this is a low alpine zone area and most species from surrounding areas likely do not have the capacity to live at the low temperatures and harsh conditions. Moreover, this area is a pure mountain beech forest, so resource selection is limited. These characteristics could translate in low invertebrate abundance, hence less competitive interactions.

When analyzing competition scores versus Sites with the interaction of Site and Food Type, we saw a statistically significant interaction, which suggests that competition in invertebrates varies by Site, but the pattern of variation is different for each Food Type. This not only supports the methodology for accounting for dietary preferences, but also conveys that invertebrates that prefer one Food Type may behave and interact differently than those with other dietary preferences. The different visitor counts for each Food Type could be because of the composition of species at each Site as some may have more species with preference for one food type over the others.

In terms of Location, it appears that the type of vegetation cover does not affect competition much, possibly since some species can smell out food from large distances and will travel to them (Baker, 2017).

For some analyses, I used competition scores with values less than 23 to remove the three very high scores from the pool. Taking these out illustrates that when ignoring them, competition scores across Sites remain at a range with upper bounds lower than a score of 16. The three anomalous scores were part of the Fat and Protein trials in Amazon H (Figure A4 in Appendix), and were high because in those trials there were large visitor counts (i.e. crickets, wasp, four different ant species, fruit flies, arthropod, etc). Even though these trials included multiple ant species, the number of individuals per species was low (1-10) and no ant colony flooded the food source. This meant that other insects were able to get to the resource, in contrast to many other trials in the study, which suggests that ants (particularly social species) have a competitive advantage to other invertebrates, since normally once the colony settles, less insects visit the lure. Studies support this and suggest a combination of physical and chemical deterrents against competitors (Miner & Rankin, 2023).

As explored so far, the variation in competition scores could be mainly from idiosyncrasies of Sites. Through quantitative analyses, I conducted regressions to test if NPP values and geological age (Age) of each Site are possible predictors of competition scores. At first, NPP and Age did not appear to be significantly predictors. However, when the anomalous high competition scores were removed, the regression revealed that Age was a significant predictor for the Fat food type scores. This indicates that the geological age of an area could be an important factor in shaping the competition dynamics in invertebrates with a dietary preference of fat. My hypothesis that age could be a predictor of competition is supported. The negative correlation found, on the other hand, is opposite of the hypothesis of positive relationship between age and competition. This is unexpected as the Fat boxplot (Figure 3b) illustrates considerably different range of scores between the two Site with same age (Whakatiwai vs Craigieburn). Perhaps there are other unknown sitespecific variables interacting with geological age that affect competition. Nevertheless, if age is indeed a universal predictor for competition, we could categorise regions into experiencing high or low competition, and then model how movement of species from high competition regions to low, or vice versa, could have an effect on local flora and fauna. This serves to identify potential invasive species that have a competitive advantage by for example being freed from its natural competitors (ecological release) (Kelley et al., 2019).

NPP was found to be non-significant in all the regressions, which contradicts my predictor hypothesis. Perhaps NPP in this study did not represent environmental conditions and biomass well, or these are not impactful to competition. The non-significant results of Age and NPP for Sugar and Protein may indicate that other factors are larger drivers of competition, factors are interacting with each other, or there are no universal drivers of competition in these.

The results in this study may have been limited from its small sample size as NPP and geological age were only one data point per Site (n=10 Sites), making the degrees of freedom small. This may affect the accuracy of the predictor analysis and so for a better regression it is recommended that in future work more Sites are sampled (in different geographical regions with varying geological ages). By having a larger sample size, the predictor relationship of NPP and Age on competition may be determined with higher confidence. I recommend using NPP values that are averages of more current months and years. Additionally, the values of geological ages may differ from the true ages of the ecosystems surveyed, since the geological history of each Site is varied and experienced great changes over millennia, making it complex to pinpoint the start of the ecosystems as we know them today. Therefore, it would be beneficial to use data from novel tools that accurately date each ecosystem. Other suggestions of future work include testing alternative variables such as biomass and a quantification of dispersal, as possible predictors of competition as suggested by the qualitative analyses.

The outcomes and information gathered from this research are valuable to the process of understanding competition dynamics in invertebrates. This study provides an analysis of the factors that may or may not affect competition in various ecological and geographical regions.

Learning about competition allows us to understand the forces structuring invertebrate communities (Parr & Gibb, 2010), predict new community assemblies from introduction or disturbance, and model how organisms will interact in these new arrangements. In real world applications, this information is useful in the movement of species to cooler regions due to global warming, in analysing the impacts of introduced species through the heightened interconnectedness of our modern world (Baker, 2017), or in the dispersal of disease carrying insects. Thus, research on the factors affecting competition dynamics is highly necessary, and this study is a step towards that.

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# Appendix A—Comparison Graphs

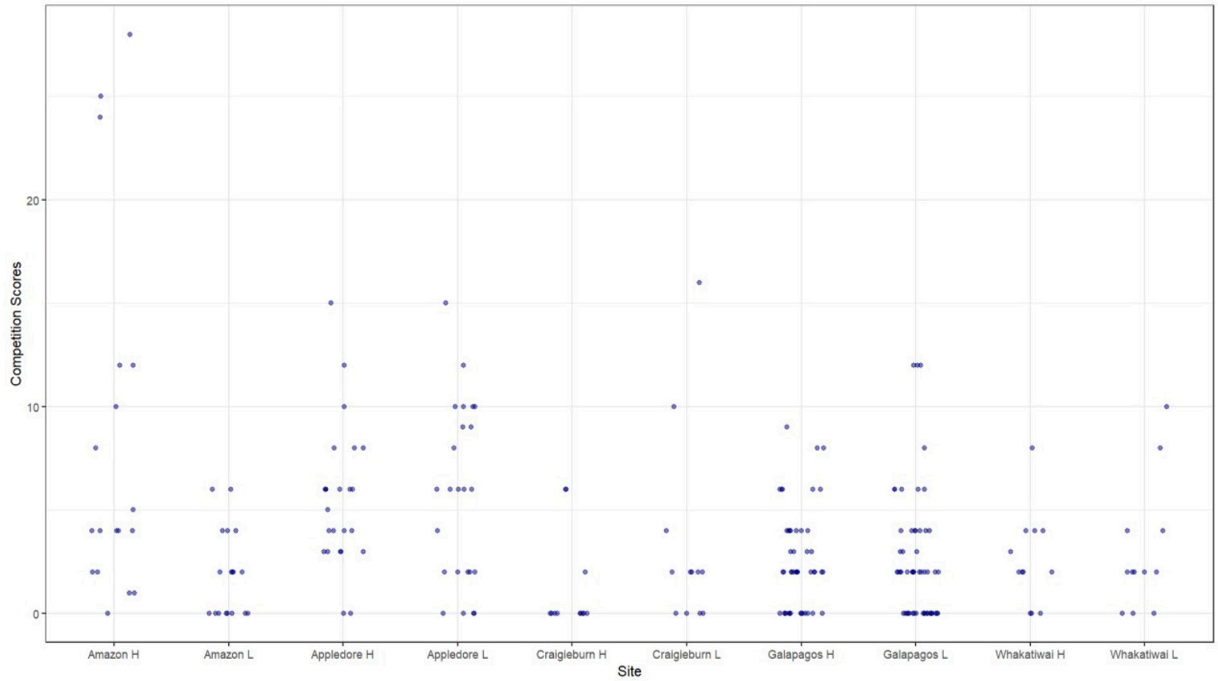


**Figure A1**. Scatterplot of Competition Scores versus Sites

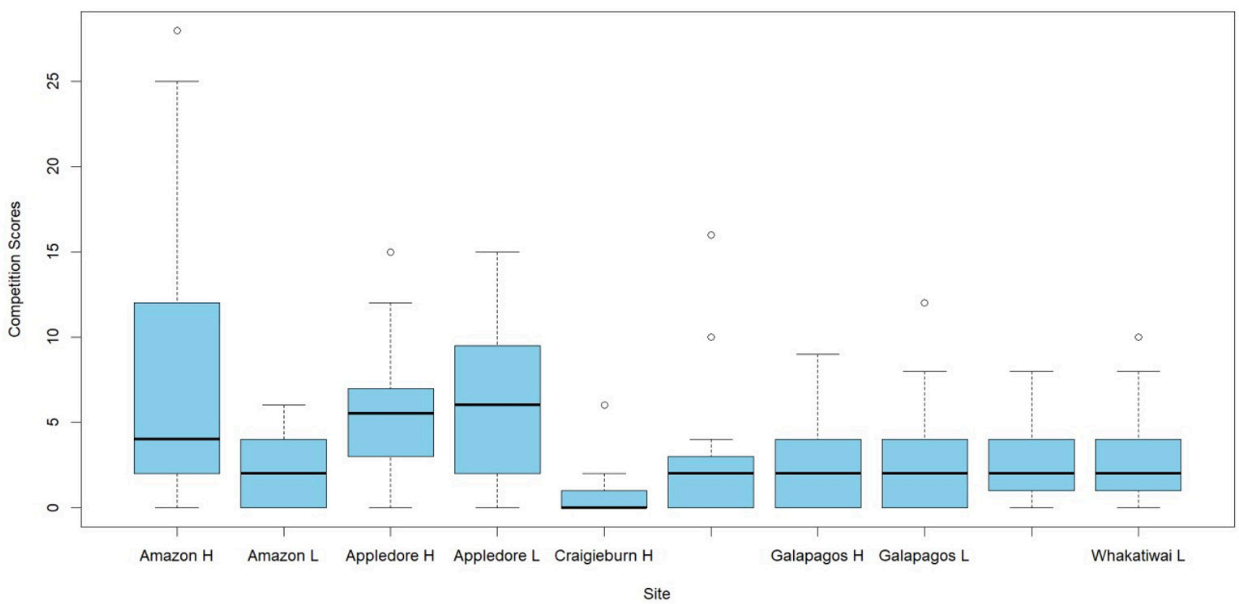


**Figure A2**. Boxplot of Competition versus Sites

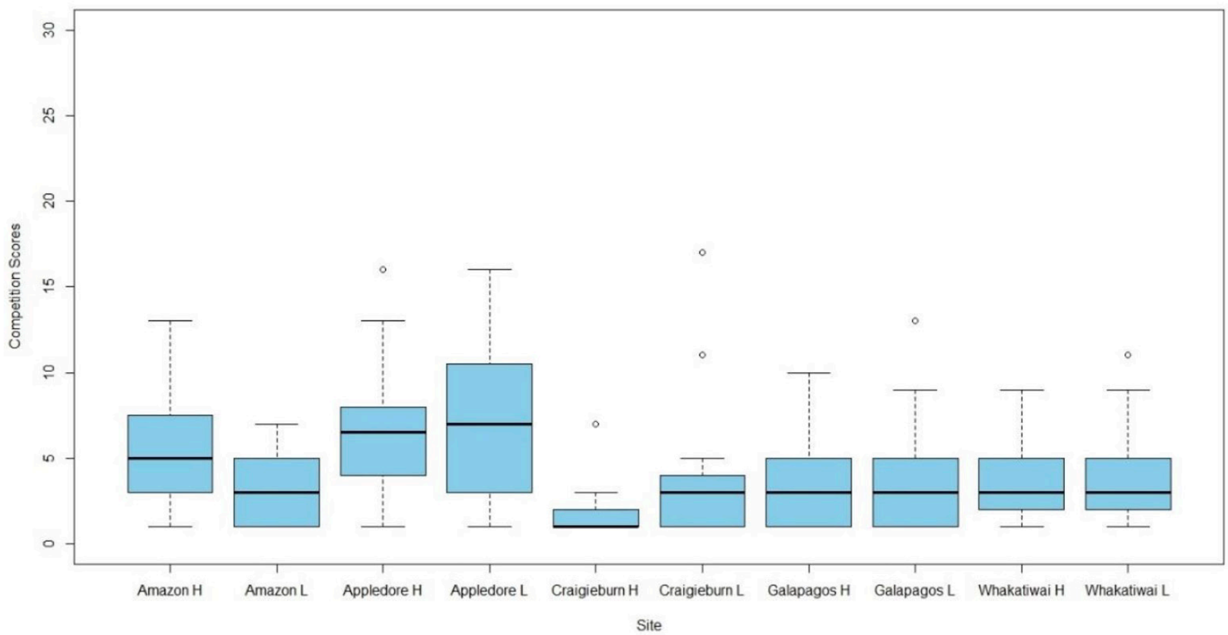


**Figure A3**. Boxplot of Competition Scores (with values < 23) versus Site. The y axis range was kept the same as Figure A2 for visual comparison.

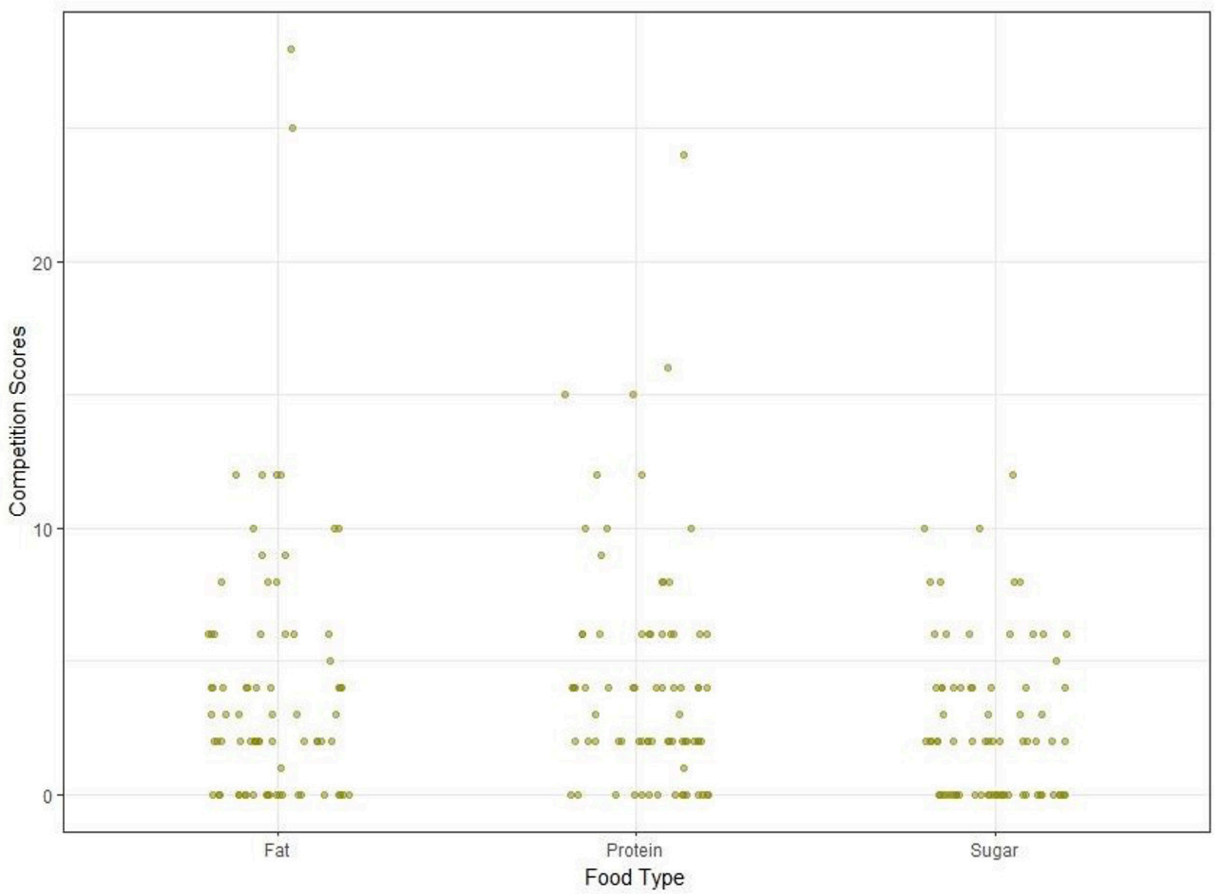


**Figure A4**. Scatterplot of Competition Scores versus Food Types

## Appendix B—Coordinates of Sites

| Site | Longitudinal Coordinates | Lateral Coordinates |
|---|---|---|
| Galapagos H | 0.9014 S | 89.6075 W |
| Galapagos L | 0.8868 S | 89.5416 W |
| Amazon H | 0.6367 S | 76.1503 W |
| Amazon L | 0.6380 S | 76.1501 W |
| Appledore H | 42.9871 N | 70.6155 W |
| Appledore L | 42.9891 N | 70.6152 W |
| Whakatiwai H | 37.0877 S | 175.3022 E |
| Whakatiwai L | 37.0873 S | 175.3032 E |
| Craigieburn H | 43.1519 S | 171.7137 E |
| Craigieburn L | 43.1515 S | 171.7121 E |

## Appendix C—List of the Orders of Species Present on Baits at Each Site

| Site | Hymenoptera | Orthoptera | Dermaptera | Diptera | Araneae | Hemiptera | Isopoda |
|---|---|---|---|---|---|---|---|
| Galapagos H | ✓ | ✓ | ✓ | ✓ | ✓ | | |
| Galapagos L | ✓ | | | ✓ | | | |
| Amazon H | ✓ | ✓ | | ✓ | | | |
| Amazon L | ✓ | ✓ | | ✓ | ✓ | | |
| Appledore H | ✓ | | | ✓ | | | ✓ |
| Appledore L | ✓ | | | ✓ | | | |
| Whakatiwai H | ✓ | | | ✓ | | | |
| Whakatiwai L | ✓ | | | ✓ | | ✓ | |
| Craigieburn H | ✓ | | | ✓ | | ✓ | |
| Craigieburn L | | | | ✓ | | | |