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The Foraging Areas of Attine Ants at the Firestone Reserve, Costa Rica

A Thesis Presented

By

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Of the Claremont Colleges

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Abstract

In tropical forest systems, attine ants are the dominant herbivores. They construct large nest structures that include foraging trails that extend to multiple plant sources throughout the forest. These foraging areas vary from nest to nest and they are highly dynamic over time and season changes. It was expected that characteristics of both the nest structure and the surrounding environment would affect the size of nest foraging areas. In this study, COMPASS survey software and ArcGIS were used to map the foraging trails and calculate the foraging areas of 12 attine ant nests located on the Firestone Reserve, over the course of 6 weeks. Data collected at the ant nest sites on nest area, flow rate, trail number and neighboring nest proximity were combined with data collected from previous studies on soil pH and light fractions in order to test correlation hypotheses between these factors and foraging area. The mean foraging areas differed significantly from each other and significant correlations were found between foraging area and trail number, flow rate, neighbor distance and soil pH. Understanding foraging behavior of attine ants is important in the field of restoration ecology because these ants are important in determining overall structure and nutrient distribution in tropical forests.

Introduction

One of the first things a person will notice upon stepping out of the airport and onto Costa Rican soil are the trails of leaf fragments seemingly moving by themselves. When examined more closely, a person will see that these leaves are in fact being carried in the pincers of thousands of large ants. These leaf-cutter or attine ants (Hymenoptera; Formicidae; Attini) are distributed throughout the Neotropics, from northern Mexico to the southern regions of Argentina. There are 190 known species, however the two most abundant species found in Costa Rica are *Atta cephalotes* and *Atta columbica*. Unlike any other type of ant, attine ants are uniquely fungus growers, meaning they use harvested living plant matter to farm fungus gardens in their nests (Hölldobler and Wilson, 1990). This fungus is their sole food source, and the plant fragments act as the substrate for these gardens.

Attine ant nests are amazing feats of architectural ingenuity. Their nest areas can range in size anywhere from 0 to over 50 m^2 and reach depths of over 6 meters (Wirth *et al.*, 2003). Generally, the size of a nest mound correlates with the age of the ant colony, which can persist for up to 15 years. Larger nests can contain over 1900 underground chambers with 250 fungus gardens and house 1 to 7 million ants, depending on the species (Wirth *et al.*, 2003). The nests also tend to have multiple entrances and are situated on slopes, which facilitate air ventilation and water expulsion during heavy rains (Hölldobler and Wilson, 1990).

Figure 1: Attine ant nest

The foraging trails that wind through the forest are an extension of the central nest structure. Attine ants form very distinct foraging routes to and from harvesting sites, which in the case of *A. cephalotes* and *A. columbica* are canopy trees, rather than grasses. These trails are chemically marked with secretions from the ants' poison gland sac that assist in both recruitment and orientation (Wirth *et al*., 2003). Actual leaf cutting is very energetically expensive for the ants, more so than even locomotion and therefore is important in determining foraging behavior (Wirth *et al*., 2003). This behavior includes things like the type of leaves they choose to harvest, the size of the fragment they cut and how far they are able to go before the costs outweigh the benefits. Understanding this behavior is vital to understanding tropical forest dynamics, considering these ants can consume between 12 to 17 percent of all tropical forest leaf production (Cherret, 1968).

Foraging trails generally consist of a main trunk trail from which multiple other trails branch off (Howard, 2001). The trunk trail is well established and generally persists for months or even years, while the diverging trails are much more dynamic. Attine ant colonies are able to clear trails quite rapidly, with relatively low energetic cost, which suggests that the persistence of these trunk trails is due to their optimal locations (Howard, 2001), i.e. they lead to patches of high-quality plant material. The colonies also invest a lot of time in maintaining the trunk trails and keeping them free of debris and this effort is paid off in the form of decreased travel time for the foragers (Rockwood and Hubbell, 1987).

In this study the foraging trails of 12 different attine colonies were mapped over the course of 6 weeks. The trails were surveyed using a Suunto compass and clinometer readable to 0.5 and 1 degree respectively, in order to determine the foraging areas around each nest. The mean nest foraging areas were compared to determine if there were any size differences between the nests. Lastly variations in physical nest factors (area, foraging trail number and flow rate) and environment factors (proximity of neighboring nests, soil pH and light fraction) were compared between nests in order to determine if they had any relationship to a nests foraging area.

It was expected that larger nests would have larger foraging areas because they were older, and therefore more likely to have a large population size. It was also expected that larger nests would have greater flow rates because of the increased number of workers available to forage. Though this could be dependent on the number of foraging trails. Flow rates will probably be higher for a nest of a fixed population size that has 2 foraging trails versus 7 foraging trails because the work force is dispersed over a larger number of trails. However, decreasing the length of the trail, thereby shortening travel time, could compensate for this decreased flow by increasing the number of potential trips an ant could make. So, it is important to look at how these factors come together and interact with one another to effect foraging area.

This study also looked at the possible competitive effect neighboring nests could have on the foraging areas of nests. This was done by calculating the potential foraging areas around each and counting the number of neighboring nests that were within this area. It was expected that as the number of neighbors increased, the foraging area would decrease.

Past students at the Firestone Center for Restoration Ecology (FCRE) collected data on canopy light fractions and soil pH. A light fraction is a measurement of the percent of forest area that is not occupied by canopy cover, meaning light can penetrate to the forest floor (Pera, 2010). Light availability is a major limiting factor in the growth and survival of many tropical forest plant species. Primary forests tend to have higher canopy leaf densities and lower light fractions than secondary and bamboo forests, indicating a lower amount of productivity (Pera, 2010). Since *A. cephalotes* and *A. columbica* are mainly canopy foragers, it was expected that there would be an increase in light fraction values around larger nests as a consequence of foliage loss.

Attine ant nest construction changes the physical and chemical properties of the soil they are in. Studies have shown that ants are as important as earthworms in soil turnover, while leaf-cutters are the most important agents of soil modification in the tropics (Alvarado *et al*., 1981). The leaves carried by the attine ants to the nest are rapidly decomposed by the fungus rather than going through the normal multi-step leaf decomposition process, resulting in nutrients being more quickly returned to the soil. (Lugo *et al.*, 1973). Overall, the soil of attine ant nests is more porous, and more nutrient rich (K, N, K, Ca, Mg, Na) than neighboring non-nest soils and this promotes root growth on and around the nest site (Haines, 1975; Farji-Brener and Medina, 2000; Moutinho *et al*., 2003). Soil pH affects the solubility of plant minerals and nutrients, with most being more soluble in acidic soils than in neutral or slightly alkaline soils (Chen and Mahlab, 2009). Therefore it is beneficial to surrounding plants if the nest soil is more acidic because this means that the minerals that the ants are concentrating in their nest soils/refuse piles are more readily available for uptake by plant roots. It was expected that as trail flow rate increased, nest soil pH would decrease.

Methods

Research location:

This study was carried out at the FCRE, a facility owned and operated by Pitzer College on the southwest coast of Costa Rica. This 60 hectare reserve was cleared for cattle grazing in the 1950s and 60s, and then later for bamboo plantations. Restoration of the land to its original tropical moist forest state began in 1993, and efforts were continued by Pitzer College when it acquired the land in 2005. For this reason much of the reserve is dominated by secondary growth forest, however there are also regions of primary, bamboo and banana forests. The area gets 4487±1003 mm of precipitation annually and has an annual temperature of 25°C (Firestone, 2013). The reserve is situated on a slope, with the west end at an elevation about 300m higher than that of the east end, which is at around sea level (Roberts *et al*., 2009).

Locating the Nests:

Previous studies conducted by Christopher Wheeler (2005) and Rachel Poutasse (2010) located and mapped the locations of attine ant nests throughout the FCRE. Many of these nests were inspected, using a Trimble Juno ST GPS unit, to ensure they were still active and then 12 were selected at random to conduct the study on. Two of the nest centers, EG10 and EGEK33, were located a few feet outside the perimeter of the reserve in Hacienda Barú, but they were deemed suitable to study, since their trails were primarily within the reserve.

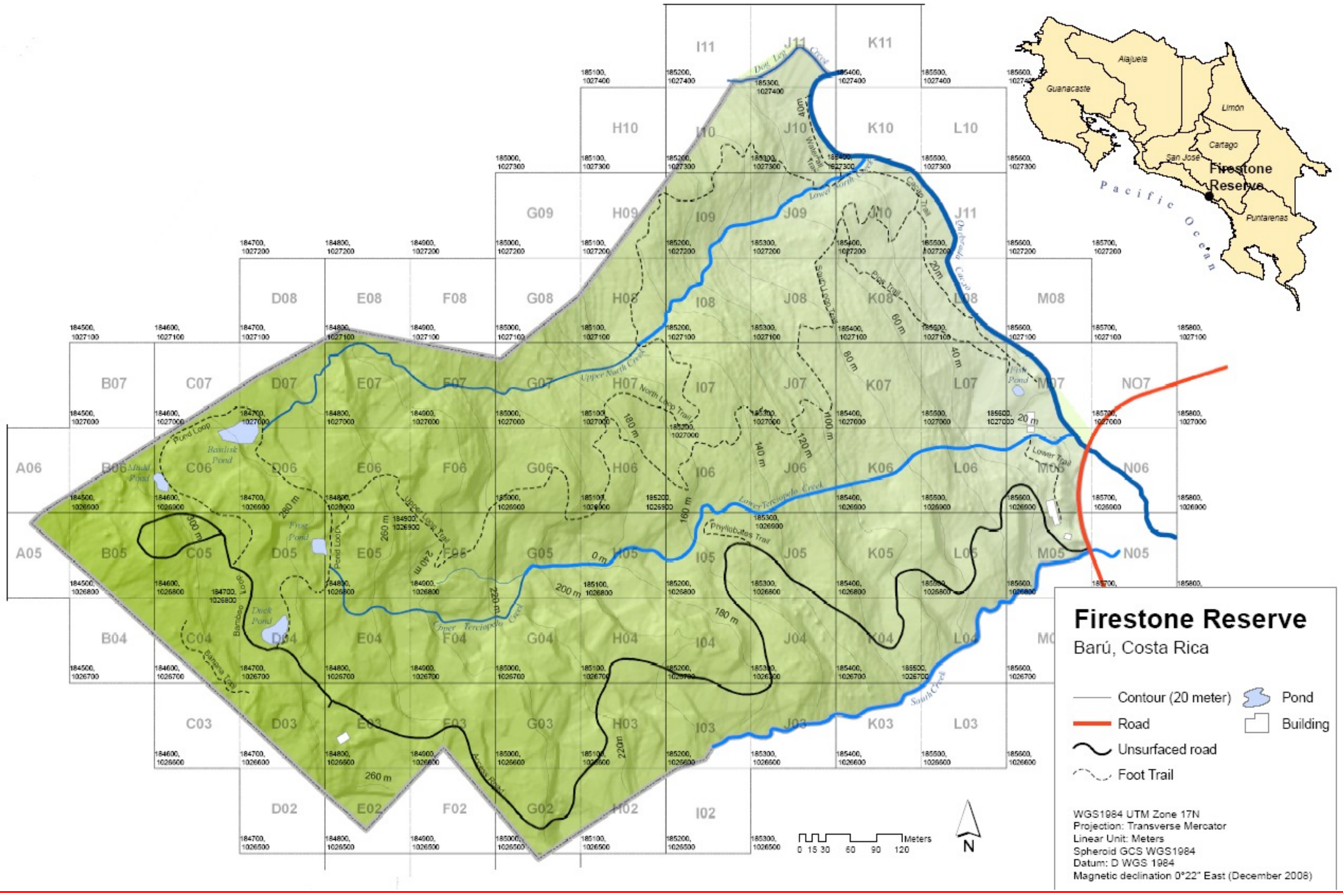

Figure 2: Map of FCRE

Measuring length, incline, direction and flow rate of each foraging trail:

Before following the foraging trails, the flow rate of each trail was recorded using a digital stopwatch. This ensured clear readings prior to following the trail, since the survey process often resulted in disturbance of the trail flow. The flow rate was recorded as the number of leaf fragments that passed a fixed point on the trail in 1 minute.

Figure 3: Attine ant foraging trail

Standard survey techniques were used to map the foraging trails of each ant nest. Equipment included a Suunto PM5 clinometer, a Suunto KB-20 compass, a Sirchie 30m tape measure and two 1.5m survey sticks. My partner and I followed the trails out from nest center to the plant source, making incremental measurements along the way. There was often no direct line of sight to the plant source because of intervening trees or bushes, and some of the trails were much longer than 30m, so generally multiple intermediate measurements were taken before the source was reached. Also, during light rains, or under decreased light conditions it was difficult to take long distance measurements, so multiple short distance measurements were taken to ensure accurate reads. Plant sources were marked with tape and labeled with the nest name and week number. Foraging trails that were on trees that were less than a meter from the nest center were given zero distance measurement and their flow rates were recorded as usual. The nest size was calculated by measuring two perpendicular maximal and minimal diameters across the mound and calculating the area as an ellipsoid (Wirth *et al.*, 2003).

Surveying the Nests:

The 12 nests selected were surveyed once a week for 6 weeks from May 27th to July 21st of 2013. Each day 2-3 nests were surveyed, depending on weather conditions, from 8:00 in the morning until about 12:30-1:00 in the afternoon. This ensured measurements were taken before the afternoon rains. However, on some days it would rain earlier in the morning or most of the day, which either delayed or totally prevented survey taking. This is due to the fact that ants seek cover and disband foraging lines while it is raining.

Some of the nests were entirely inactive some weeks, with no trails leaving the nest mound. This was the case for nest EGEK87 during week 4, nest EGJB05 during weeks 4 and 5 and nest EG10, which became totally inactive after week 3.

Figure 4: Surveying a nest on the FCRE

COMPASS Mapping, ArcGIS and Statistical Analysis:

Each day the field survey data were imputed into COMPASS cave survey software (http://www.fountainware.com/compass/) to generate a map of the foraging trails. Separate maps were generated each week for each of the 12 nests and then at the end of the study the 6 weeks of data were combined into one map for each nest.

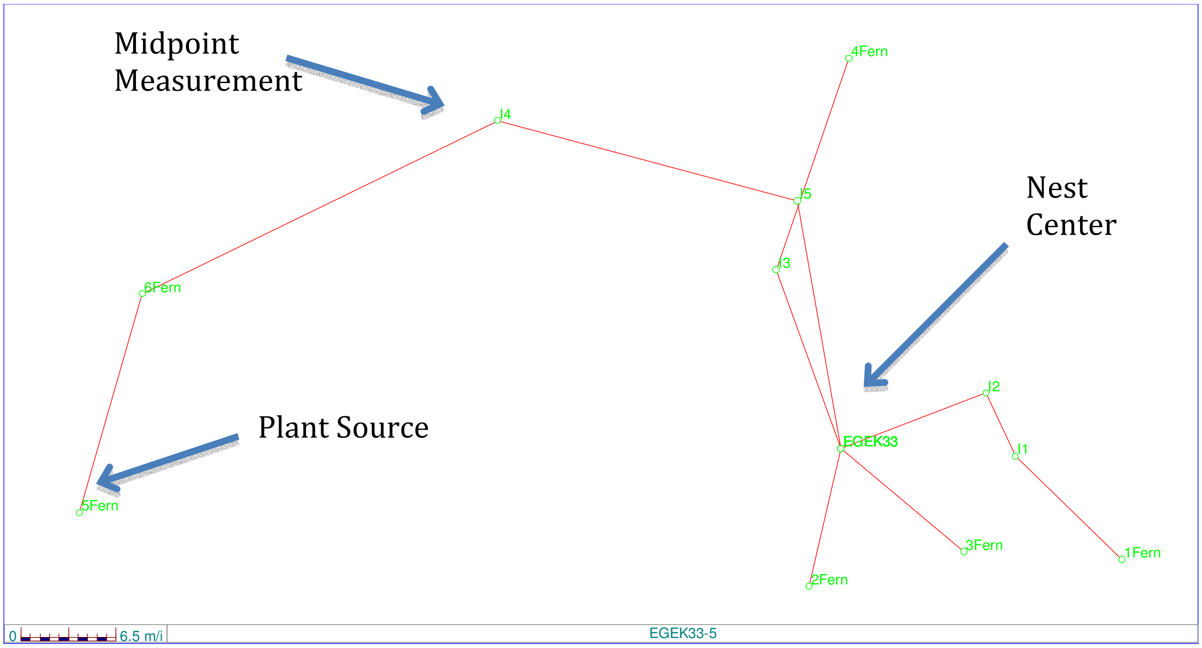

Figure 5: Nest EGEK33, week 5 trails

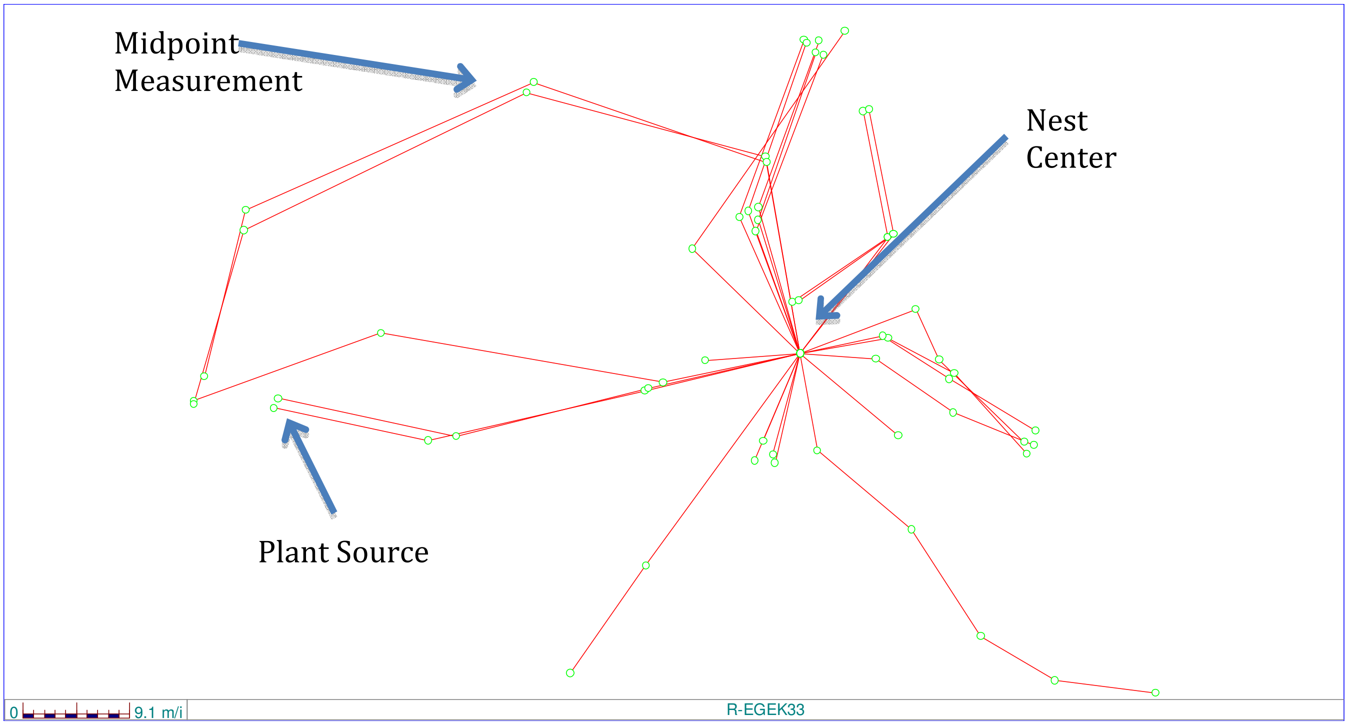

Figure 6: Nest EGEK33, weeks 1-6 trails

In Figure 5 the nest center is indicated by the point that is labeled with the nest name: EGEK33. The red lines represent the trails mapped and the points along the trail are points of measurement. In the first figure there are five foraging trails mapped. The end points represent the locations of the plant sources. Figure 6 displays all six weeks of data for that particular nest.

The COMPASS data were then transferred into ArcGIS. A minimum convex polygon formula was used to find the weekly and total foraging areas for each nest. To analyze the effect neighboring nests had on foraging area, the potential areas for each nest were calculated. This involved taking the longest foraging trail for each nest and using it as the radius for the potential area. Then the number of neighboring nests that fell within this area were counted and recorded. Additionally, the distance to the closest neighbor was also calculated for each of the 12 nests. Data collected from previous studies on soil pH (Chen and Mahlab, 2009) and canopy light penetration (Pera, 2010) were used to analyze possible environmental factors that may be affecting foraging area. Kernel density plots were created for each of these two factors and the conditions around each nest were recorded. However, since nests EG10 and EGEK33 were offsite, they were not included in the light and pH measurements. Lastly, the vegetation type the nests were located in was also recorded.

Comparing nests to each other involved multiple correlation tests using SPSS. I tested whether any of the nest characteristics (mound elliptical area, the flow rate, the trail number) had a significant relationship to the nest foraging area. I also looked for any correlations between foraging area and light penetration, soil pH, and neighbor proximity and number. To test for significant differences in foraging area size between nests, the mean foraging area over the six weeks for each nest were compared using a repeated measure 1-way ANOVA test and Tukey's HSD tests.

Results

Six sets of foraging trail survey data were collected for each of the 12 nests. Nest EG10 was inactive during the last 3 weeks, nest EGEK87 was inactive during week 4 and nest EGJB05 was inactive during weeks 4 and 6. Therefore, a total of 66 foraging areas were calculated. The total foraging area around each nest can be seen in the ArcGIS image in Figure 7. The potential foraging area was calculated using the length of the longest foraging trail as the radius of the circle (Figure 8). The green dots represent the locations of neighboring nests. The number of nests that fell within the potential area were counted and recorded for each nest.

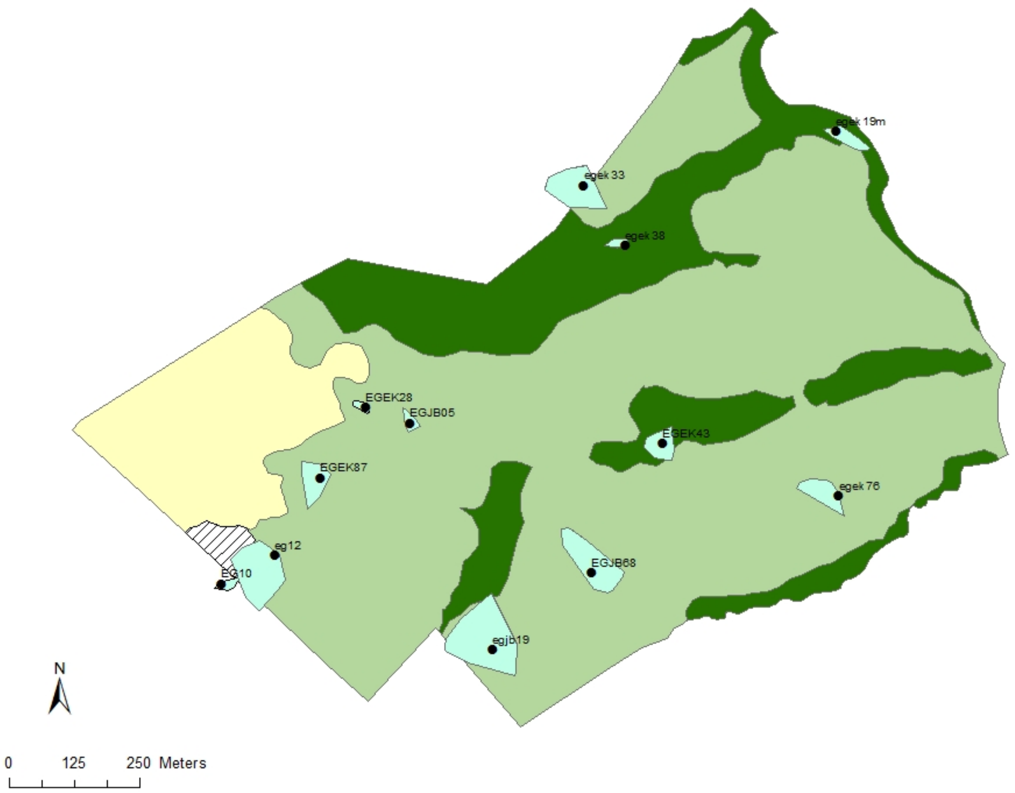

Figure 7: Minimum convex polygons of total foraging areas around each nest on the FCRE

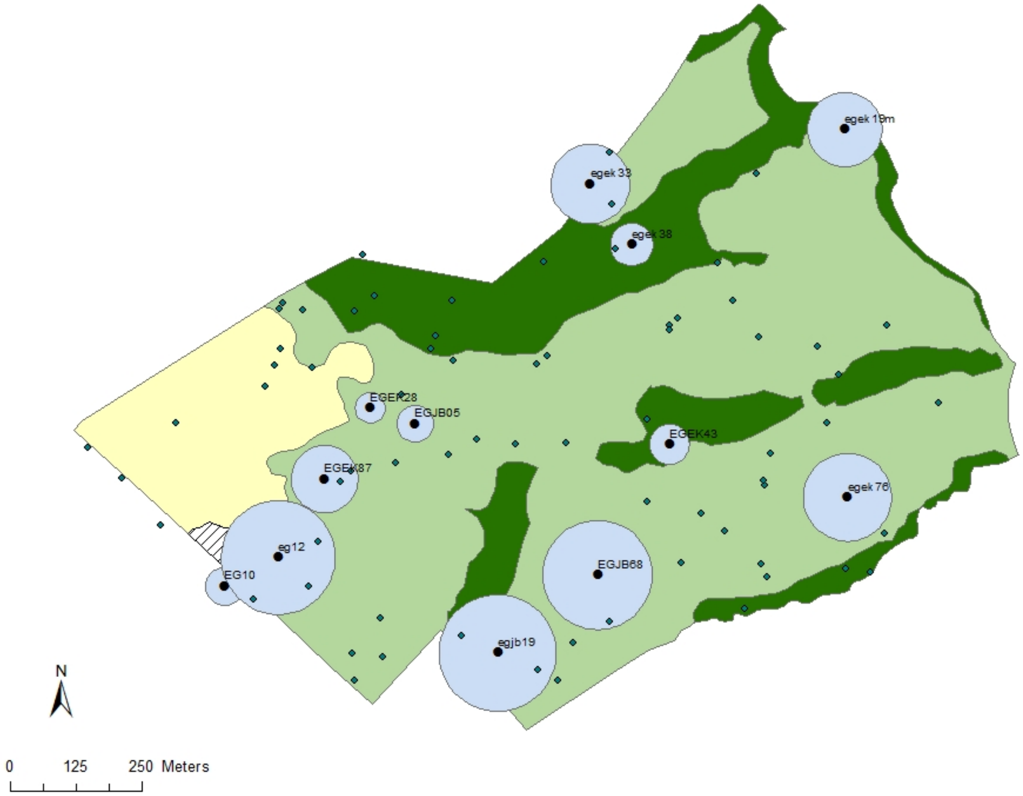

Figure 8: Potential foraging areas for each nest on the FCRE

Kernel density plots:

The kernel density plot displays the light fraction gradient throughout the reserve (Figure 9). The lighter pink color represents the area with the greatest light fraction, meaning that the percent canopy cover is low, and the darker red represents areas with lesser light fractions, meaning the canopy is denser in those locations. The light fraction region each nest was located in was recorded. Figure 10 is a kernel density plot of the soil pH gradient; with the lighter regions represent the more acidic pH's and the darker regions representing the more basic soil pH’s. The soil pH each nest was located in was recorded. Only nests EGEK33 and EG10 were excluded from these measurements because they were located just outside the boundaries of the reserve.

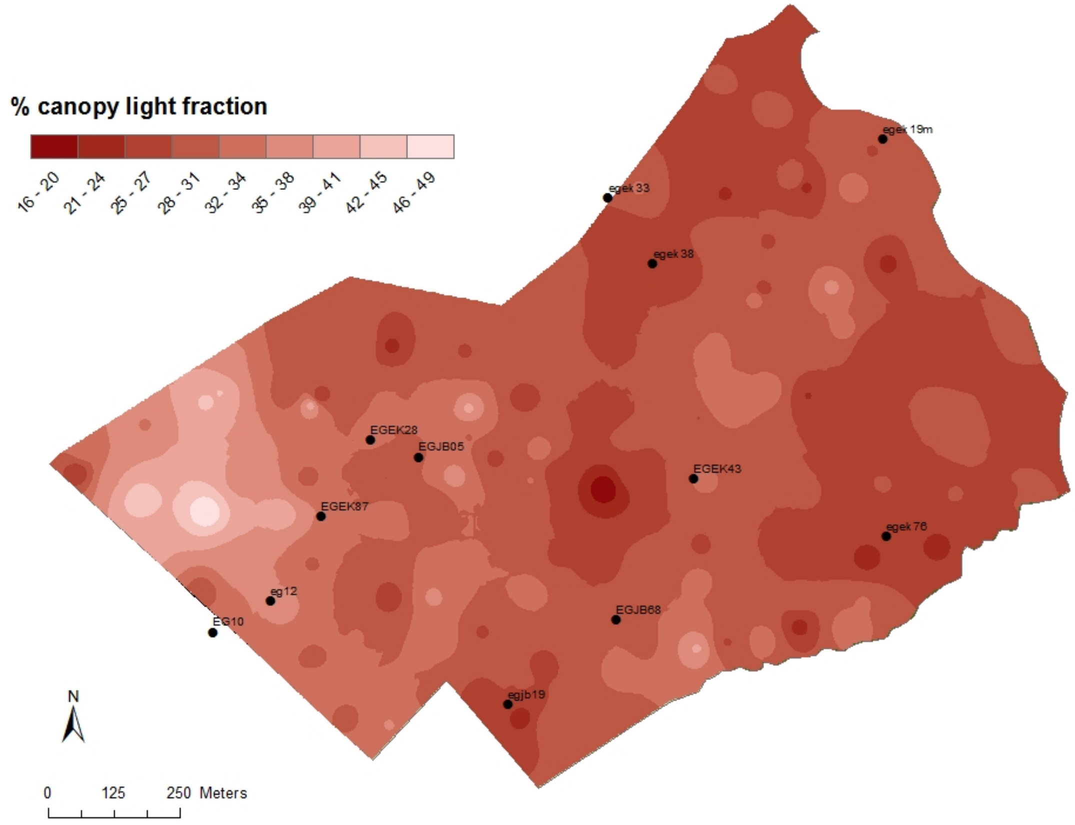

Figure 9: Kernel density plot of light fractions on the FCRE (Pera, 2010, n=720)

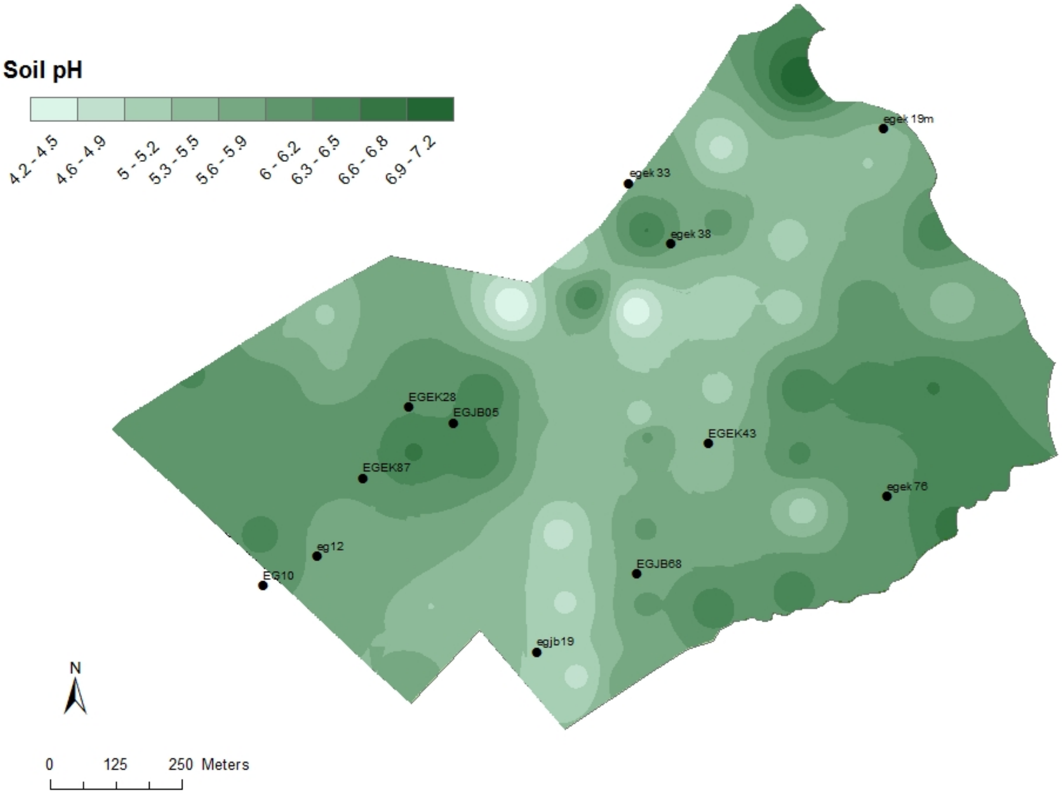

Figure 10: Kernel density plot of soil pH on the FCRE (Chen and Mahlab, 2009)

Comparisons of foraging areas between nests:

There is a clear size disparity in foraging areas between nests as seen by Table 1. Total weekly foraging areas were measured as well as the overall total foraging area over the course of six weeks. An ANOVA test could not be performed to test if the overall total foraging areas were significantly different between each other. However, an ANOVA and Tukey’s HSD test could be performed on the mean weekly foraging area data. This is because each nest only had one overall total value, but 6 weekly total values. The group sample size has to be larger than one to perform an ANOVA test because it is an analysis of variance between group means. Overall, there was a significant difference in mean foraging areas between nests (F=26.86, df=11,52,63, $p<0.001$).

Nest EGJB19 was significantly larger than every other nest (Tukey's, $p<0.001$), except for nest EG12 (Tukey's, p=0.544). Nest EG12 was the second largest, but its mean foraging area did not differ significantly from nest EGJB68 (Tukey's, p=0.054). The third largest nest was EGJB68, and this nest did not differ significantly from nest EGEK33 (Tukey's, p=0.974). Lastly the fourth largest nest foraging area was for nest EGEK33, however, this nest did not differ significantly from nests EGEK19m (Tukey's, p=0.079), EGEK43 (Tukey's, p=0.191), EGEK87 (Tukey's, p=0.161). The remaining 8 nests did not differ significantly from each other (Tukey's, $p>0.05$).

Table 1: Foraging area measurements of the 12 nests of study (n=66)

Nest ID	**Average Weekly Foraging Area ± SD (m^2)**	**Total Foraging Area (m^2)**	**Potential Foraging Area (m^2)**	**Relative Significance[*]**
EG10	117.02 ± 35.56	304.79	1963.50	A
EG12	2849.29 ± 176.41	4216.70	17671.46	B
EGEK19M	341.91 ± 145.22	858.60	7542.96	A
EGEK28	100.57 ± 29.78	197.21	1256.64	A
EGEK33	1364.98 ± 395.85	3052.26	8494.87	E
EGEK38	47.28 ± 37.46	261.16	2463.01	A
EGEK43	466.10 ± 160.49	1264.86	2123.72	AE
EGEK76	185.12 ± 227.76	1471.13	10568.32	A
EGEK87	395.25 ± 358.40	1473.14	6082.12	AE
EGJB05	83.95 ± 78.96	375.87	1809.56	A
EGJB19	3549.79 ±1601.91	6215.59	18626.50	CB
EGJB68	1778.51 ± 384.90	3354.98	16286.02	DBE

*Tukey's HSD, significant at $p<0.05$, same letter indicates no significant difference between average nest foraging areas

Correlations:

Trail number vs. foraging area

As the number of foraging trails from a nest increases, the foraging area of that nest significantly increases ($r=0.819$, $p<0.001$, $n=66$; Figure 11).

Flow rate vs. foraging area

As the flow rate of each foraging trail increases, the foraging area significantly increases ($r=0.855$, $p<0.001$, $n=66$; Figure 12).

Neighbor count vs. foraging area

As the number of neighbors within the potential foraging radius increases, the foraging area significantly increases ($r=0.687$, $p<0.001$, $n=66$; Figure 13). To reiterate, sample size is 66, rather than 72 because a few nests were inactive during some weeks.

Closest neighbor distance vs. foraging area

For the 6 nests that had neighboring nests within their potential foraging radius: as the closest neighbor nest gets further away, the foraging area for the nest increases ($r=0.697$,$p<0.001$, $n=35$). The nests that had no neighbors within their potential radiuses were not included in this graph (Figure 14). The sample size here is 35, rather than 36 because one out of the 6 nests was inactive one week.

Soil pH vs. foraging area

As the soil pH increases, becoming more alkaline, the foraging area significantly decreases (r= -0.554, p<0.001, n=55). The data for nest EG10 and EGEK33 were not included in this graph since their nest centers were located outside the reserve boundaries, thus sample size is 55, rather than 66 (Figure 15).

Light fraction vs. foraging area

There is no significant correlation between foraging area and canopy light fraction (r=0.113, p=0.410, n=55).

Elliptical nest area vs. foraging area

There is no significant correlation between the elliptical nest areas and the foraging areas of the nests (r=-0.147, p=0.647, n=66).

Trail number vs. flow rate

As the number of foraging trails from a nest increases, the flow rate of each trail increases (r=0.752, p<0.001, n=66; Figure 16).

Flow rate vs. elliptical area

As the flow rate of each trail increases, the elliptical area of the nest decreases (r = -0.284, p=0.016, n=66; Figure 17).

Flow rate vs. soil pH

As the soil pH increases, the flow rate of each trail decreases (r= -0.492, p<0.001, n=55; Figure 18).

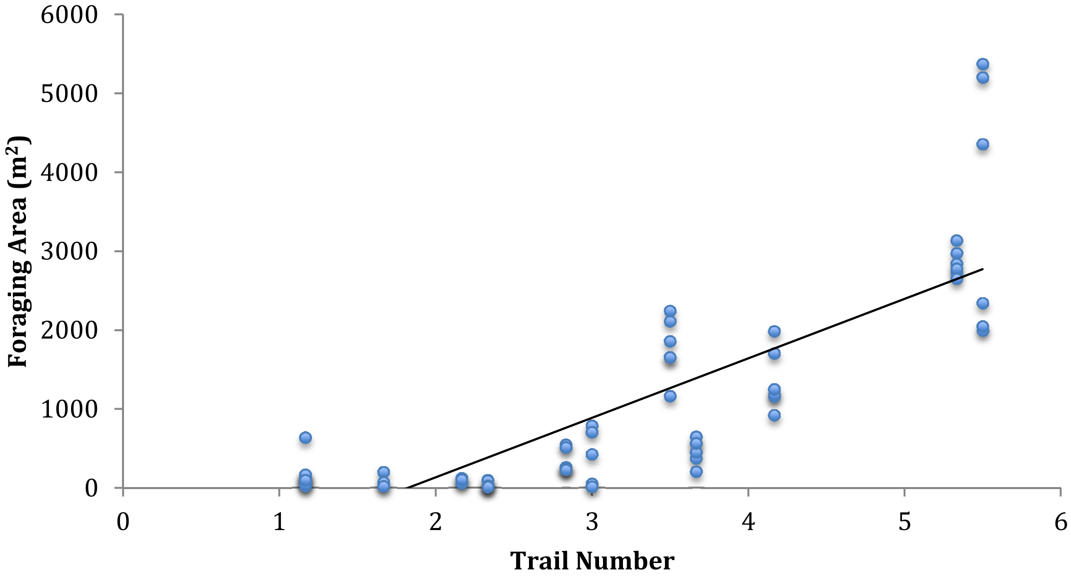

Figure 11: Relationship between the number of foraging trails and the foraging area of the nests (m=753.06, r=0.819, p<0.001, n=66).

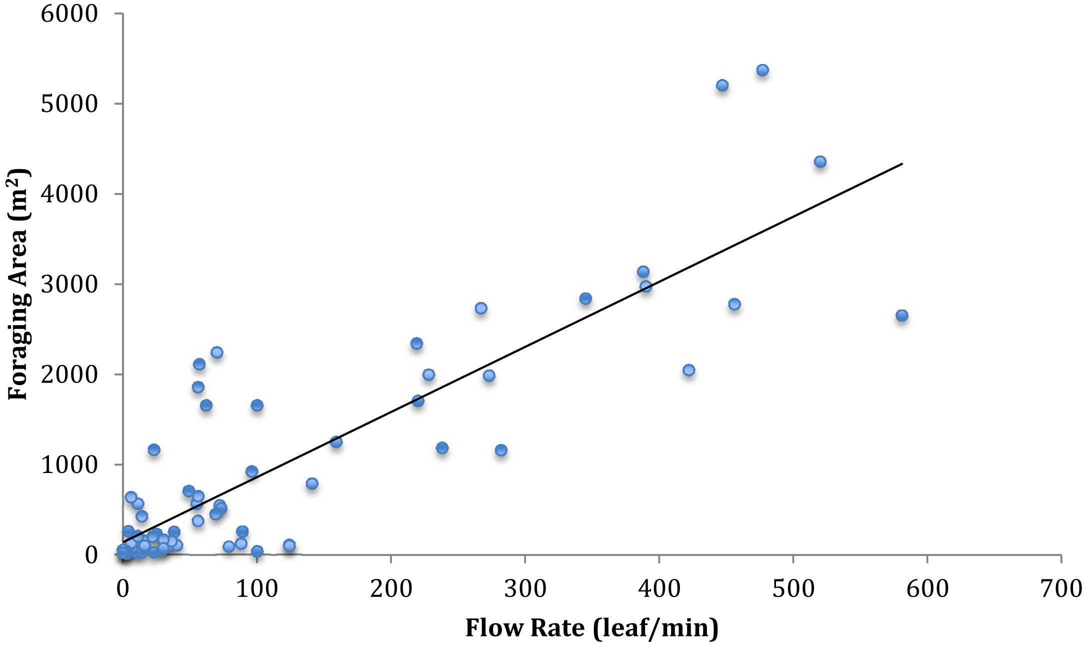

Figure 12: Relationship between trail flow rate and foraging area (m=7.21, r=0.855, p<0.001, n=66).

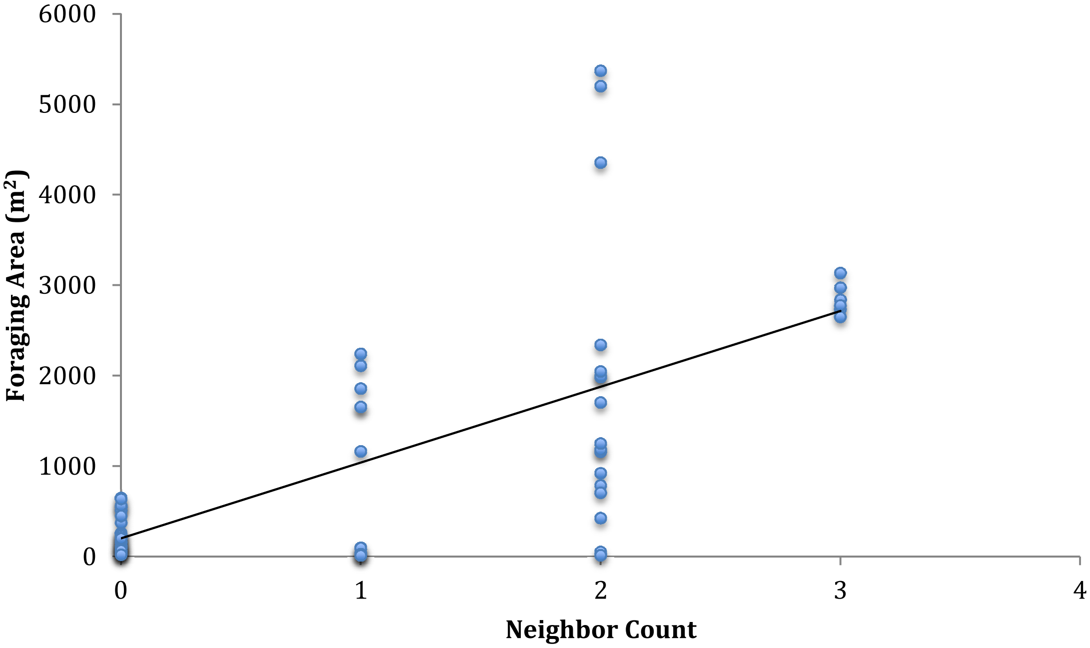

Figure 13: Relationship between the number of neighbors within the potential area of each nest and their respective foraging areas (m=837.26, r=0.687, p<0.001, n=66).

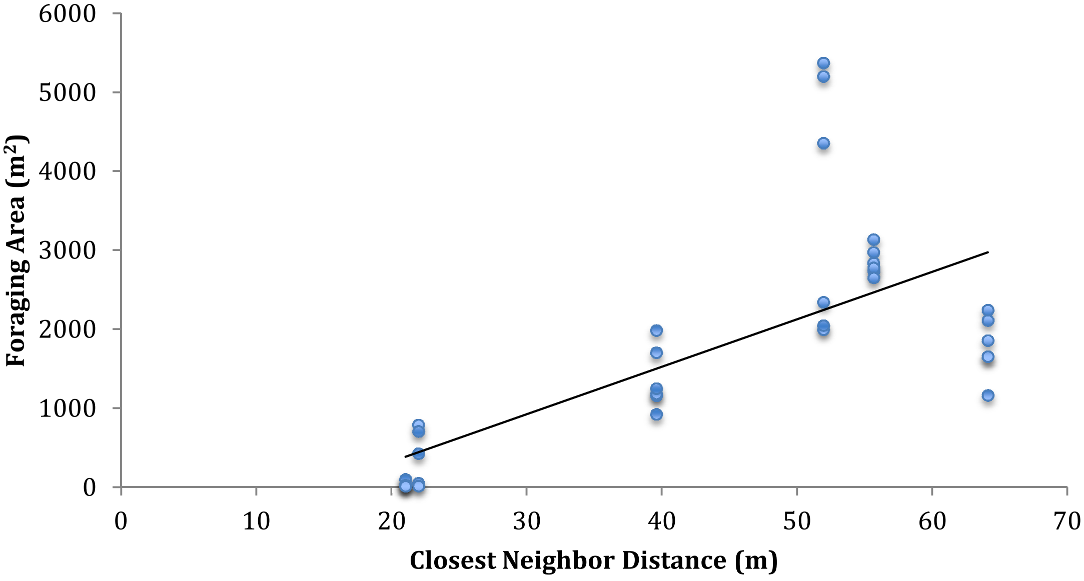

Figure 14: The distance of the closest neighbor in relation to foraging area for the six nests that had a neighbor fall within their potential foraging areas (m=60.10, r=0.697, p<0.001, n=35).

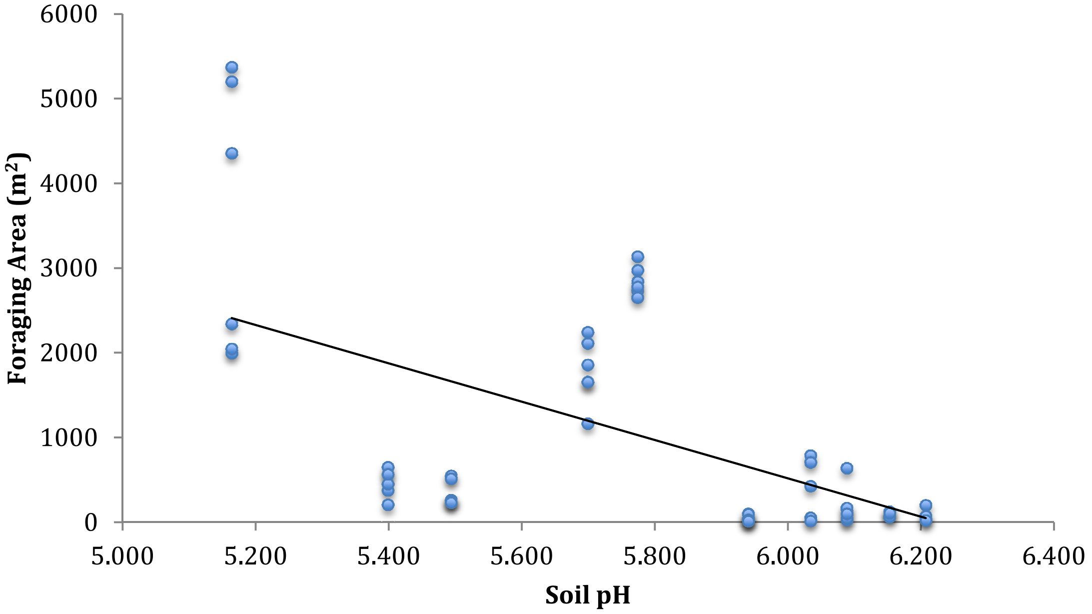

Figure 15: The correlation between the pH of the soil around the nest and the foraging area (m= -2261.50, r= -0.554, p<0.001, n=55).

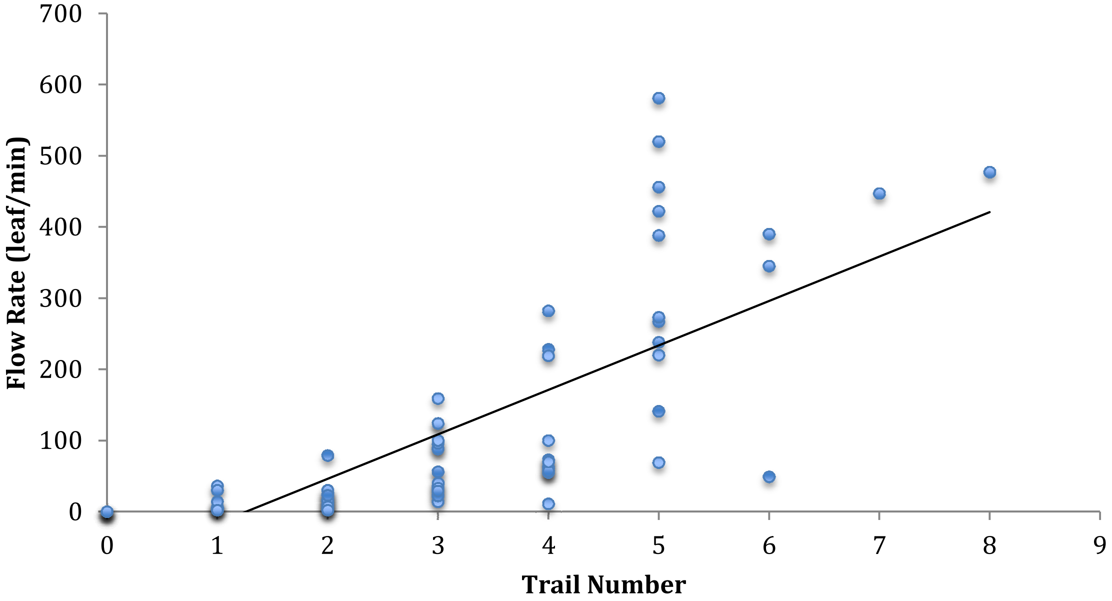

Figure 16: Relationship between the number of foraging trails and flow rate (m=62.44, r=0.752, p<0.001, n=66).

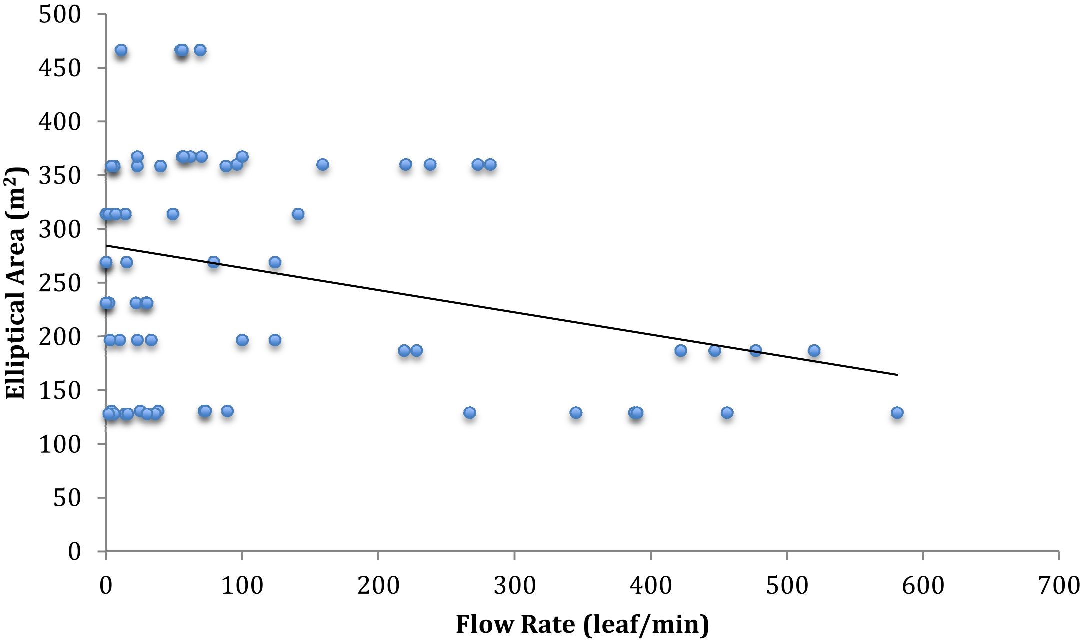

Figure 17: Relationship between the foraging trail flow rate and the elliptical area of the nest (m= -0.21, r= -0.284, p=0.016, n=66).

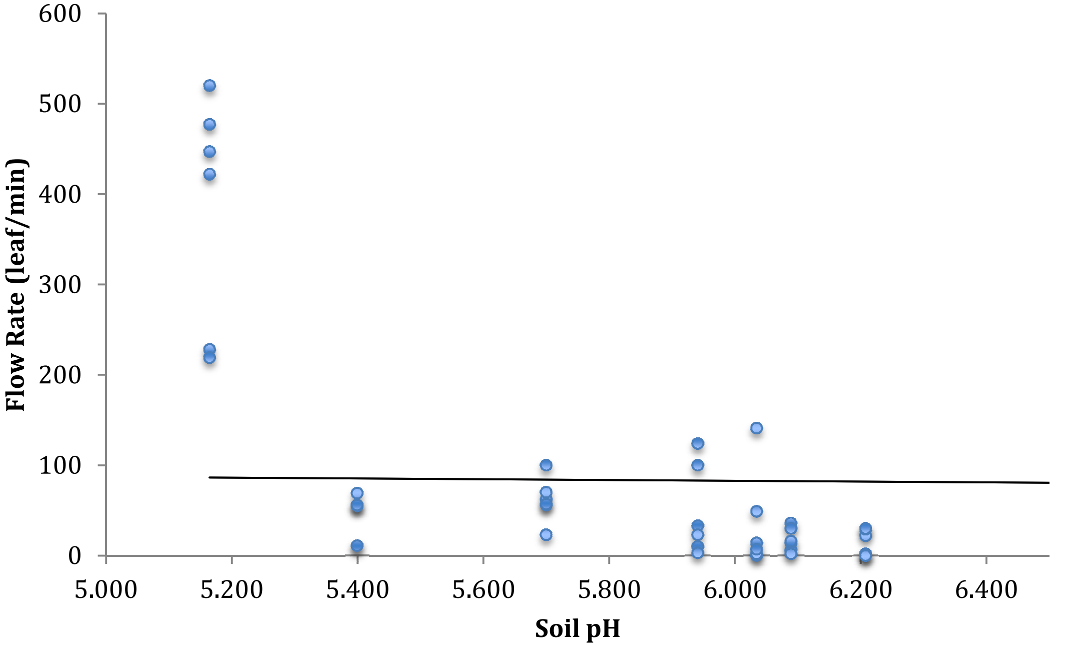

Figure18: Relationship between soil pH and flow rate (m= -0.29, r= -0.492, p<0.001, n=55).

Discussion:

Overall there were differences in foraging areas between the 12 nests, and these differences correlated with differences in flow rate, trail number, neighbor distance and soil pH. No correlations were found between foraging area and nest elliptical area or light fraction.

Foraging area increased as expected as trail number (Figure 11) and flow rate (Figure 12) increased. My utilizing more trails, the ants are able to divvy up and cover more ground, thus increasing area. From week to week the number of trails did not dramatically change for each nest; they tended to either gain or lose 1 trail. And this makes sense since it is more energetically costly to establish a new trail than to maintain an existing trail (Howard, 2001). Increased foraging area also corresponded with increased flow rate, thus the ants were covering more ground more quickly, meaning increased foraging efficiency for the colony.

It was expected that as the number foraging trails increased, the flow rates would decrease because there would be fewer ants to allocate to each individual trail. However the correlation was strongly the opposite (Figure 16). This could be that larger, more populous nests had more foraging trails and thus their flow rates were high. However, no significant relationship was found between elliptical area and the number of foraging trails. It could also be that ants with larger populations have a larger scout workforce and therefore are more likely to spread out and find multiple suitable plant sources (Beckers *et al*., 1989). They could then recruit worker ants via pheromone markers and a trail would be established.

The area of an ant nest mound is an indicator of the colony age, with larger nests being older (Wirth *et al*., 2003) Therefore it was expected that larger, older nests would have higher flow rates than smaller nests because they would have higher populations and be more efficient than smaller nests. This was not the case. However, the correlation between flow rate and mound area was relatively weak (Figure 17). This could possibly be the result of other confounding factors, such as the location of the nest with regard to animal trails and human activity. If the trail is in an area of high disturbance, then the foraging rate will slow.

All the nests fell within a soil pH that was between 5 and 6.5. The nests with larger foraging areas were situated in more acidic soils, while smaller foraging area nests were found in soils that were closer to a neutral pH (Figure 15).

Reliability of the soil pH data comes into question since the researchers who conducted the study did not directly sample the nests selected. Rather the pH values were extrapolated from a kernel density plot of pH data points collected randomly across the reserve (Figure 10). So while a significant negative correlation between soil pH and flow rate is observed (Figure 18), this may be more a representation of the pH of the soil within a large area around the ant nests. This can be fixed by performing a more focused nest-soil assay project on the reserve in the future, then reexamining the results. However, according to Haines (1975), pH probably does not significantly impact ant behavior so it may be more interesting to look nutrient levels in the soil. In a study done on Barro Colorado Island, Panama it was found that attine ant refuse piles had nitrogen concentrations and carbon concentrations that were 26 times and 12 times greater, respectively, than the surrounding forest floor (Wirth *et al.*, 2003).

No significant correlation was found between light fractions and foraging area. However, according to Haines (1975), ants change the light conditions around the smaller understory cover and not in the larger canopy cover. The ants tend to clear out all understory vegetation growing on the nest mound, which results in understory gaps near the nests. This can be seen in Figure 1, where all the small saplings have had their leaves stripped. Since the measurements taken by Pera in 2010 were of canopy light fractions, it makes sense that there were no significant differences between nests. Therefore it would be interesting to carry out a project measuring the understory light fractions around nest and non-nest sites to see if they are significantly increasing light penetration within their foraging area.

Contrary to predictions, the number of neighboring ant nests had a positive correlation with foraging area. Meaning that as the number of neighbors increased the foraging area increased (Figure 13). However, this actually makes sense since it would be expected that larger foraging areas would randomly intersect more neighbors.

Interestingly, the further away the closest neighbor was, the larger the foraging area was (Figure 14). This suggests that perhaps there is competition for foraging space between neighboring nests. Competition has not been widely studied among attine ants and there is not a lot of literature on it. Hölldobler and Lumsden (1980) studied territoriality in harvester ants, *Pogonomyrmex barbatus* and *P. rugosus* and found that trails of intraspecific neighboring nests never crossed. And while foraging areas of neighboring nests can overlap, there tends to be very little aggression since there is very little actual contact. The ants tend to stay on their respective trails and diverge in different directions. However, they saw that when trunk trails did cross there was heavy aggression until the trails diverged again. Thus neighboring nests influence the directionality and length of each other's foraging trails. They also found that forager recruitment partly depended on the presence or absence of foreign foragers at the resource patch. Sites previously occupied by foreign foragers were deemed less attractive than unoccupied sites. It would be interesting to see if this is the case with attine ants as well. There is a claim that *A. cephalotes* deposits territorial pheromones along its trails (Jaffe *et al.,* 1979), however follow-up studies have been unable to verify this (Hölldobler and Wilson, 1990).

Some nests ceased activity during the period of study. This could be the result of nest movement, which was most likely the case for nest EG10, or of nest death. Short periods of inactivity can be explained by sensitivity to particularly heavy rainstorms, thus making the ants slow to get back into an active foraging rhythm (Hölldobler and Wilson, 1990).

In conclusion, it appears that leaf-cutter ants have a major impact on tropical forest dynamics and are thus an important organism to look at when discussing restoration ecology and secondary forest growth in Costa Rica. They are considered ecological engineers because they alter the availability of resources to other organisms (Jones *et al.,* 1994). Tropical forest soil is relatively nutrient poor because a lot of the nutrients are contained within the standing vegetation. Attine ant harversting enables some of these nutrients to be recycled and concentrated back into the soil more rapidly and frequently (Haines, 1975). This creates an environment around the nests that favors new plant growth. In fact it was found that abandoned *A. cephalotes* nests had 58% greater understory diversity and 73% greater understory abundance than the surrounding forest (Garrettson *et al*., 1998).

In a study done at La Selva, Perfecto and Vandermeer (1993) estimated the turnover rate and size of *A. cephalotes* nests. They suggested, given the abundance of leaf-cutting ants in tropical forests, that these ant nests could occupy the entire forest area every 200-300 years. If this holds true, then the Firestone Reserve, which is about 25 times smaller than La Selva, could have total soil turnover in a much shorter period of time.

These ants also can affect the competitive ability of certain species. Attine ants harvest the flowers of many trees, thus either destroying their seeds or dispersing them somewhere where they are more likely to survive (Schupp, 1992; Haines 1975). Also the preferred individual trees can have as much as 40% of their total leaf production harvested, which greatly reduce the plants ability to compete for light (Wirth *et al.,* 2003), but improves the light conditions for understory vegetation (Oberbauer and Donnelly, 1986). Thus, disturbances caused by ants are not only assisting with secondary forest growth, but it is also helping maintain species richness in tropical forests (Farji-Brener and Ghermandi, 2000).

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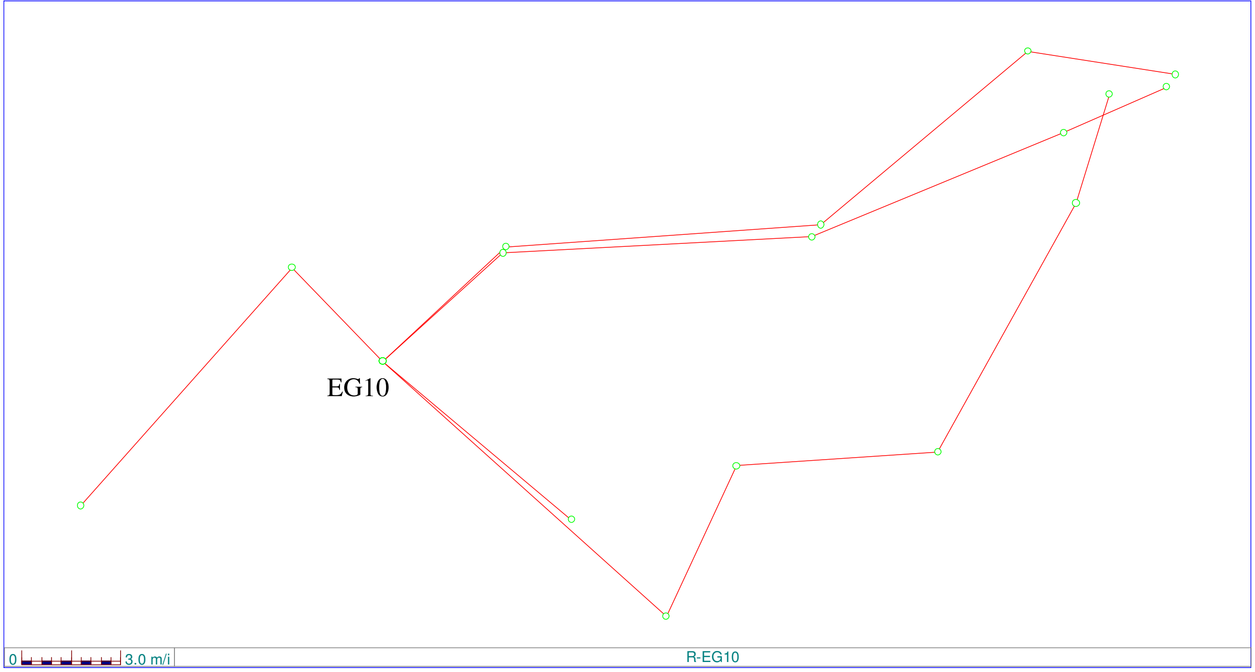
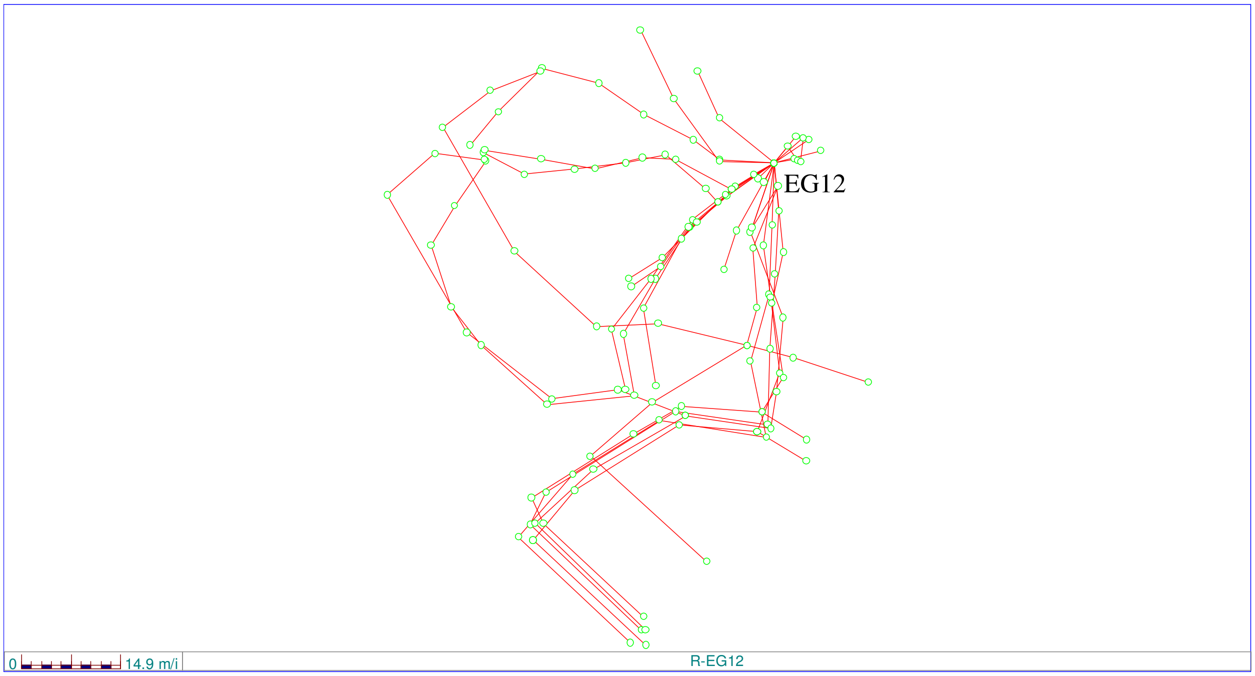
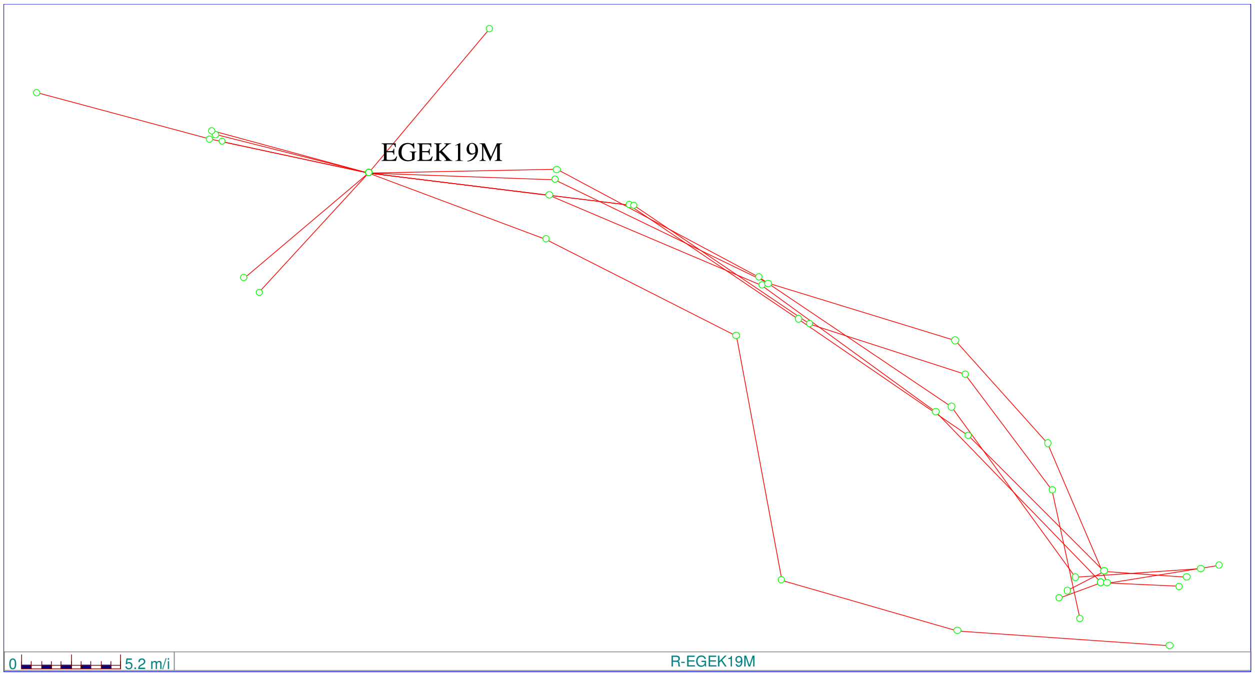
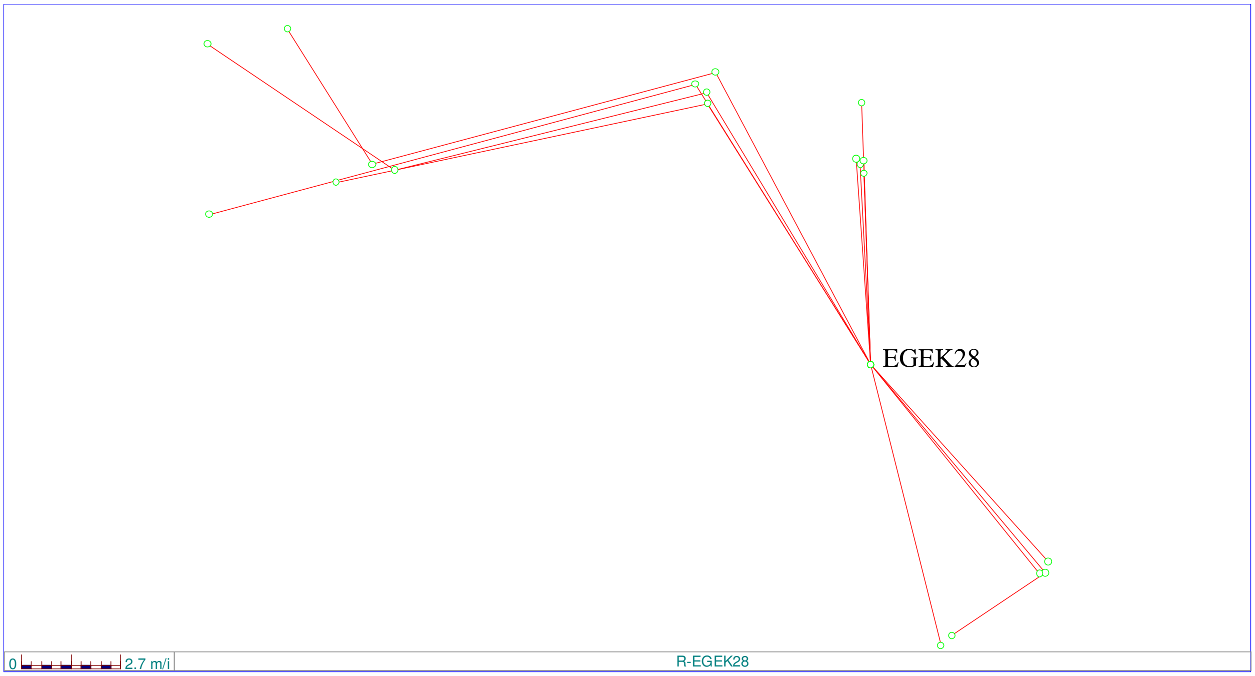
Appendix

Appendix 1: COMPASS maps of total trails for each of the 12 nest over 6 weeks






EGEK19M
0
5.2 m/i
R-EGEK19M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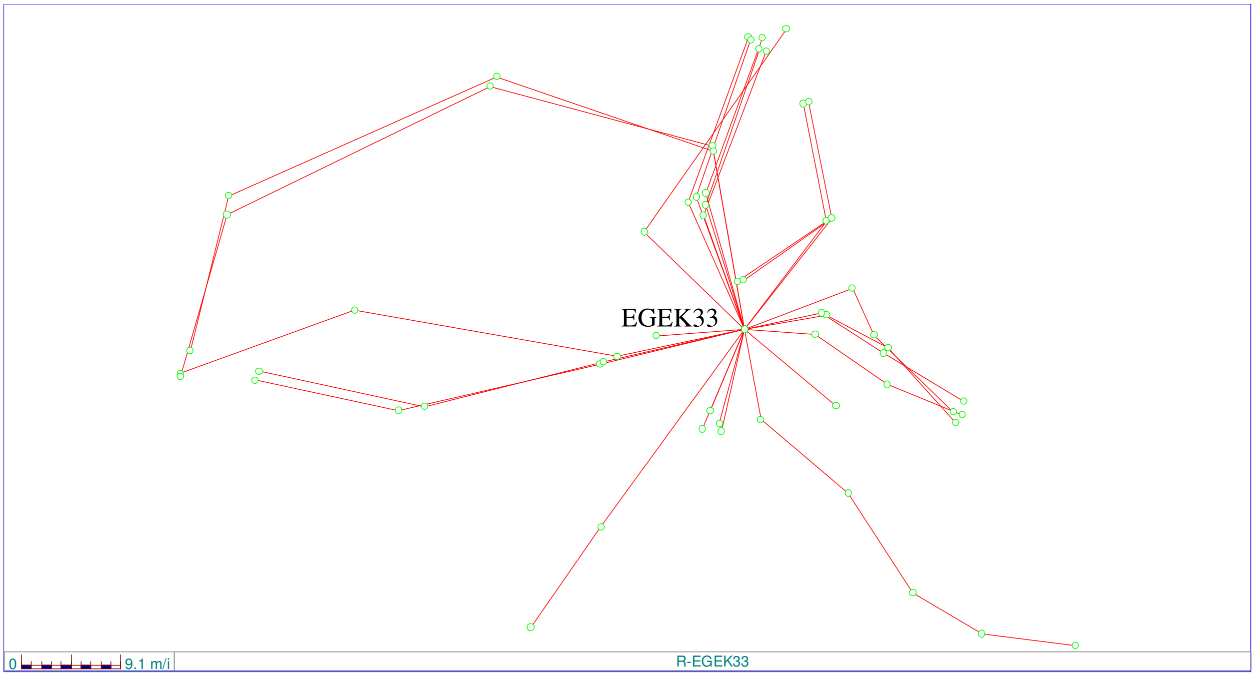
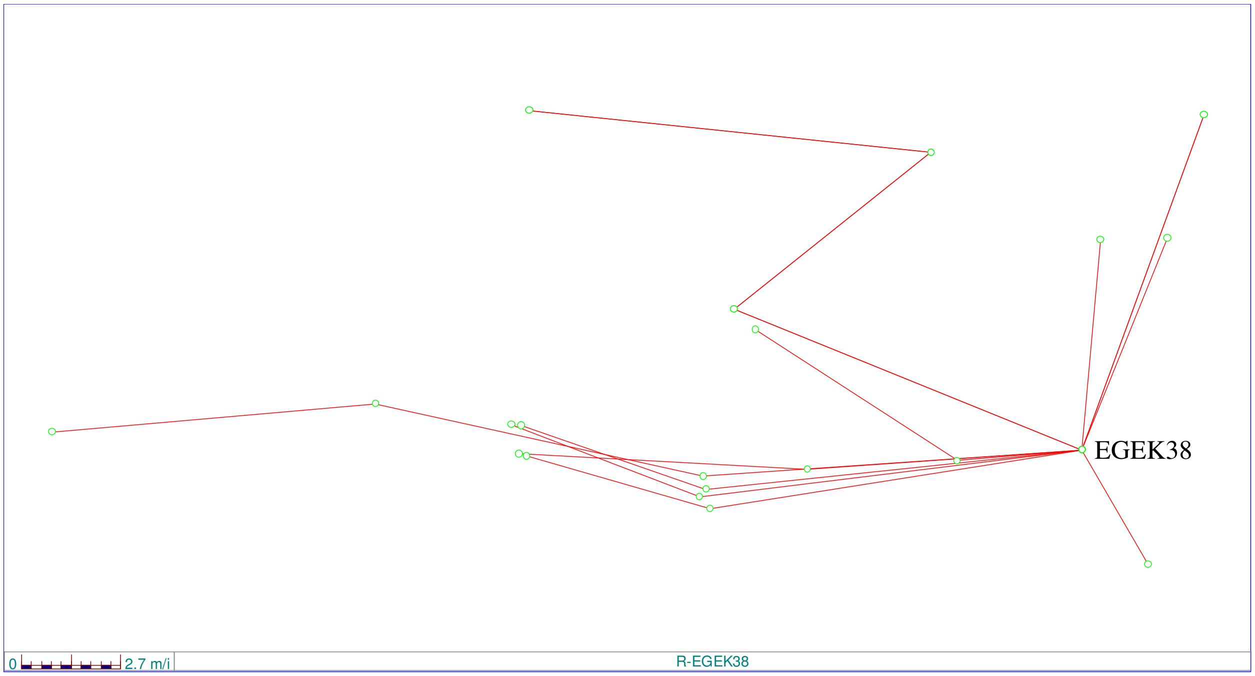
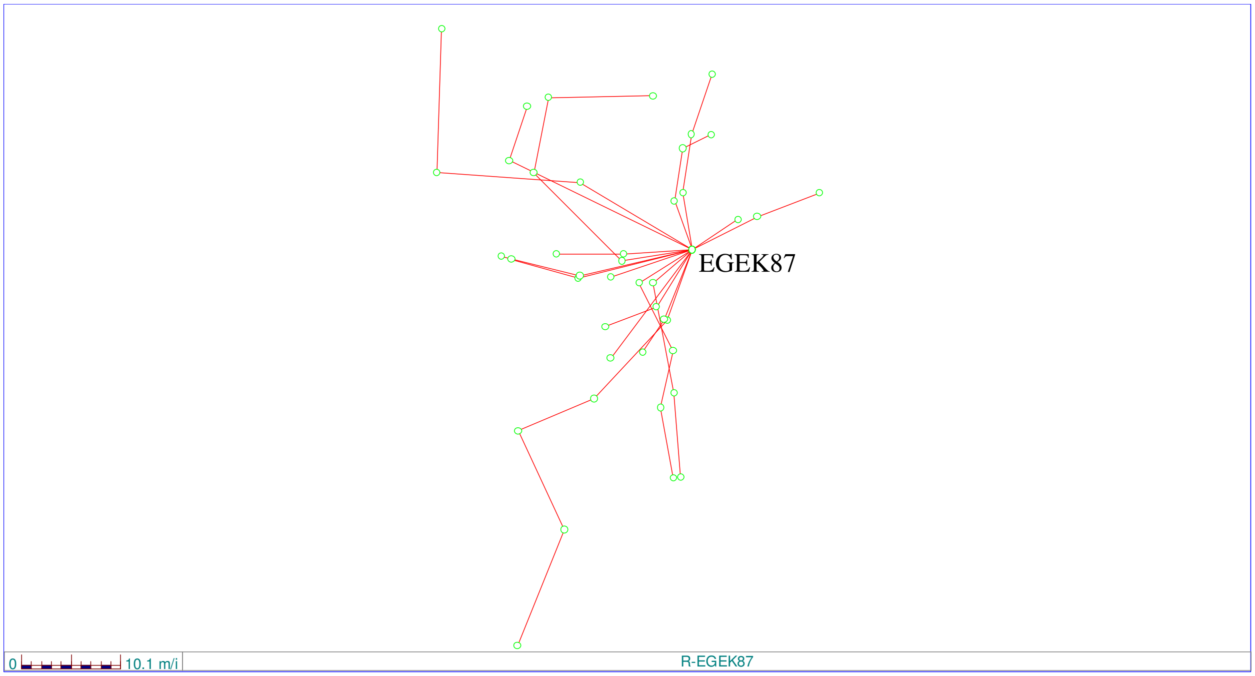
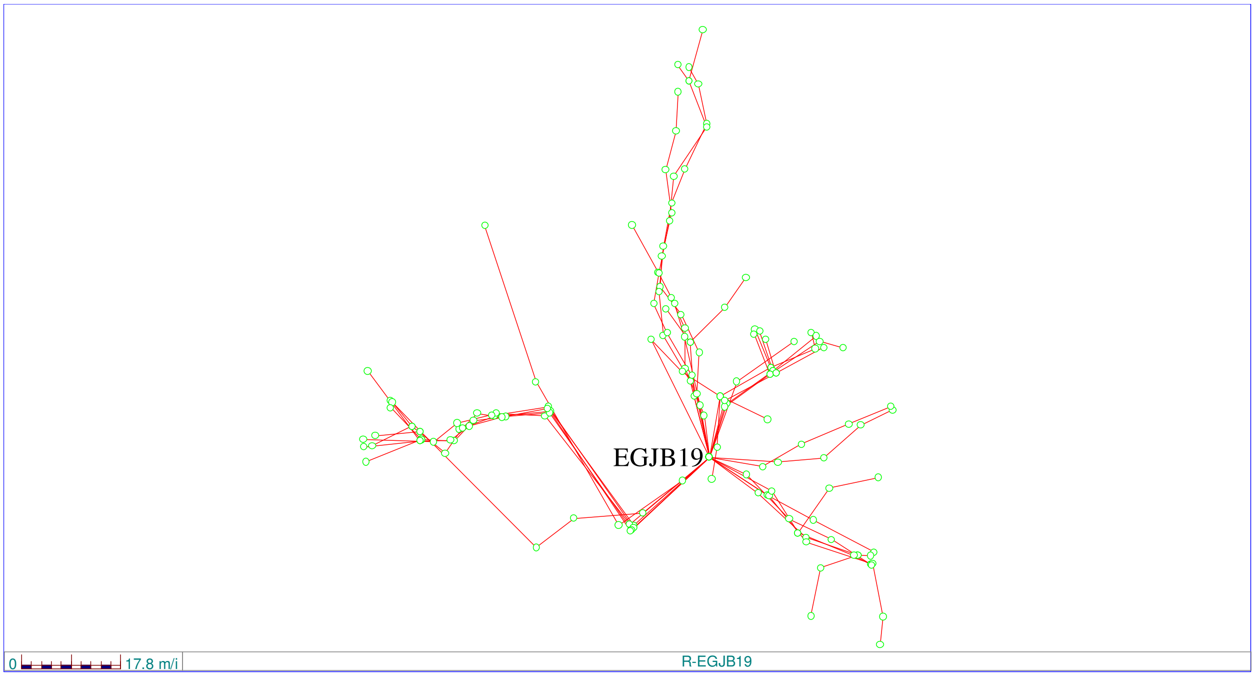
2.7 m/i
R-EGEK28

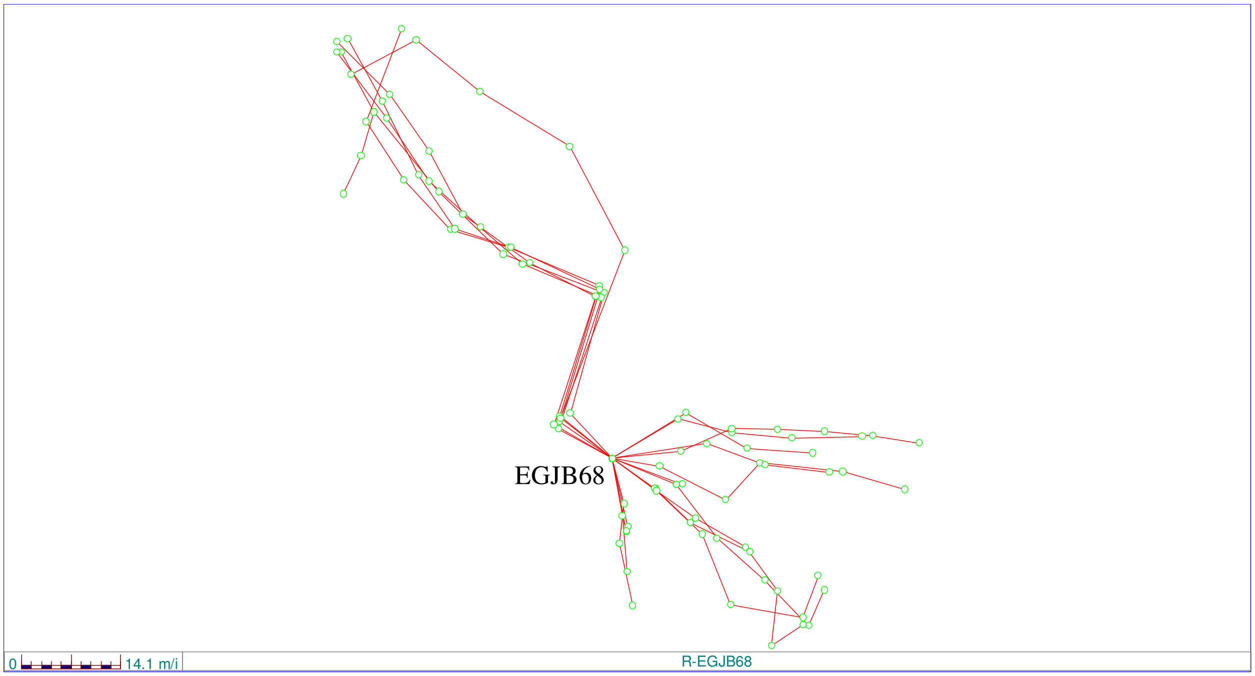

EGEK33
0
9.1 m/i
R-EGEK33

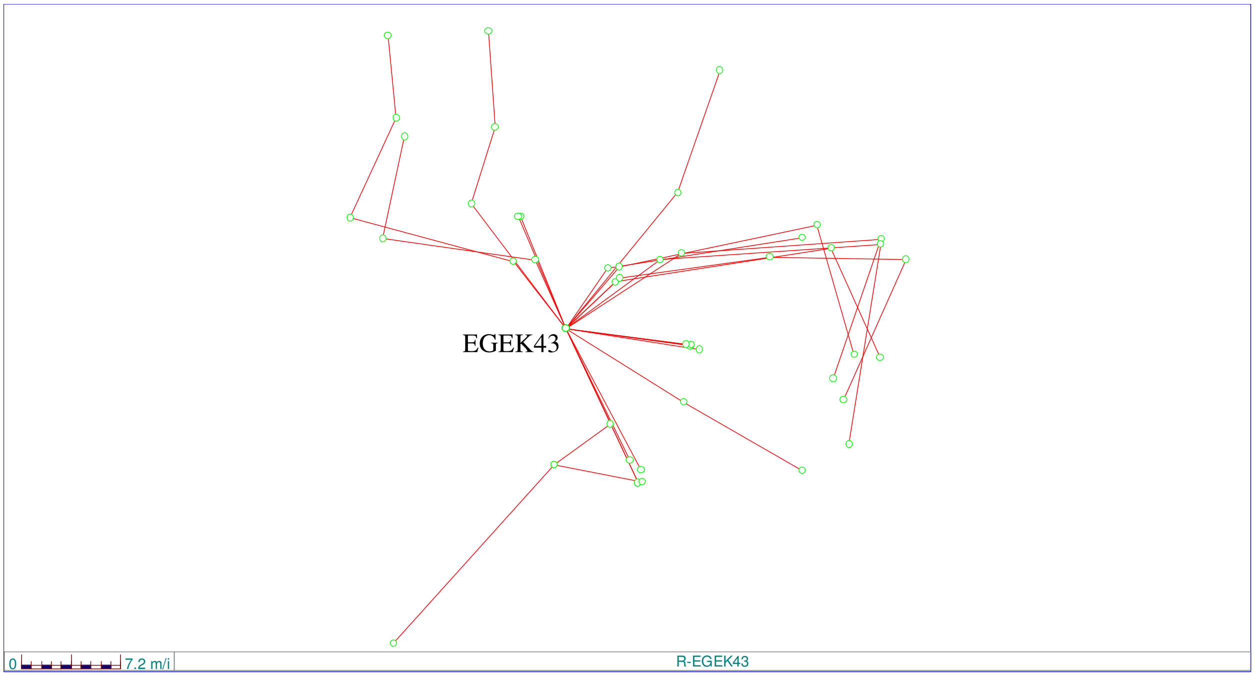

EGEK38
0
2.7 m/i
R-EGEK38


EGEK76
0
7.8 m/i
R-EGEK76


EGEK87
0
10.1 m/i
R-EGEK87


EGJB19
0
17.8 m/i
R-EGJB19


EGJB68
0
14.1 m/i
R-EGJB68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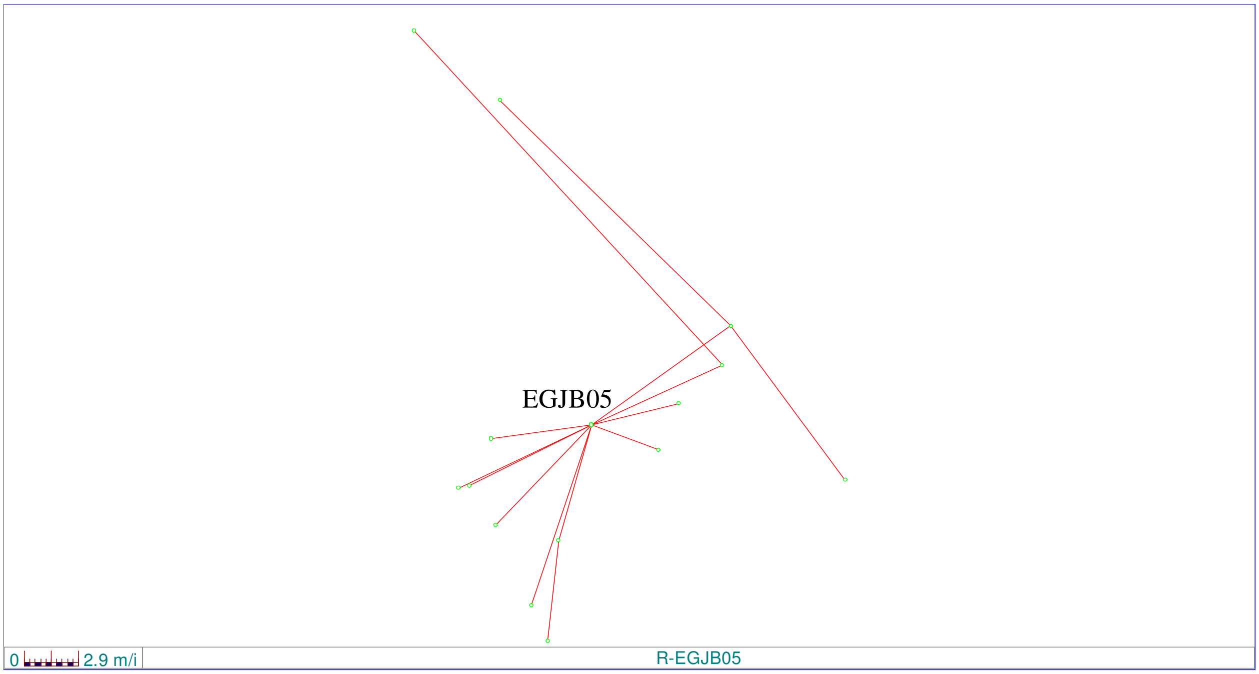
0
7.2 m/i
R-EGEK43


EGJB05
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2.9 m/i
R-EGJB05