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Habitat Fragmentation and Aculeate Wasps in San Diego County

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Habitat Fragmentation and Aculeate Wasps in San Diego County

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in

Biology

by

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

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ABSTRACT OF THE THESIS

Habitat Fragmentation and Aculeate Wasps in San Diego County

by

Kayleigh Cassidy

Master of Science in Biology

University of California San Diego, 2024

Professor David Holway, Chair

Habitat loss and fragmentation collectively are a leading cause of biodiversity decline, including in a variety of insect groups. However, the effect of habitat fragmentation on solitary Aculeate wasps is unclear. To contrast Aculeate wasp populations in areas affected and unaffected by fragmentation, we used bowl traps to sample these wasps in scrub fragments (small, isolated patches of habitat) and scrub reserves (large expanses of habitat) in San Diego County in 2015, 2016, and 2022. No significant differences were observed between reserves and fragments in the total number of wasps captured or in the number of Crabronid (family Crabronidae) wasps sampled in either of the three years. However, in 2016, reserves had significantly more wasp genera, more Crabronid genera, and more Pompilid (family Pompilidae) individuals compared to fragments. Due to there being no significant difference in any category

in at least two of the three sampling years, it appears that Aculeate wasps are resistant to fragmentation-driven changes, although this varies by year and by family. Further investigation using different sampling methods, greater number of years, and a closer examination of specific families and genera could shed light on this relationship.

INTRODUCTION

Habitat fragmentation is increasingly recognized as a leading form of biodiversity loss worldwide (Haddad et al. 2015). Habitat fragmentation describes when habitats are broken up into smaller, separated areas, often as a result of human development; roads, urban areas, and agriculture can all contribute to fragmentation (Haddad et al. 2015). Even if the habitat present in fragments remains intact, biodiversity can plummet due to population isolation, loss of genetic diversity, and altered physical conditions (Haddad et al. 2015, Suarez et al. 1998). Edge habitat, or the area most directly affected by human development, makes up a greater portion of fragments, leading to shifts in biotic interactions (e.g., predation, herbivory, and parasitism) and increased vulnerability to invasion (Achury et al. 2020, Haddad et al. 2015). Negative effects of fragmentation are especially prevalent when combined with decreased fragment size and increased fragment isolation (Achury et al. 2020, Haddad et al. 2015). These effects can cascade across entire ecosystems, from altered physical conditions (such as in the losses of old trees in fragmented rainforests), to changes in abundance, diversity, and community composition (Haddad et al. 2015, Laurance et al. 2000). These effects can be radical, and often incredibly complex and varied depending not only on the traits of the species, but that of the environment (Haddad et al. 2015, Hung et al. 2019). Understanding them further is key to conservation efforts of species and ecosystems alike.

It is important to understand the impact of habitat fragmentation on insects due to their ecological importance and potential for decline. Insects are important pollinators, as well as a source of food for many other animals and share close relationships with innumerable plants and animals (Cardoso et al. 2020). Beyond this, they contribute to ecosystem services that benefit humanity, from detritivores, to pollinators, to pest control (Cardoso et al. 2020). The loss of insect biodiversity worldwide, in large part due to land use changes such as fragmentation, is increasingly recognized as a environmental concern (Cardoso et al. 2020). This biodiversity loss is a major ecological threat not only due to the sheer variety of insect species, as they consist of an estimated 5.5 million species total, but also due to the myriad of services they provide (Stork, 2018). Of particular importance are the members of the Hymenoptera, which includes sawflies, ants, bees, and wasps. Functionally, Hymenoptera include many predators, pollinators, and parasitoids.

Previous studies of the effects of habitat fragmentation on insects, including studies within San Diego County, include investigations of bees and ants. Bee diversity, especially range-restricted, native species, suffers greatly in fragmented habitats (Hung et al. 2019, Olynyk et al. 2021). While the vulnerability of bees may result from a number of factors, including their nesting requirements and dependence on plants for food, fragmentation can drive losses even when native plants persist within fragments (Hung et al. 2019). Likewise, studies on native ant species showed even more dramatic losses, driven mostly from invasion by the Argentine ant (Achury et al. 2021, Suarez et al. 1998). The Argentine ant worsened the effects of fragmentation by outcompeting and attacking native ant colonies, and fragmentation allowed for greater invasion due to greater edge habitat, and changes in abiotic conditions (Achury et al. 2021).

There is a substantial gap in knowledge on the effects of fragmentation on Aculeate wasps, the close relatives of bees and ants. Aculeate wasps are known as the “stinging” wasps, and consist of both social and solitary wasps (excluding the parasitoids that made up the “Parasitica”) (Brock et al. 2021, Brothers 2019). They provide incredibly important ecosystem services, including but not limited to their roles as pollinators and predators or parasitoids (Brock et al 2021). As adults, Aculeate wasps feed off of nectar, but hunt and provision prey for their young. Many plant species rely on Aculeate wasps specifically for pollination, and there are many more arthropod species for which Aculeate wasps are predators, with prey type varying among families (Brock et al. 2021). Despite their importance, Aculeate wasps remain relatively understudied (Brock et al. 2021). The threat that habitat fragmentation poses to Aculeate wasps is unclear; individual studies show mixed results, with some species benefiting from increased edge habitats, and others suffering in small fragments (Coudrain et al. 2013, Schüepp et al. 2011, Török et al. 2022). The previous investigations of ants and bees, their close relatives, indicate the possibility of diversity declining from fragmentation. However, Bolger et al. 2008 showed how populations of spiders increased within fragmented ecosystems, with potential links to the consumption of Argentine ants by non-native spiders. Numerous Aculeate wasps feed on spiders, and if this pattern persists, then it is possible that the spider-feeding Pompilids may increase in abundance and diversity, rather than decrease. In addition, as Aculeate wasps consume nectar as adults (as bees do), but likewise predate on other arthropods (as spiders do), it is unclear whether fragmentation would decrease their diversity and abundance, in the case of bees, or increase, in the case of bees.

In this project, we aimed to examine the potential effects of habitat fragmentation on Aculeate wasps by comparing wasps found in preserved sites ("reserves") versus those in fragmented sites ("fragments"). We surveyed 15 sites across San Diego county to assess whether or not the number of Aculeate wasp genera or the number of individuals sampled varied between reserves and fragments over three sampling years. This effort provided an overview of Aculeate wasps as a whole. As results were expected to vary by family, as wasp families vary in food and nesting requirements, results for both sample count and genus count were conducted a the level of family. Of the families present, Crabronidae and Pompilidae were examined due to being the most numerous. We predicted that fragmentation effects would vary between families, and would show a greater impact on genera count in comparison to capture count due to how genera may vary in their vulnerability to fragmentation. In addition, we expected Pompilid count to be more affected by fragmentation than Crabronids as a whole due to the sheer diversity of Crabronids, as well as the reliance of Pompilids on spiders as a food source.

METHODS

We designated sites within coastal sage scrub ecosystems across San Diego County as either reserves (internal area > 500 ha) and fragments (internal area 2.7 - 117 ha), to allow for comparison between areas affected and unaffected by habitat fragmentation (Table 1). Fragments were surrounded by urban development, and all sites have comparable plant assemblage compositions (Hung et al. 2017). Within each site, we designated 1-ha study plots. Bowl traps, or 96 mL (7 cm diameter) white, blue, or yellow bowls filled with 60 ml detergent solution and were placed along linear transects within each study plot (15 bowls per plot). All sites in Table 1 were sampled in 2015, 2016, and 2022, except for MTS7, MTI2, and SCR. The 2015 and 2016 sampling periods consisted of the habitat fragmentation project started by Keng-Lou James Hung (Hung et al. 2019, 2021). These efforts were continued by Jess Mullins in the 2022 sampling year. These projects aimed to assess the effect of habitat fragmentation on native bee assemblages; however, wasps were caught in addition to bees.

All wasp samples were removed from bowls, washed, dried, pinned, labeled, and identified, first to overall grouping, and then to family and genus. The majority of genus identifications were done professionally. We focused on genus-level identifications, rather than species-level, due to the high level of specificity and expertise necessary to identify certain genera to species. Identifying to genus allowed for a broader, but more timely, examination. Intra-year, rather than inter-year, analyses were done in order to account for potential differences in sampling times and lengths, as well as the sites that were added in 2022 (Table 1).

All analyses were done within R version 4.3.2. Within each year, overall capture count was compared between fragments and reserves using Welch's t-test. The number of genera found at each site was also compared across site type within each year, likewise using Welch's t-test.

These two analyses assessed whether overall Aculeate wasp sample count or genera count were affected by fragmentation in each of the three years, separately.

In order to investigate whether specific families showed different patterns than the aggregated Aculeate wasps overall, Aculeate wasp families were examined separately. Those families with a sufficient number of samples within each site type and year were Crabronidae and Pompilidae. For each family, the number of samples (belonging to that family) was compared across site type and year. In addition, we examined genera count in each site by site type and year for Crabronidae. Pompilidae was not analyzed in this manner due to the number of early samples not identified to genus, and the fact that the vast majority of samples belonged to a single genus: Aporinellus. All of these analyses were performed using the same protocol of within-year Welch's t-test between fragments and reserves.

Table 1: Sites, their designation as reserves or fragments, locations, and years sampled. Modified from Hung et al. 2021.

Plot	Type	Years sampled	Latitude	Longitude	Internal area (ha)
ECR5	Reserve	2015, 2016, 2022	32.900	-117.075	> 500
ECR4	Reserve	2015, 2016, 2022	32.893	-117.092	> 500
MTE3	Reserve	2015, 2016, 2022	32.822	-117.076	> 500
MTE4	Reserve	2015, 2016, 2022	32.835	-117.075	> 500
MTI2	Reserve	2022	32.842	-117.065	> 500
SWEA	Reserve	2015, 2016, 2022	32.732	-116.956	> 500
SWI4	Reserve	2015, 2016, 2022	32.727	-116.940	> 500
MTS1A	Fragment	2015, 2016, 2022	32.792	-117.061	2.72
MTS2	Fragment	2015, 2016, 2022	32.856	-117.188	12.89
MTS6	Fragment	2015, 2016, 2022	32.722	-117.119	52.79
MTS7	Fragment	2022	32.740	-117.086	12.01
SCR	Fragment	2015	32.875	-117.248	36.38
SWS1	Fragment	2015, 2016, 2022	32.750	-117.032	46.55
SWS3	Fragment	2015, 2016, 2022	32.720	-117.078	28.06
SWS10	Fragment	2015, 2016, 2022	32.786	-116.989	6.23

RESULTS

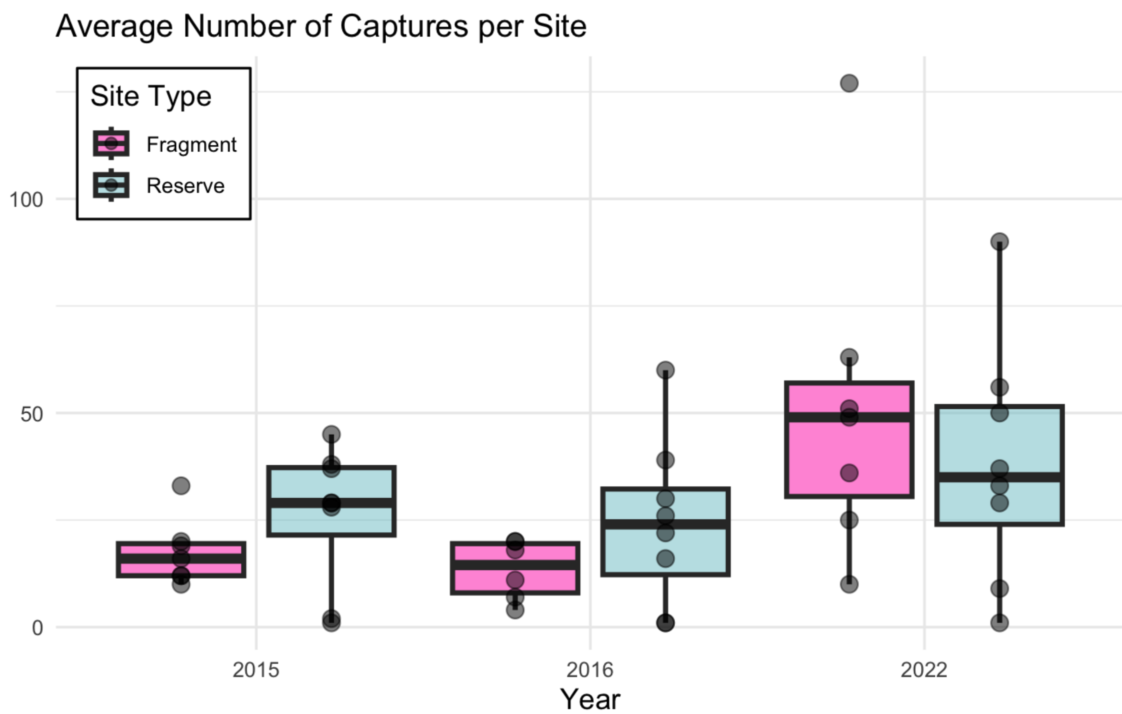
The average number of captures (number of individual wasps) within each site was compared across site type and within each year (Figure 1A). Within each year, there was no significant difference in captures between fragments and reserves, indicating a lack of overall effect of fragmentation on wasp assemblages in aggregate. The number of genera found at each site was compared across site type and within each year (Figure 1B). Generic richness did not differ in 2015 and 2022 between fragments and reserves, but more wasp genera were found in in reserves than in in fragments in 2016.

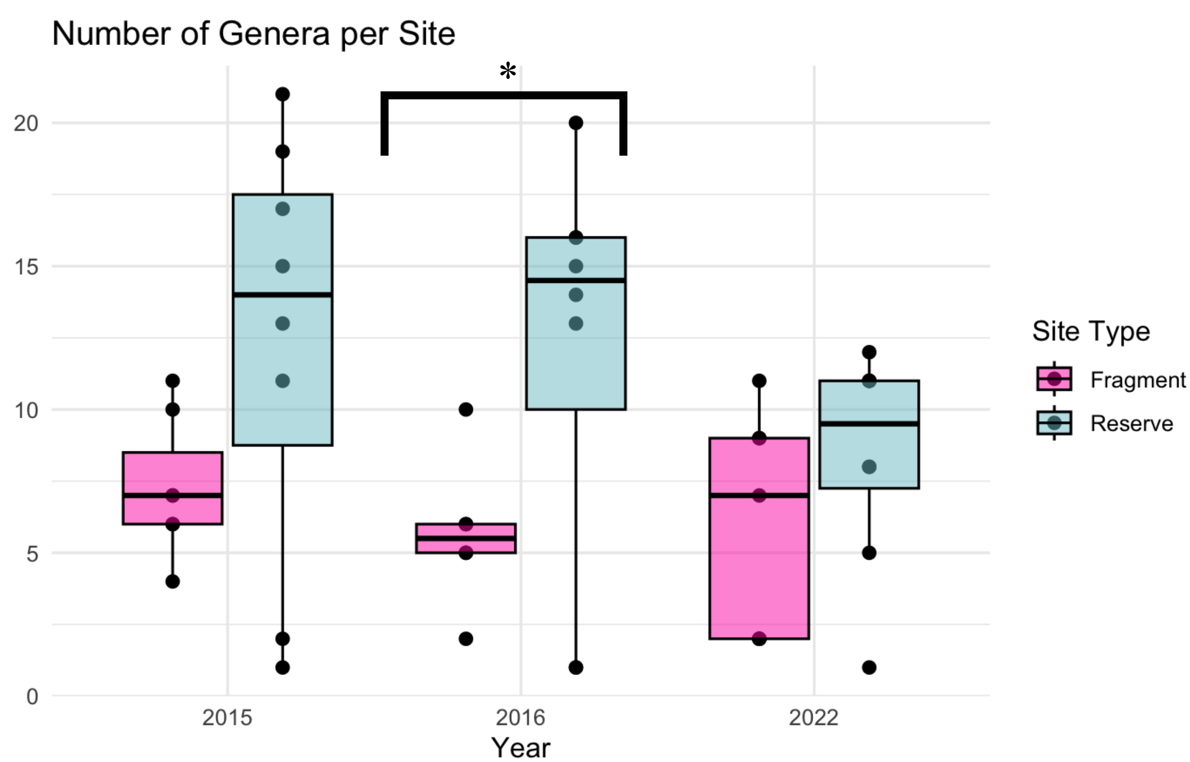
Crabronidae and Pompilidae were present in all years and site types. The number of individuals in the Crabronidae did not differ between reserves and fragments in any of the three years (Figure 2). In contrast, Pompilidae (Figure 3) were less abundant in fragments than in reserves in 2016.

We examined genus count in each site by site type and year for Crabronidae. Within Crabronidae, there was a significant difference in the number of genera found at each site between fragments and reserves in 2016, but not 2015 and 2022.

Figure 1: Captures & genera count across years and site types.

1A: There was no significant difference in wasp capture count per site between fragments and reserves in any year: 2015 (Welch two-sample t-test, df = 10.355, p = 0.2072), 2016 (Welch two-sample t-test, df = 9.199, p = 0.1737), 2022 (Welch two-sample t-test, df = 11.005, p = 0.4543).
1B: There was a significantly lower number of genera found per site in fragments compared to reserves in 2016, but not 2015 or 2022. 2015 (Welch two-sample t -test, df = 8.667, p = 0.1018), 2016 (Welch two-sample t-test, df = 9.287, p = 0.04401*), 2022 (Welch two-sample t-test, df = 12.59, p = 0.2555).


Average Number of Captures per Site
Site Type
Fragment
Reserve
100
50
0
2015
2016
2022
Year


Number of Genera per Site
*
20
15
10
5
0
2015
2016
2022
Year
Site Type
Fragment
Reserve

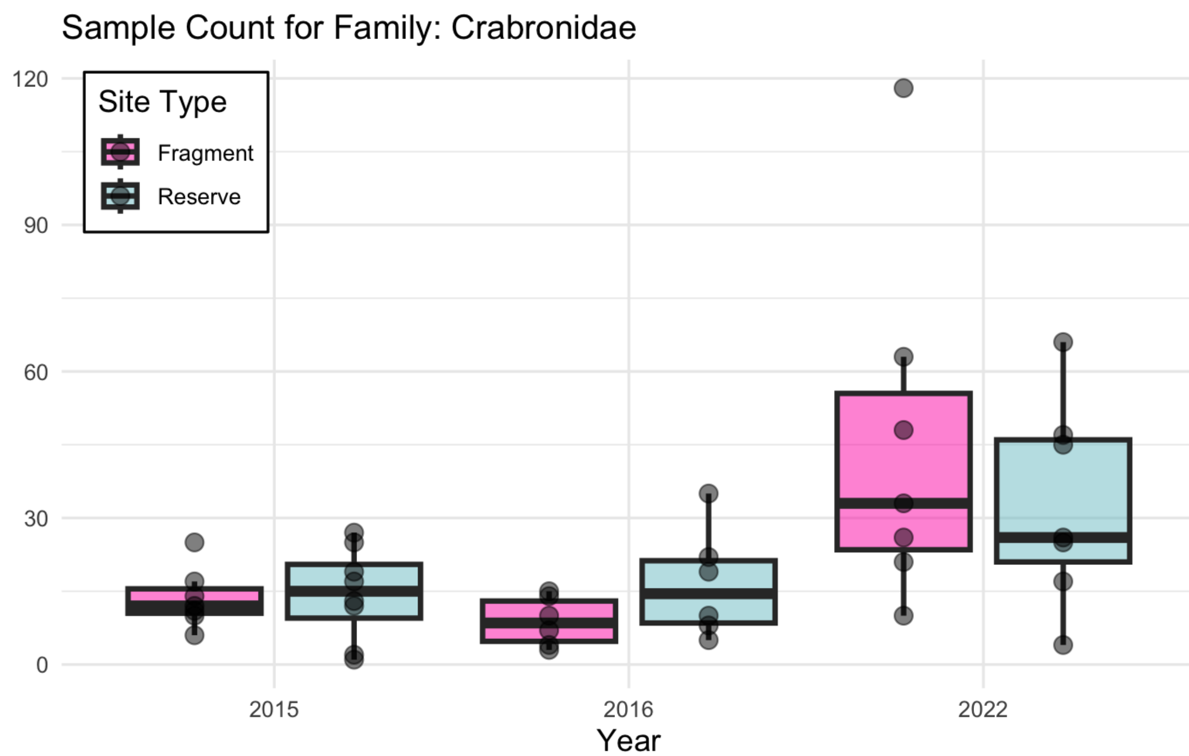


Figure 2: Number of captures within each site, across site type and year.

Intra-year results: 2015 (Welch two-sample t-test, df = 10.355, p = 0.2072), 2016 (Welch two-sample t-test, df = 9.1995, p = 0.1737), 2022 (Welch two-sample t-test, df = 11.005, p =0.4543). There was no significant difference between reserves and fragments in any of the three sampling years.

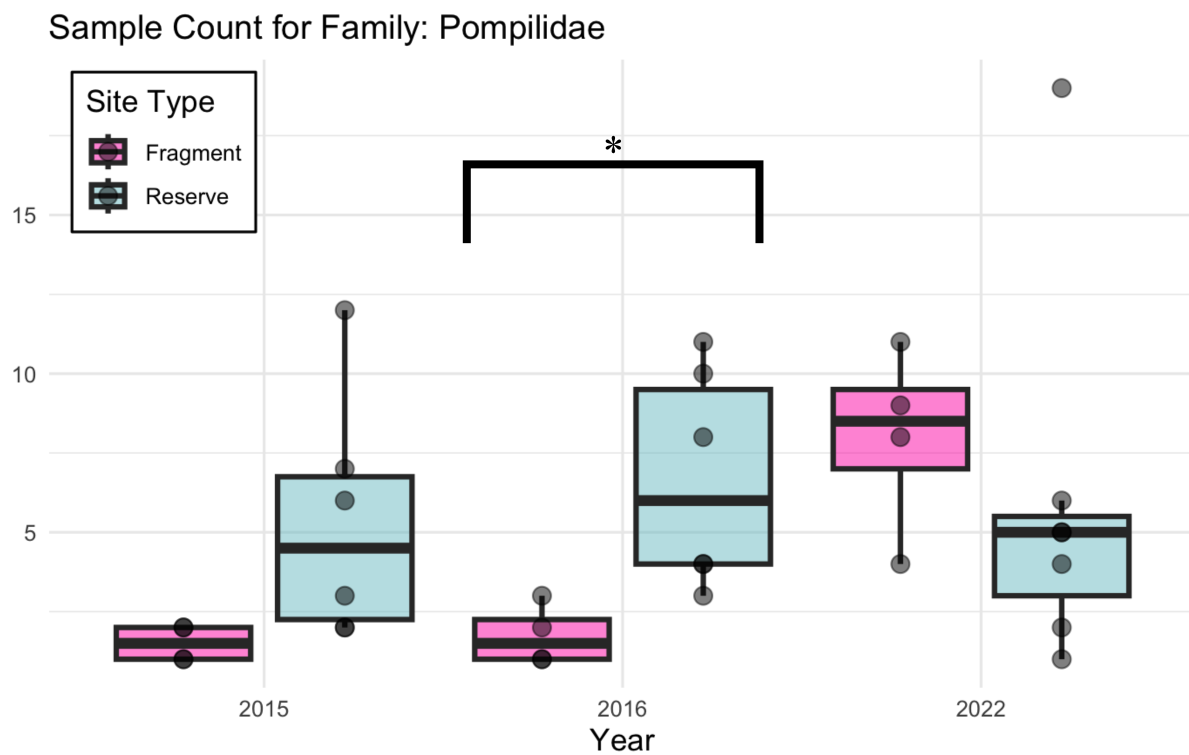


Figure 3: Number of Pompilid captures within each site, across site type and year.

Intra-year results: 2015 (Welch two-sample t-test, df = 5.3276, p = 0.06006), 2016 (Welch two-sample t-test, df = 6.089, p = 0.01586*), 2022 (Welch two-sample t-test, df = 8.9451, p = 0.4784). 2016 displays a significantly lower number of captures found in fragmented sites in comparison to reserve sites.

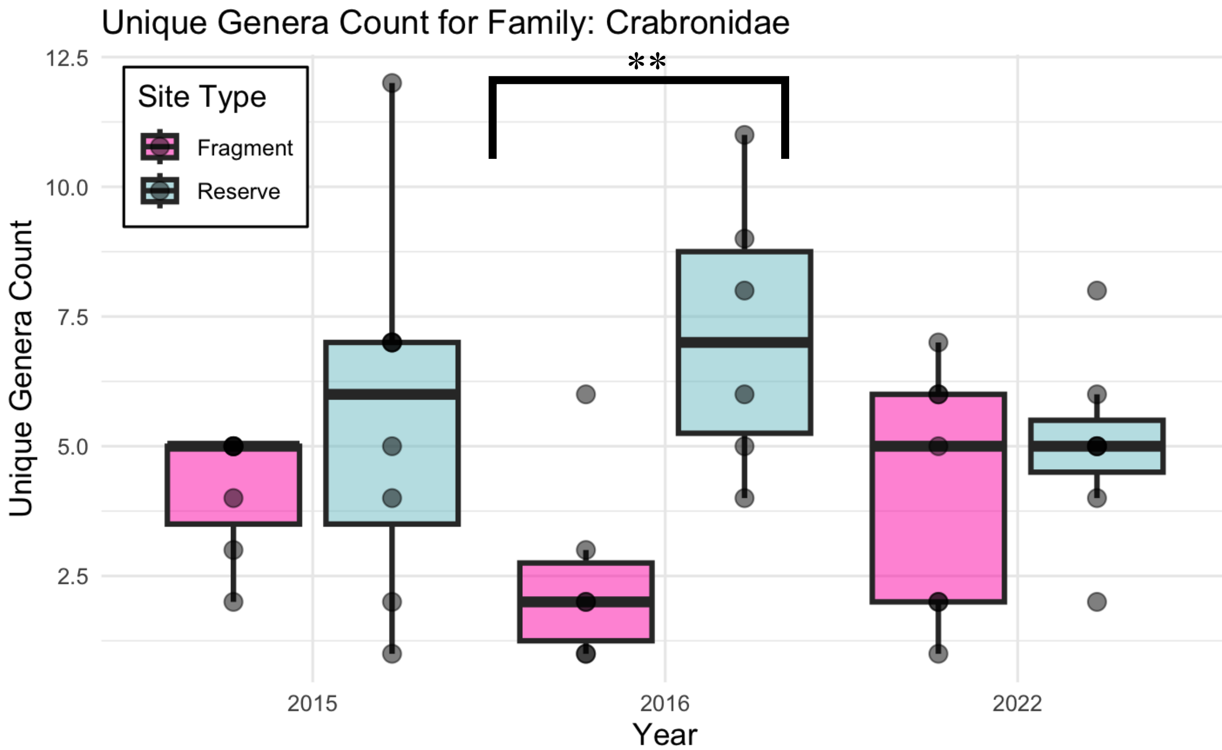


Figure 4: Number of Crabronid genera within each site, across site type and year.

Intra-year results: 2015 (Welch two-sample t-test, df = 8.904, p = 0.2865), 2016 (Welch two-sample t-test, df = 9.011, p = 0.006368*), 2022 (Welch two-sample t-test, df = 11.18, p = 0.4687). 2016 displays a significantly lower number of genera found in fragmented sites in comparison to reserve sites.

DISCUSSION

We sought out to assess whether wasp assemblages are affected by habitat fragmentation, with a particular focus on the effects on the number of genera and the number of individuals. As shown in Figure 1A, within each year, the overall number of Aculeate wasps sampled did not appear to be affected by fragmentation. This finding could potentially indicate that Aculeate wasp populations overall are resilient to fragmentation, or that the effects of fragmentation may be insignificant when compared to other ecological phenomena. This resilience appears to be mirrored in genus count in 2015 and 2022, but not 2016, potentially indicating that certain genera are more vulnerable to fragmentation effects than others.

The lack of large differences in wasp sample count between reserves and fragments, with the exception of generic richness in 2016, stands in contrast to the research done on ants, bees, and spiders, while partially aligning with previous research on wasps. Native ants (Achury et al. 2021, Suarez et al. 1998) and bees (Hung et al. 2019, Olynyk et al. 2021) decline in diversity, abundance, and richness in fragmented ecosystems as a result of increased invasion of introduced species, human interference, losses of necessary native plants, population isolation, and other losses of necessary conditions for survival (Haddad et al. 2015). Spiders, on the other hand, were shown by Bolger et al. 2008 to increase in abundance in fragments, possibly due to increased invasion by the Argentine ant (*Linepithema humile*), which some spiders may consume as prey.

Previous studies on different wasps across different types of fragmented ecosystems show mixed results (Coudrain et al. 2013, Schüepp et al. 2011, Török et al. 2022). Wasp populations can increase in relationship to fragment size and floral availability (Török et al. 2022), decrease in relationship to fragment isolation (Coudrain et al. 2013, Schüepp et al. 2011), both increase and decrease in relation to forest cover (Coudrain et al. 2013, Schüepp et al. 2011), with other studies showing varying results between different wasp families (Steffan-Dewenter, 2003).

The results for 2016 indicate a negative relationship between fragmentation and generic richness, which aligns more closely with the previous results for native ant and bee species. This finding could indicate that certain wasp genera are more negatively affected by fragmentation than others, causing a dip in generic richness, but because this pattern does not hold across the other two sampling years, the implications are limited. Certain factors can make species more vulnerable to loss in fragmentation; a higher trophic level, range restriction, dispersal capacity, competition from invasive species, and other traits are implicated as such risk factors (Bolger et al. 2008; Haddad et al. 2015; Holt, 1996; Hung et al, 2019; Van Nouhuys et al. 2005). Because these traits may vary between families, genera, and species, it is important to examine the effects of fragmentation on these levels. As explored later on in this paper, 2016 did not differ from 2015 and 2022 in temperature or rainfall, so the causes of inter-year differences should likewise be examined in combination with analyses by family, genus, and species.

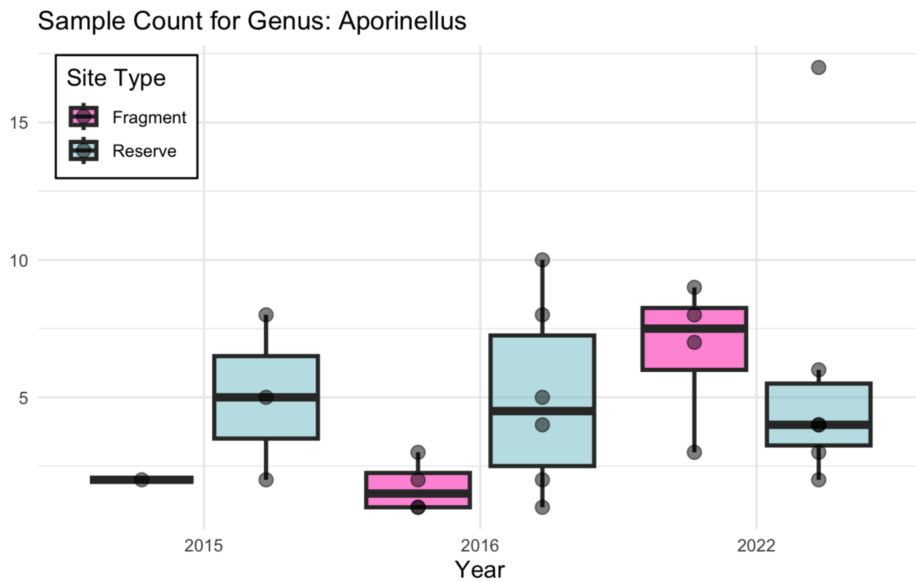
Crabronidae made up the majority of samples found. Crabronidae is a remarkably diverse grouping of wasps, consisting of thousands of species, and paraphyletic with respect to bees (Brothers, 2019; Debevec et al., 2012; Ohl & Engel 2007, Sann et al. 2018). Due to this diversity, there is also a great diversity in their arthropod food sources. Even within genera, this diversity persists, with different species within Solierella (the most abundant genus in our samples) noted as hunting hemipterans, psocids, and short-horned grasshoppers, and favoring the flower Euphorbia albomarginata (Williams 1950). This remarkable diversity may bolster this grouping's stability, or it may obscure finer differences, which require investigation to the species level. This potential gap is indicated by the drop in genera count in 2016 fragments; however, since this is only present in one of the three sampling years, implications are limited.

The second most commonly found family was Pompilidae, with the most commonly found genus therein being Aporinellus. Members of Pompilidae nearly exclusively hunt and provision spiders (Kurczewski & Kurczewski 1968). However, as this grouping showed no significant difference in capture count in 2015 and 2022, and a decreased number of captures in fragments in 2016, their capture count stands in contrast to the increase in spider abundance in fragments. This difference, however, may be due to a variety of life factors, including a potential difference in the spiders being consumed; Aporinellus feeds on Salticids ("jumping spiders"), which Bolger et al. (2008) found not be significantly affected by fragmentation.

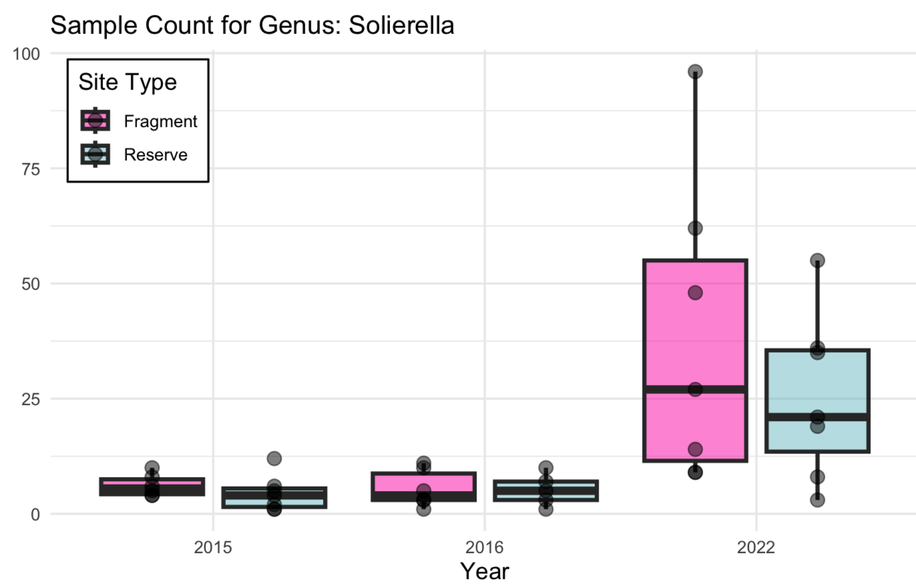
The reason why 2016 differed from 2015 and 2022 in total genera count, Crabronid genera count, and Pompilid captures is unclear. Rainfall could be a potential factor, given that it drives primary production (and, by extension, herbivore abundance) in coastal sage scrub (Hung et al. 2021). However, 2016 did not differ from 2015 and 2022 in rainfall. Annual rainfall in San Diego County was recorded as 30.25 cm in 2015, 20.77 cm in 2016, and 13.3 cm in 2021 (San Diego County Water Authority). Examining rainfall from 2014 and 2020, to potentially account for generation times, also showed no pattern (2014 recorded 12.92 cm, and 2020 had 34.5 cm). Rainfall alone cannot explain the difference found. The same pattern holds true for temperature, with 2015 having a mean temperature of 19.72 degrees F, 2016 averaging 19.05, and 2021 averaging 18.2 (NOAA). Overall, the reason behind why 2016 differed from other years in generic richness and Pompilid sample count does not appear to directly link to rainfall or temperature, despite the role that both play in the environment. Further investigation across more sampling years is required.

In addition, there are limitations imposed by the use of bowl traps: exclusive use of this method can be over- or under-represented bee diversity (Kuhlman et al. 2021, Portman et al. 2020, Roulston et al. 2007). The effectiveness and drawbacks of bowl traps are debated (Kuhlman et al. 2021, Portman et al. 2020), but it is unclear if this pattern holds true for wasps. In regards to the effects of fragmentation on wasp diversity, future directions of investigation should include more pointed examinations of specific wasp genera, as well as studying why these effects occur. The use of beating nets or nest examinations on specific families or genera could round out this investigation and cover potential gaps left by bowl-exclusive captures. Overall, a more in-depth and whole-ecosystem approach could shed light not only on the effects of fragmentation, but the ecological relationships of wasps.

This work has given an overview of the effect of fragmentation on Aculeate wasps, indicating a high resilience to fragmentation in most years and measures. These results provide some baseline information to work off of for future study, and indicate that Aculeate wasp populations may not be suffering the dramatic losses in abundance and diversity that ants and bees suffer, nor the gains that are felt by spider populations. This potential stability is a positive note for the roles that these wasps play within their ecosystems, as their stability indicates that their relationships with prey and plant species may be maintained, even in this environmental disturbance. By understanding this resilience, as well as the factors that cause the observed losses in 2016, we can better understand the different ways in which habitat fragmentation affects ecology.



Supplemental Figure 1: Capture count per site for genus Aporinellus (Pompilidae).



Supplemental Figure 2: Capture count per site for genus Solierella (Crabronidae).

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