A Survey of Queen Anne's Lace on Nantucket and an Assessment of its Effect on Native Pollination

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Keywords: *Daucus*, density, non-native, pollination, population density, *Sericocarpus*

Abstract

Queen Anne's Lace (*Daucus carota*, QAL) is a non-native plant species that was introduced to North America from Europe during the early colonial period. Its presence on Nantucket has been documented since at least the nineteenth century. Research in other plant systems has investigated whether native pollination was affected by the presence of a non-native, and the results have been mixed. Depending on the system a native may be negatively affected, may not be affected or may be positively affected, but there are characteristic features of natives that make them more susceptible to the effects on non-natives. As yet, there has been no survey of QAL on Nantucket, and no study known to the authors has investigated the effect of QAL on a native species. In June and July 2015 a survey of QAL populations was performed on properties owned and managed by the Nantucket Conservation Foundation, Linda Loring Foundation and Nantucket Islands Land Bank, as well as other, public properties. Following this, a pollination observation study was performed on QAL and a native species, Toothed White-top Aster (*Sericocarpus asteroides*, TWTA), as the native's morphology and life history appeared to put it at risk of the effect of presence of QAL. Pollinators were observed for three hours per day and five days each for the two species individually and both species cohabitating together. Queen Anne's Lace was found to be abundant across the island, with an average density of 12.2 plants/m^2 and a high density of 109.4 plants/m^2. While both plant species are generalist pollinated, QAL attracted 15 insect families and TWTA attracted only eight, the majority of each were flies and bees.

Introduction

Humans have been facilitating the movement of species past natural borders for millennia. For the majority of that time the effects on native species were little known. Within the last century though, researchers began documenting that species introduced to non-native habitats were having several effects on native flora and fauna. Most early research focused on the consequences of non-native animal introductions, such as rats, cane toads, fire ants and zebra mussels, into non-native environments. These species overpopulate their introduced environments, decimate native competing animals and prey on other, native species[1,2]. However, many non-native plants, often unobtrusive, are now considered to be highly invasive species in their own right[3–8]. Consequences of plant invasions may appear more subtle than animal invaders which interact with their environment to a more noticeable degree than plants. Nevertheless, plants are keystone species in many environments so the effects of non-natives may cascade to affect entire ecosystems. Successful plant invaders often outcompete native plant species for limited resources such as water, nutrients, space or sunlight[3,4,8,9]. Well-known early examples include kudzu, common dandelion and Japanese honeysuckle[7,10].

In addition to outcompeting for resources, it has become increasingly recognized that non-native plants may compete with native plant species and communities at the ecological level[4,11,12]. Most intriguingly, evidence shows that non-native plant species effectively interact with native plant species for pollinator services. In some cases the effects of these interactions are positive. Non-natives with more attractive flowers than natives increase pollinator species richness and number of pollinator visits which together may provide enhanced pollination to native species[3,8,12]. In these systems it appears that the non-native attracts more pollinators to the community than would normally be present, and those pollinators visit the natives, in turn. In species that are pollen- or pollinator-limited, an increase in pollinator visits would increase seed set of the native, yet if the species experiences neither limitation, there would no increase in seed set. For example, in *Raphanus sativus*, seed set increased with increasing pollinator diversity, but at the highest species richness investigated, there was a slight reduction in seed set[13]. It is possible that at high pollinator visitation or diversity, a reduction of native pollen occurs, being effectively diluted by non-native pollen on stigmas.

A meta-analysis of 40 studies obtained an overall significantly negative effect of non-native species on native species via pollination disruption[8]. Although increases in visits and

diversity may occur, non-native species may disrupt pollinator services and eventually, fecundity of native species. For instance, the presence of non-natives alters how pollinators behave towards natives. In a similar fashion to how non-natives may attract pollinators to a community, non-natives may alter pollinators' behavior, once present. A pollinator drawn to a community may follow two scenarios. It may initially visit the non-native before visiting the native, or it may visit the native but shift to non-natives before revisiting another native. In either case, the native's stigma will be "contaminated" with non-native pollen, called heterospecific pollination[6,14]. The non-native pollen may overload the stigma's capacity or simply dilute the native pollen that is present such that it negatively interferes with pollen germination and ultimately, fertilization. Subsequently, this shift in pollinator behavior has reduced seed set in native plant species[4,7,15].

Although the effects of non-natives on natives are variable, there is a consistent pattern to those effects. Native flowers that morphologically resemble a non-native will be affected more than a native that does not resemble the non-native[7,8]. If both species co-flower and are found in the same community, the effect on natives is more pronounced as pollinators will be able to directly interact with both species at spatial and temporal scales[9,11]. Likewise, when both species are generalist pollinated, they can compete for the same pollinators[4,8,11]. These effects are most prevalent when the non-natives are at high densities relative to the natives[5,9,12,14].

This project had two objectives and was performed in June and July 2015. The first objective was to map the distribution and density of a non-native, Queen Anne's Lace (QAL) on the island. The second objective was to determine the effect of the presence of QAL on the pollination of a native similar to QAL, Toothed Whitetop Aster (TWTA). We hypothesized that QAL was abundant on the island, and that QAL has disrupted the pollination of Toothed Whitetop Aster. This native species was chosen based on its abundance, generalist pollination strategy and similar morphology, flowering time and habitat preference as QAL[16].

Methods

Study Species

A common non-native species is Queen Anne's Lace (QAL), or wild carrot (*Daucus carota* ssp *carota*, L.). It is the wild relative of crop carrot (ssp *sativus*), a biennial member of the Apiaceae (Umbelliferae) family and considered a highly invasive plant species in numerous locations. The species is biennial, as it grows a rosette during the first year of growth and bolts

(flowers) May – August in the second year before dying. The inflorescence of QAL is a compound umbel composed of hundreds of white florets. The species can reach between one and two meters tall[17]. It is generalist pollinated, with Diptera (flies) being the largest group of pollinators[18]. QAL grows easily along roadsides and in disturbed landscapes and can produce several thousands of seeds per individual which facilitate its spread into new environments[17]. It was introduced to New England with the earliest settlers for medicinal purposes but quickly escaped into the wild[17,18]. It was described on Nantucket Island, Massachusetts in 1888 as being "Too common, a great pest; over-running entire fields"[19].

Two native Nantucket Asteraceae (Compositae) species with morphologies and life histories similar to QAL are *Sericocarpus asteroides* (L.), Toothed Whitetop Aster (TWTA), and *S. linifolius* (L.), Narrowleaf Whitetop Aster. These asters are putatively rhizomatous clonal, as is a related species that occurs in the Pacific Northwest, *S. rigidus*, although sexual reproduction does occur[20]. Like QAL, they also produce a rosette of leaves during vegetative growth and an upright stem when bolting. The inflorescence is the head (composite), which in these species are themselves organized into a corymb-like structure, resembling a compound umbel. The florets are white, which gives the inflorescences an overall morphology similar to QAL (Figure 1). On Nantucket both species co-flower with QAL and each other. Both species are smaller than QAL, but *S. linifolius* is generally smaller still and has a more limited distribution than *S. asteroides*, creating fewer places on the island in which it co-occurs with QAL.

Queen Anne's Lace Population Survey

The presence of QAL was investigated on properties owned and maintained by the Nantucket Conservation Foundation, Nantucket Islands Land Bank and the Linda Loring Nature Foundation, in addition to properties under public domain. When populations of QAL were located, up to five density measurements were taken randomly within the population with a PVC square meter, and an average density for the population was calculated. Latitude and longitude of each population were recorded using Smart Compass Pro (Smart Tools) installed on an Android smartphone. Distances from the population to the ocean were measured using Google Maps, a regression was performed on average density of the population by distance to the ocean and a line of best was added in Microsoft Excel (2013). A population distribution map was generated by uploading the completed dataset to Google Fusion Tables and using default settings. A density map was then generated by using the heat map feature of Google Fusion Tables,

weighted by the average density for each population and a radius of 10. A small population survey was also performed for TWTA, although this survey was less thorough than the one for QAL.

Pollination Observation Study

A random site was observed between 8:00 and 11:00 am each morning, selected from the treatments of 1) QAL in the absence of TWTA, 2) both species present and 3) TWTA in the absence of QAL. In the sites with one species present and the other absent, one square meter was observed, and in populations where both species were present, 2-one square meters were observed, one that contained QAL and one that contained TWTA. Time of pollinator visits was recorded, and pollinators were identified to the lowest possible taxon, following Ahmad and Aslam[18]. Some pollinators were identified to the species level, but all statistics were ran with pollinators maintained at the family level. Families of beetles and ants were left out of the statistical analyses as they appeared to be poor pollinators for either species. A total of 15 sites were observed for a total of 20 treatment plots, five each of QAL (-TWTA), QAL (+TWTA), TWTA (+QAL) and TWTA (-QAL) (Table 3, Figure 5). The number of pollinator visits was standardized to the number of inflorescences per treatment plot and normalized using log transformation, as in Vanparys *et al*.[15]. ANOVAs were performed on the standardized number of visits to each treatment and the number of families of pollinators to each treatment using R version 3.2.2. Shannon index, the Simpson diversity index and evenness were all calculated in Microsoft Excel (2013), and ANOVAs were ran in JMP pro 12.0.1.

Results

Queen Anne's Lace Population Survey

A total of 209 QAL populations were located on Nantucket, and a single population was discovered on Tuckernuck Island (Table 1). The average population density was 12.2 plants/m^2 across the island. The population density ranged from a low of 1 plant/m^2 to a high of 109.4 plants/m^2 on the seaside cliff of Baxter Rd in Sconset (Figures 2 and 3). Many of the populations of QAL on the island were found along roadsides and in highly disturbed areas. Population number decreased with increasing distance from the ocean, and population density decreased with increasing distance from the ocean ($p = 0.023$, $R^2 = 0.024$, Figure 4). Few populations were found within the island's numerous conservation properties (Table 1).

Pollination Observation Study

Toothed Whitetop Aster was found to co-occur with QAL in several locations on the island (Table 3, Figure 5), however, the two species were not found to be direct neighbors. They were at least 1 meter apart at all sites investigated. Both species were confirmed to be generalist pollinated, but clear differences were found between them. Queen Anne's Lace attracted 15 insect families (Andrenidae, Apidae, Calliphoridae, Crabronidae, Dolichopodidae, Empididae, Halictidae, Ichneumonidae, Lycaenidae, Muscidae, Nymphalidae, Sphecidae, Syrphidae, Tabaninae and Vespidae, Figure 6), whereas TWTA attracted only eight (Andrenidae, Apidae, Crabronidae, Halictidae, Lycaenidae, Muscidae, Nymphalidae and Syrphidae, Figure 7), a subset of the pollinator families found on QAL. The distribution of the number of pollinators was similar between the species. The majority of each were sweat bees (Halictidae) followed by families of flies (Calliphoridae, Muscidae and Syrphidae).

Toothed Whitetop Aster received a total of 149 pollinator visits and QAL received a total of 477 visits, over 30 observation hours each (Table 4). At the treatment level, QAL (-TWTA) received 290 visits, QAL (+TWTA) received 187 visits, TWTA (-QAL) received 56 and TWTA (+QAL) received 93 visits (Table 5). After standardizing by the number of inflorescences, QAL (+TWTA) received the most average visits, 20.06 +/- 11.28, followed by QAL (-TWTA) with 11.38 +/- 4.03, TWTA (+QAL) with 2.85+/- 1.72 and TWTA (-QAL) with the fewest average visits, 0.63 +/- 0.32 (Figure 8).

No significant different exists between the two TWTA treatments ($p = 0.08$), although the treatment set of QAL (-TWTA), QAL (+TWTA) and TWTA (+QAL) is significantly different than the treatment set of TWTA (+QAL) and TWTA (-QAL) ($p = 0.001$, Figure 8). There is no difference between the average number of pollinator families between species treatments, QAL (-TWTA) with 5.8 +/- 1.36 and QAL (+TWTA) with 4.4 +/- 0.93 and TWTA (-QAL) with 2.4 +/- 0.81 and TWTA (+QAL) with 2.8 +/- 0.49. However, the average number of families per treatment is significantly different between the species ($p = 0.0131$, Figure 9).

The Shannon diversity index is significantly different between the two species (QAL = 1.37, TWTA = 0.83, $p = 0.03$), and the Simpson (QAL = 0.71, TWTA = 0.48) and Evenness (QAL = 0.82, TWTA = 0.57) indices are not significant ($p = 0.06$ for both, Table 4). At the treatment level there is no significant difference in any diversity index, although each index is higher for TWTA (+QAL) versus TWTA (-QAL) ($H = 0.96$, $D = 0.54$ and $H = 0.69$, $D = 0.41$, respectively, Table 5).

Discussion

Queen Anne's Lace is a tenacious, non-native plant that can be found across the island. There are localities where it tends to be found most often, including sites close to the ocean and along roadsides. Additionally, it is found in the highest densities close to the ocean (Figure 3). Historically, QAL was found in a more widespread distribution, rather than being confined to currently disturbed landscapes[19]. It is highly probable that land use strategies on the island have changed which has decreased the prevalence of QAL in protected properties and farther inland from the ocean. Historic sheepherding on the island would have permitted consistent disturbance and facilitated QAL's incursion on the landscape, but as much of the island is now protected property, that disturbance has subsided within the last century[16]. Unfortunately, QAL produces thousands of seeds which are easily dispersed by two common island mammal species, rabbit and deer. Its seed can have a long dormancy[21], so the possibility that QAL is hidden in the seed bank cannot be overlooked, even on conservation properties. Nonetheless, it seems likely that the distribution of QAL has decreased from historic levels, and continued proper land management strategies will continue that trend.

We have confirmed that both plant species are generalist pollinated. We found that the majority of pollinator visits to each species are non-specialist pollinators, i.e. flies and bees. By far the largest pollinator family on both species is the sweat bees, Halictidae, followed by three families of flies, the Muscidae, Calliphoridae and Syrphidae, although the Calliphoridae were not found on TWTA. Consistent with previous research which investigated the effects of a non-native on native pollination, TWTA has the less attractive inflorescence of the two species, and it generally receives fewer pollinator visits and has less diverse pollinators.

One would expect the presence of an attractive non-native, like QAL, to increase the number of visits and the diversity of the visitors. Here, we show that the presence of QAL does increase the number of visits and the diversity of the visitors to TWTA, even though that increase is not always significantly different. In this situation, we obtained only five replicates for each treatment, limiting our statistical power. In addition, within each treatment there is a great amount of variation which further reduces our statistical power. Even so, we report p-values that are near significant, so with an increase in sample size it is possible that significance would appear.

As yet, a causation cannot be applied to this pollination system. We have not investigated the actual fitness consequences of QAL on TWTA, nor have we experimentally manipulated the system in any way. The next steps are to manipulate the system to determine if QAL is directly affecting the pollination of TWTA and lowering its fitness in some way. Doing so would be relatively straightforward. We propose to revisit the same locations in which both species co-occur and observe pollinator activity again over the course of a few weeks. In so doing, we would increase our replicate size by adding to the data presented here, and we would manipulate the system by removing QAL umbels after the first day to reveal if pollinator activity would decrease back to the levels found on TWTA without QAL nearby. Additionally, I expect to assay TWTA populations at specific distances from QAL for the presence of QAL pollen. It is possible that even though QAL is not present in a community with TWTA, its pollen will have traveled on pollinators and will be present.

Queen Anne's Lace is currently listed as non-native on Nantucket, but elsewhere in the United States it is classified as highly invasive, posing serious risks to native plants and communities. This project revealed valuable information regarding the distribution and density of QAL in relation to native species in Nantucket habitats. In combination, the pollination disruption data and the completed distribution and density maps of QAL on Nantucket will help to determine the risk to Toothed Whitetop Aster on Nantucket and, more generally, native plants. Island ecosystems are known to be at greatest threat from invasion by non-natives. The equilibrium theory of island biogeography and ecology posits that island ecosystems can maintain only a specific number of species which might be compromised during the establishment of non-natives. Nantucket is unique in its habitats and native flora; it encompasses many diverse landscapes which allows it to be home to several hundred species of plants, though only 48 out of its 100 sq. miles are land. In addition to its significance as an island, species interactions found in Nantucket's diverse habitats may well be applicable to broader landscapes such as those found on continental North America.

Acknowledgements

We thank Sarah Oktay, Jennifer Karberg, Karen Beattie, Sarah Bois, Kelly Omand and Rachael Freeman for being available for assistance on Nantucket. We also thank Bruce Mandel and Woody Lindley for their hospitality and transportation to Tuckernuck. We thank all of the wonderful conservation foundations (Nantucket Islands Land Bank, Nantucket Conservation

248 Foundation and Linda Loring Nature Foundation) for their permission to perform this research
249 on properties they manage. AJR particularly would like to thank the Nantucket Biodiversity
250 Initiative for funding this project through the NBI Small Research Grants program. Without its
251 assistance this project would not have been possible.

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325 Table 1. Populations and average densities of Queen Anne's Lace on Nantucket Island.

Location Number	Location Site	Latitude	Longitude	Ocean Distance	$D_{Average}$
1	Eel Point, LLF Property, Roadside.1	41.293211	-70.166959	98.15	6.2
2	Nantucket Field Station, Driveway	41.295078	-70.040414	115.76	21.2
3	Nantucket Field Station, field	41.296003	-70.040036	34.69	11.2
4	Nantucket Field Station, Sea Bluff	41.296756	-70.038981	6.77	8
5	M6 Condo, Backyard.1	41.273378	-70.101272	944.09	10
6	M6 Condo, Backyard.2	41.27305	-70.101806	1001	3
7	Eel Point, LLF Property, Roadside.2	41.291406	-70.1761	265.77	63.8
8	Eel Point, LLF Property, Roadside.3	41.291969	-70.174836	217.2	13.4
9	Eel Point, LLF Property, Roadside.4	41.292106	-70.174275	204.55	28.4
10	118 Bellevue, Eel Point Rd	41.292469	-70.172203	181.45	30.2
11	5 Little Neck Rd	41.279497	-70.193125	273.86	18.6
12	Entrance Rd, Little Neck	41.2793	-70.193572	250.08	17.6
13	Little Neck Parking Lot, Beachside	41.279739	-70.194125	6.57	53.5
14	10 Blue Heron Way	41.281669	-70.190483	111.26	8.4
15	NILB Parking Lot	41.280792	-70.191964	192.9	1.333333
16	NILB, Pine Tree	41.281281	-70.192036	80.57	1
17	NCF, Sanford Farm Overlook	41.282867	-70.137364	1190	8.2
18	NCF, Sanford Farm, Tile Silo	41.281158	-70.138186	1381	7
19	Waste Options, Madaket Bike Path	41.282293	-70.165449	1294	4.8
20	D.P.W. Office Entrance	41.283211	-70.167539	1209	3
21	East of DPW Entrance	41.282215	-70.163963	1291	3.666667
22	Madaket, 3 Brick Stone, Roadside	41.28184	-70.155236	1288	17.6
23	Madaket Rd @ Worth Rd	41.281937	-70.158176	1297	13.6
24	NCF, Madaket Rd, West of Worth Rd	41.28197	-70.159481	1291	16.4
25	Madaket Rd, Bridge	41.282031	-70.160954	1289	7.2
26	Miacomet Rd, Loop.1	41.24551	-70.111783	360.52	12.8
27	Miacomet Rd, Loop.2	41.244813	-70.111481	276.07	27
28	Miacomet Beach Parking Lot	41.243391	-70.110958	107.43	13.4
29	Miacomet Rock Walking Trail	41.247051	-70.113998	466.27	42.4
30	Starbuck Rd, South Loop	41.269422	-70.197896	73.07	4.8
31	Starbuck Rd, SE Loop	41.26919	-70.196855	68.15	14.8
32	Proprietor Rd, Madaket Beach Parking Lot	41.263089	-70.180581	75.7	3
33	48 Proprietors Rd	41.270349	-70.193943	176.02	8
34	Pinetops, 54 Proprietors Rd	41.271343	-70.193644	285.84	12
35	Arkansas Ave @ S. Cambridge St.	41.27675	-70.186914	519	6.4
36	Head of Plains @ Red Barn Rd	41.270219	-70.184565	678.35	1.5
37	Red Barn Rd Near Head of Plains	41.269786	-70.184042	647.23	8.4
38	Red Barn Rd @ WNTX Driveway	41.26839	-70.182701	567.55	10.8
39	Long Pond Sanctuary, Parking Lot	41.272142	-70.18483	844.7	16

40	Massasoit Bridge Rd, Fork	41.273084	-70.172899	1342.56	8
41	36 Washington St.	41.281249	-70.095751	50.5	1
42	2 Fairgrounds Rd	41.280439	-70.094462	12.1	10
43	N Beach Rd @ Brant Pt Rd, field	41.291075	-70.102912	255.78	6.6
44	Bathing Beach @ Hulbert Ave.	41.293333	-70.105077	193.68	24.4
45	Jetties	41.294102	-70.104937	179.64	6.2
46	Cliffside Beach Club	41.293786	-70.107584	192.29	30.6
47	Brant Point Beach	41.290041	-70.091453	0	5
48	New Ln @ Franklin St.	41.286068	-70.10865	955.1	3.25
49	68-70 W. Chester St	41.286859	-70.111984	873.76	38.4
50	96-98 W. Chester St	41.28642	-70.116057	876.96	7.4
51	Crooked Ln @ Cliff Rd	41.289146	-70.120874	552.21	9.333333
52	The Tupancy Links	41.290455	-70.128081	365.44	13.8
53	The Sound Bluff, The Tupancy Links	41.293541	-70.129546	12.49	2.5
54	The Tupancy Links, Trail.1	41.291761	-70.128326	214.25	5.25
55	The Tupancy Links, Trail.2	41.290435	-70.126774	364.9	11
56	Cliff Rd Bike Path	41.288998	-70.123423	507.51	3
57	186 Cliff Rd	41.287781	-70.128167	656.31	6
58	7 Washing Pond Rd	41.288916	-70.131837	546.41	9
59	27 Washing Pond Rd	41.291606	-70.135708	220.8	32.8
60	26 Washing Pond Rd	41.292192	-70.13403	160.11	6.5
61	39 Madaket Rd	41.281561	-70.115386	1416.8	11
62	Christian Science Society	41.281393	-70.109525	1166.66	1.666667
63	Nantucket Cottage Hospital	41.275806	-70.101462	777.51	15.4
64	Nantucket Tackle Center	41.27194	-70.093871	628.41	17
65	Milestone Bike Path, 67 Milestone Rd	41.26989	-70.064775	1947.31	2.5
66	Larsen Acres, 4M	41.26309	-69.982122	1625.44	2.5
67	Milesone Overlook Trial, P.L. Entr.	41.262497	-70.0127889	2558.86	37.5
68	Milesone Bog	41.264006	-70.007298	2574.95	17.33333
69	220 Milestone Rd	41.262276	-70.008678	2430.11	14
70	Milesone Bog, North.	41.274297	-70.005266	2655.42	3
71	199 Polpis Rd, Polpis Bike Path	41.290289	-70.03809	702.49	6.8
72	180 Polpis Rd, Polpis Bike Path	41.290369	-70.040239	568.9	18.8
73	153 Polpis Rd, Polpis Bike Path	41.290029	-70.045708	465.56	2
74	Polpis Bike Path	41.288712	-70.05017	744.56	22.4
75	82 Polpis Rd, Polpis Bike Path	41.282928	-70.062417	785.45	9.6
76	55R Polpis Rd, Polpis Bike Path	41.278809	-70.067943	958.94	15.6
77	6 Fair St	41.282543	-70.09963	341.96	1.5
78	20 Vesper Lane	41.274471	-70.101997	902.47	2.5
79	Madaket Beach	41.252382	-70.152707	27.3	8.4
80	Madaket Beach Place	41.253557	-70.151657	183.21	3.333333

81	Hummock Pond Rd @ Hellers Way	41.256951	-70.144748	734.42	1.25
82	14 Hellers Way	41.255738	-70.140388	680.44	39.33333
83	Cisco Beach Bike Path	41.258034	-70.143331	880.01	7.5
84	199R Hummock Pond Rd	41.260175	-70.140637	1195.74	1
85	167 Hummock Pond Rd	41.263877	-70.134682	1705.9	34.4
86	Advice 5Â¢	41.26884	-70.124726	2462.3	5.6
87	8 Somerset Ln	41.268573	-70.123026	2478.39	4.8
88	18 Somerset Ln	41.267152	-70.122192	2349.64	2.2
89	Raceway Dr @ Bartlett Rd	41.261214	-70.118108	1866.84	1.5
90	Tuckernuck.1	41.300877	-70.248592	70.07	24
91	Madaket Harbor	41.275581	-70.19557	7.94	14.6
92	Burnt Swamp Ln	41.2756	-70.1231	2011.68	9
93	Milestone Rd @ New St	41.262141	-69.973005	860.89	16
94	Captain Cabin, Baxter Ave	41.269039	-69.962577	136.56	9.666667
95	36 Baxter Ave	41.27038	-69.962302	117.21	11.5
96	Owl's Nest	41.272609	-69.962146	109.88	13.25
97	Baxter Field Cliff	41.278021	-69.962357	15.33	109.4
98	Sankaty Lighthouse	41.282953	-69.964926	31.07	7
99	Sankaty Rd @ Bayberry Sias Ln	41.275768	-69.964079	233.6	11.8
100	Sankaty Rd @ Isobel's Way	41.273982	-69.964068	262.26	29.2
101	Wells Guest Cottage	41.274399	-69.966146	423.23	53.6
102	Meetinghouse Ln @ Sankaty Rd	41.271142	-69.963914	245.79	25.6
103	20 Sconset Ave	41.25927	-69.965165	119.05	4.5
104	South Rd	41.266138	-69.965646	365.27	6.333333
105	W Sankaty Rd @ Coffin St	41.265698	-69.966867	449.09	2.333333
106	New St @ Shell St	41.262988	-69.964131	159.12	4
107	One Ocean Ave	41.261264	-69.9644	127.84	3.666667
108	Ocean Ave @ Carew Ln	41.258931	-69.965273	119.51	7.8
109	19 Ocean Ave	41.255411	-69.968637	217.34	15
110	Low Beach Rd Beach, NILB	41.253592	-69.968288	121.22	5
111	Low Beach Rd	41.251135	-69.975993	364.75	6.6
112	Underhill Ln @ Morey Ln	41.257856	-69.967021	210.42	15.75
113	44 New St	41.262767	-69.971146	726.17	15.8
114	15 1/2 Burnell	41.264695	-69.969164	624.81	10
115	Blackfish @ Burnell St	41.266836	-69.969198	667.51	6
116	Sconset Bike Path	41.26217	-69.979661	1391.15	3
117	Phillips Run Rd @ Milestone Rd	41.262532	-69.992394	2027.77	28.8
118	Milestone Rd @ Proprietors Way	41.26944	-70.061542	2027.77	11
119	69 Sparks Ave	41.274774	-70.09754	598.86	6
120	Ruddick Commons	41.265502	-69.976425	1245.87	4
121	Proprietors Way @ Hinsdale Rd	41.26457	-70.06464	2204.8	4

122	8 Pine Tree Rd	41.263071	-70.065034	2043.87	20.4
123	Pine Tree Rd @ Old South Rd	41.261285	-70.065675	1834.65	3.6
124	Old South Rd Bike Path	41.261605	-70.068328	1866.84	4.666667
125	Consignment Shop	41.261762	-70.076713	1866.84	1
126	Eel Pt Rd @ Dionis Beach Rd	41.289336	-70.149929	464.01	4
127	Eel Pt Rd @ Primrose Ln	41.287424	-70.144931	686.29	3
128	7 Eel Pt Rd	41.285373	-70.141659	905.47	8.6
129	Surrey Ave @ Sandsbury Rd	41.246332	-69.992348	379.94	5.5
130	Surrey Ave @ Old Tom Nevers Rd	41.245183	-69.992683	254.72	13.4
131	Wanoma Way, Tom Nevers Beach	41.243011	-69.994397	63.45	9.6
132	Nichols Rd	41.245397	-69.994875	332.62	2.8
133	3 Bosworth Rd	41.244666	-69.997374	310.62	5.2
134	JFK Bomb Shelter	41.24086	-70.004928	71.79	1.5
135	7 New South Rd	41.241281	-70.016581	200.45	3
136	Forked Pond Valley	41.241603	-70.022818	125.33	1
137	Russells Way	41.249715	-70.035886	777.14	14
138	38 Wigwam Rd	41.250922	-70.033637	934.54	5
139	Wigwam Rd @ Russells Way	41.252819	-70.036269	1124.2	17.4
140	Milestone Bike Path, New South Rd	41.267604	-70.048872	2671.51	1
141	Surfside Beach Parking Lot, East	41.244217	-70.093815	118.78	79.2
142	Surfside Beach Parking Lot, West	41.244541	-70.094735	171.25	52.2
143	Farrell Beach, NILB	41.243892	-70.098895	284.09	17.4
144	27 Western Ave	41.243947	-70.097378	213.13	3.5
145	Uncatena St @ Nonantum Ave	41.245141	-70.087922	83.49	19.6
146	Pochick Ave @ Surside Rd	41.249427	-70.094363	678.53	7.5
147	Masaquett Ave @ Surside Rd	41.250926	-70.09443	837.33	4
148	124 Surfside Rd	41.254186	-70.093802	1190.77	6.333333
149	South Shore Rd @ Surfside Rd	41.258556	-70.09794	1754.18	2.8
150	5 Wherowhero Ln	41.25767	-70.101355	1786.37	2.666667
151	Zachary Way @ South Shore Rd	41.250536	-70.102015	1050.68	4
152	85-87 South Shore Rd	41.24551	-70.104839	480.81	5.4
153	34 W Miacomet Rd, Miacomet Beach	41.243884	-70.119113	62.65	6.4
154	28-34 W Miacomet Rd.1	41.245513	-70.117981	237.28	6.8
155	28-34 W Miacomet Rd.2	41.249	-70.116256	649.56	1
156	28-34 W Miacomet Rd.3	41.250147	-70.115665	786.61	4
157	6-28 W Miacomet Rd	41.253453	-70.116991	1108.58	2.6
158	76 Millbrook Rd	41.269216	-70.130267	2365.74	6
159	Millbrook Rd, NILB Property	41.276773	-70.128003	1882.93	1
160	55 Millbrook Rd	41.276336	-70.126495	1947.31	8.6
161	19 Burnt Swamp Ln	41.275646	-70.122628	1995.59	1.333333
162	Massasoit Bridge Rd	41.274702	-70.16793	1754.18	1

163	2 Massasoit Bridge Rd	41.271366	-70.178705	965.3	3.2
164	330 Madaket Rd	41.271238	-70.201104	123.93	13.6
165	Ames Ave	41.273365	-70.204728	106.34	2
166	Massachusetts Ave	41.27372	-70.209398	0	2
167	Rhode Island Ave	41.273444	-70.206385	118.94	10
168	Tennessee Ave	41.276164	-70.193295	103.55	11.8
169	Tennessee Ave @ N Cambridge St	41.279019	-70.187565	296.78	37.8
170	Vestal St @ Winn St	41.288705	-70.110121	714.18	30.4
171	74 Monomoy Rd	41.281385	-70.07869	96.64	4.6
172	Monomoy Harbor Path	41.278941	-70.083278	167.76	3
173	47 Monomoy Rd	41.278665	-70.082199	139.64	4.6
174	Eat Fire Spring Rd	41.307359	-70.006842	146.55	5.5
175	16 Eat Fire Spring Rd	41.307206	-70.001601	586.4	9.2
176	Wauminet	41.327932	-69.9966	214.34	3.5
177	Squam Rd @ Wauwinet Rd	41.325656	-69.996205	316.9	12.4
178	Crow's Net Way @ Squam Rd	41.325624	-69.993786	132.31	30
179	Squam Rd.1	41.323439	-69.992811	170.16	39
180	Squam Rd.2	41.318395	-69.991872	336.63	36.2
181	Squam Rd.3	41.306822	-69.982728	190.87	21
182	Quidnet.1	41.304815	-69.979854	95.94	3
183	Sesachacha	41.303895	-69.979395	118.23	9.6
184	Windswept Cranberry Bog	41.296998	-70.005812	749.81	23.33333
185	Almanack Pond Rd.1	41.291832	-70.007829	1156.53	3
186	Almanack Pond Rd.2	41.297039	-70.011313	559.64	6.666667
187	Miacomet Golf Course, South	41.25555	-70.120723	1207.16	11
188	A Full House	41.244326	-70.120537	83.29	18.4
189	W Miacomet Rd.1	41.246281	-70.122066	228.96	2.8
190	W Miacomet Rd.2	41.247725	-70.122994	322.58	21.6
191	Proprietors Way @ Mioxes Pond Rd	41.251619	-70.12794	577.12	1.5
192	Proprietors Way	41.249478	-70.129174	316.32	7.6
193	Heller Way	41.254594	-70.130057	828.84	1
194	Bartlett Farm Rd	41.253752	-70.13105	717.13	10.4
195	Cisco Brewery.1	41.262923	-70.130124	1705.9	11.6
196	240 Polpis Rd	41.29052	-70.02416	444.06	5.8
197	9 Pocomo Rd	41.31474	-70.008833	599.64	7.5
198	Pocomo Rd.1	41.315213	-70.014383	328.23	3.666667
199	43 Pocomo Rd	41.314736	-70.02083	181.32	3.5
200	79 Pocomo Rd	41.31461	-70.030134	115.77	4.5
201	Pocomo Head	41.316047	-70.032346	0	18.5
202	Polpis Harbor Rd	41.302267	-70.010701	35.54	1.5
203	Red Barn Rd.1	41.264417	-70.181013	158.45	25.2

204	Sheep Pond Rd	41.264675	-70.186061	65.3	3.333333
205	Red Barn Rd.2	41.262683	-70.176769	241.86	9.75
206	Moors End.1	41.27931	-70.068967	874.03	8.666667
207	Moors End.2	41.27789	-70.070873	831.93	40.6
208	Polpis Rd @ Sesachacha Pond	41.290136	-69.983618	1190.13	4
209	320 Polpis Rd	41.297477	-69.99786	1866.84	17.2
210	Rock Face	41.293187	-70.020949	164.99	24.2

326

327 Table 2. Populations of Toothed Whitetop Aster on Nantucket Island.

Location Number	Location Site	Latitude	Longitude
1	Linda Loring Foundation.1	41.289992	-70.171492
2	Linda Loring Foundation.2	41.289914	-70.172725
3	ACK Sparkle Clean	41.286922	-70.174961
4	Linda Loring Foundation.3	41.289061	-70.174649
5	Linda Loring Foundation.4	41.291503	-70.170817
6	LLF, Beach Trail, South end	41.287781	-70.177794
7	Sanford Farm	41.278289	-70.137069
8	North Head Hummock Pond, Sanford Farm	41.277894	-70.135561
9	Sanford Farm, W of deer exclosure	41.276303	-70.137775
10	NILB, Madaket Rd to Eel Pt property	41.283573	-70.156976
11	NILB, Worth Rd property	41.285976	-70.155407
12	Dionis	41.287827	-70.159307
13	Miacomet Rd	41.244914	-70.11142
14	Head of Prairies @ Red Barn Rd	41.270177	-70.184992
15	The Tupancy Links	41.290455	-70.128081
16	The Tupancy Links, West Entrance	41.288227	-70.131163
17	Milestone Trail	41.265514	-70.012435
18	The Tupancy Links.2	41.291761	-70.128326
19	Tuckernuck.1	41.300877	-70.248592
20	Middle Moors	41.265514	-70.012435
21	West Miacomet Rd	41.251299	-70.115314
22	Ram Pasture	41.260507	-70.155101
23	Ruddick Commons	41.265995	-69.976201
24	Starbuck Rd	41.270231	-70.194051

328

329 Table 3. Sites that were observed during the pollination observation study.

Date	Population	Latitude	Longitude	Treatment	Temperature (°C)	Humidity (%)	Dew Point (°C)	Wind (kph)	Conditions
7/3/2015	Nantucket Tackle Center	41.27194	-70.093871	QAL (-TWTA)	21.7	76	17.2	11	Clear
7/4/2015	Cliffside Beach Club	41.293786	-70.107584	QAL (-TWTA)	17.8	81	14.4	10	Mostly Cloudy
7/5/2015	The Tupancy Links	41.290506	-70.128865	TWTA (-QAL)	22.2	71	16.7	14	Clear
7/7/2015	Washing Pond Rd	41.288479	-70.131772	QAL (-TWTA)	21.1	79	17.2	11	Clear
7/8/2015	Starbuck Rd	41.270231	-70.194051	Both	23.3	84	20.6	13	Clear
7/9/2015	Ruddick Commons	41.265995	-69.976201	TWTA (-QAL)	20.6	68	14.4	14	Overcast
7/11/2015	Linda Loring Foundation	41.29001	-70.171507	TWTA (-QAL)	26.1	54	16.1	9	Clear
7/12/2015	Pine Tree Rd @ Old South Rd	41.261379	-70.0659	QAL (-TWTA)	23.3	71	17.8	14	Clear
7/13/2015	Middle Moors	41.265514	-70.012435	TWTA (-QAL)	22.8	82	19.4	9	Clear
7/15/2015	Ram Pasture	41.260507	-70.155101	TWTA (-QAL)	26.1	82	22.8	7	Scattered Clouds
7/17/2015	The Tupancy Links	41.290411	-70.12783	Both	22.2	71	16.7	9	Partly Cloudy
7/19/2015	Miacomet Rd	41.24479	-70.111335	Both	21.7	87	19.4	8	Overcast
7/20/2015	West Miacomet Rd	41.251299	-70.115314	Both	23.3	90	21.7	10	Mist
7/21/2015	Red Barn Rd @ Head of Plains Rd	41.270194	-70.184774	Both	25	85	22.2	0	Scattered Clouds
7/22/2015	M6 Condo Backyard	41.2732	-70.101602	QAL (-TWTA)	24.4	62	16.7	18	Clear

330

Table 4. Pollinator diversity by species. * indicates significance difference ($p = 0.03$). Simpson and Evenness indices are not significantly different ($p = 0.06$ for each). H = Shannon index; D = Simpson index.

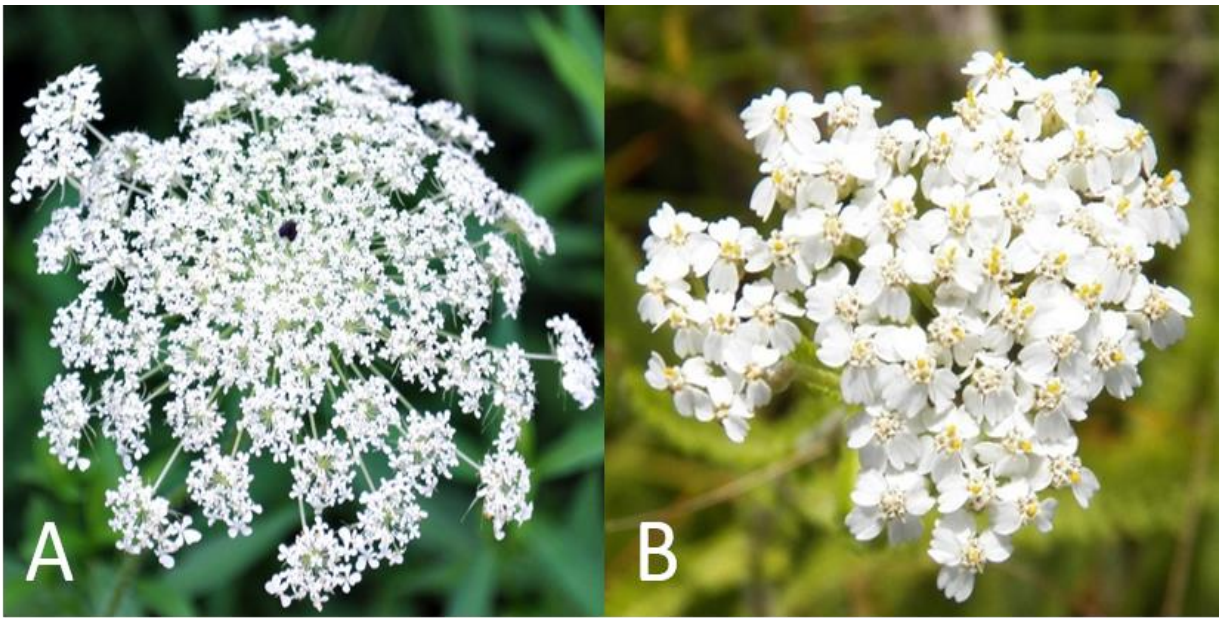
Species	Total Visits	Total No. of Families	H	D	Evenness
QAL	477	15	1.37*	0.71	0.82
TWTA	149	8	0.83*	0.48	0.57

335 Table 5. Pollinator diversity indices by treatment. No differences are significant.

Treatment	Total Visits	Total No. of Families	H	D	Evenness
QAL (-TWTA)	290	13	1.38	0.66	0.78
QAL (+TWTA)	187	11	1.37	0.75	0.86
TWTA (+QAL)	93	7	0.96	0.54	0.66
TWTA (-QAL)	56	7	0.69	0.41	0.48

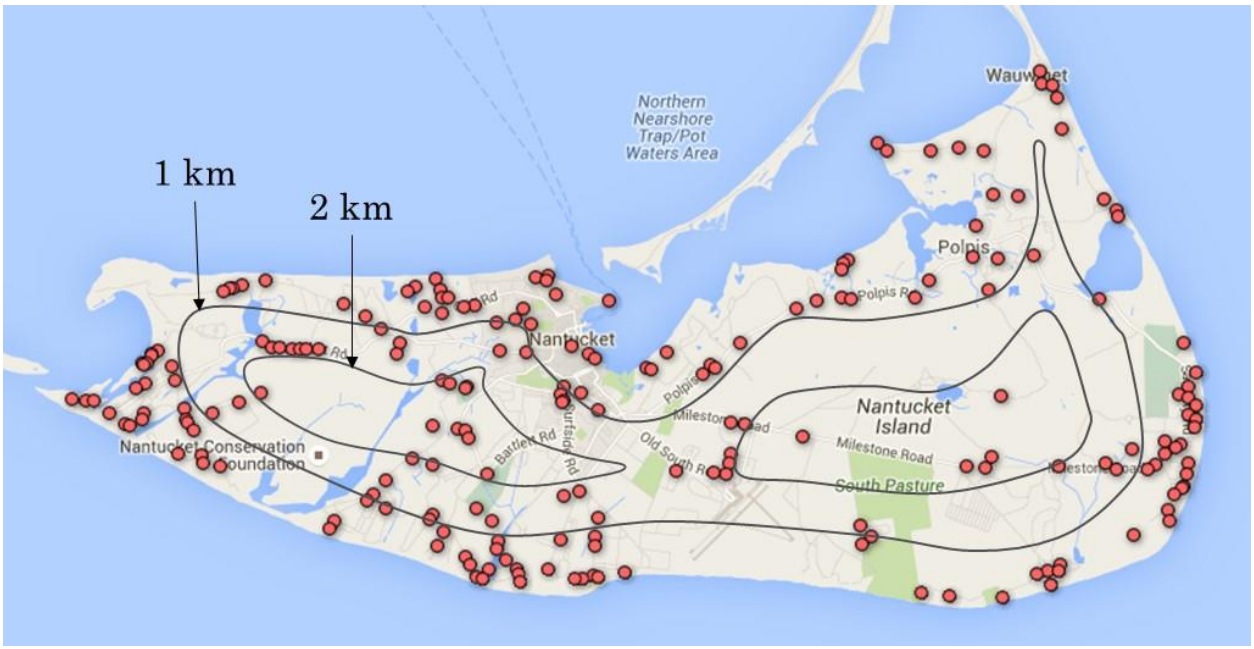
336

Figure 1. Morphological similarities between Queen Anne's Lace and Toothed Whitetop Aster inflorescences. A) Queen Anne's Lace, B) Toothed Whitetop Aster.



340 Figure 2. Map of QAL populations across Nantucket. Dots indicate one population occurrence.

341 Contour lines indicate approximate distance to the ocean.



342

Figure 3. Density heat map of Queen Anne's Lace on Nantucket. Warm colors indicate high densities, whereas cool colors indicate low densities. Contour lines indicate approximate distance to the ocean.

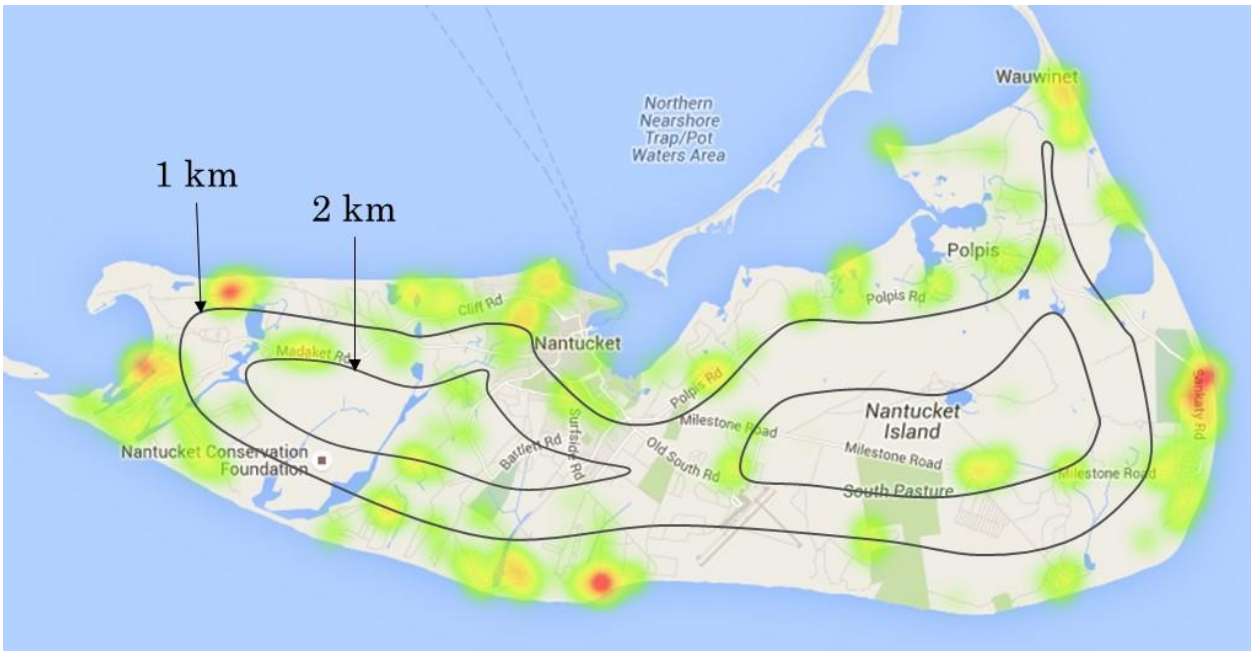


Figure 4. Linear regression of QAL population density by the distance from the ocean. Line of best fit is a shallow exponential curve with a fit of $R^2 = 0.024$ and $p = 0.023$.

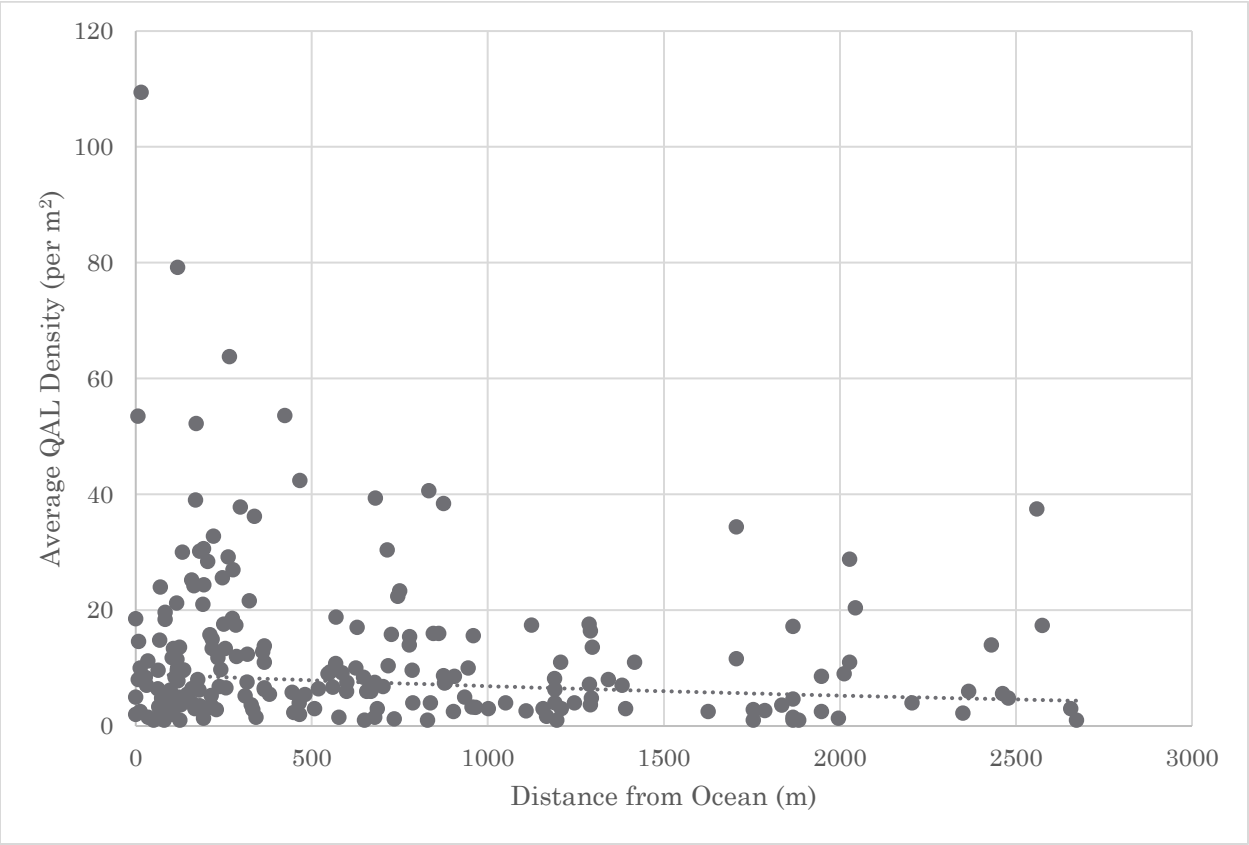


Figure 5. Map of Nantucket with observed populations pinpointed. Red indicates QAL (-TWTA), yellow indicates TWTA (-QAL) and blue indicates both species.

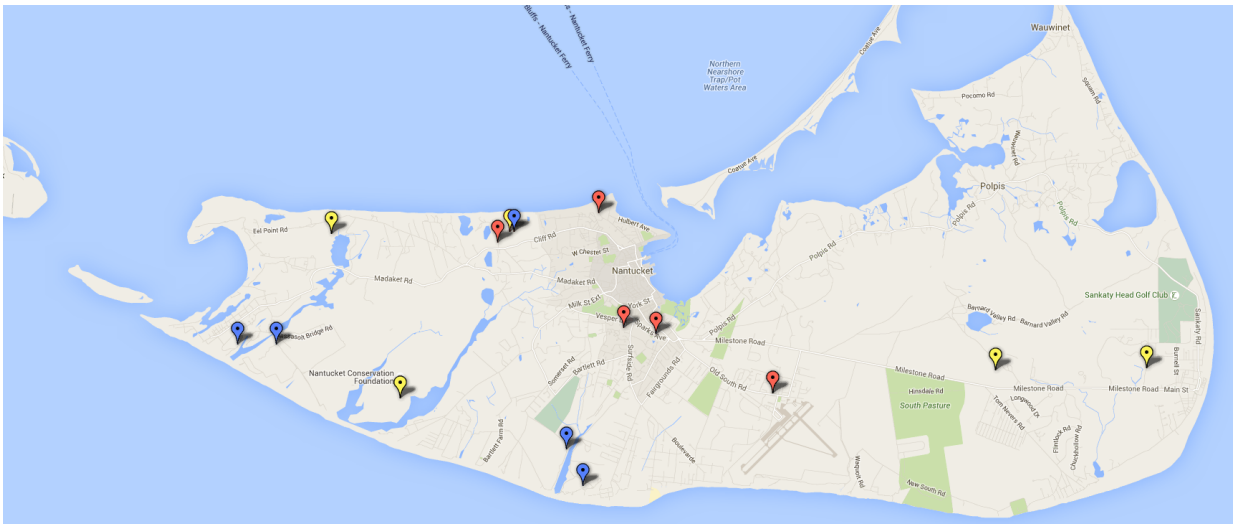


Figure 6. Queen Anne's Lace pollinator family distribution.

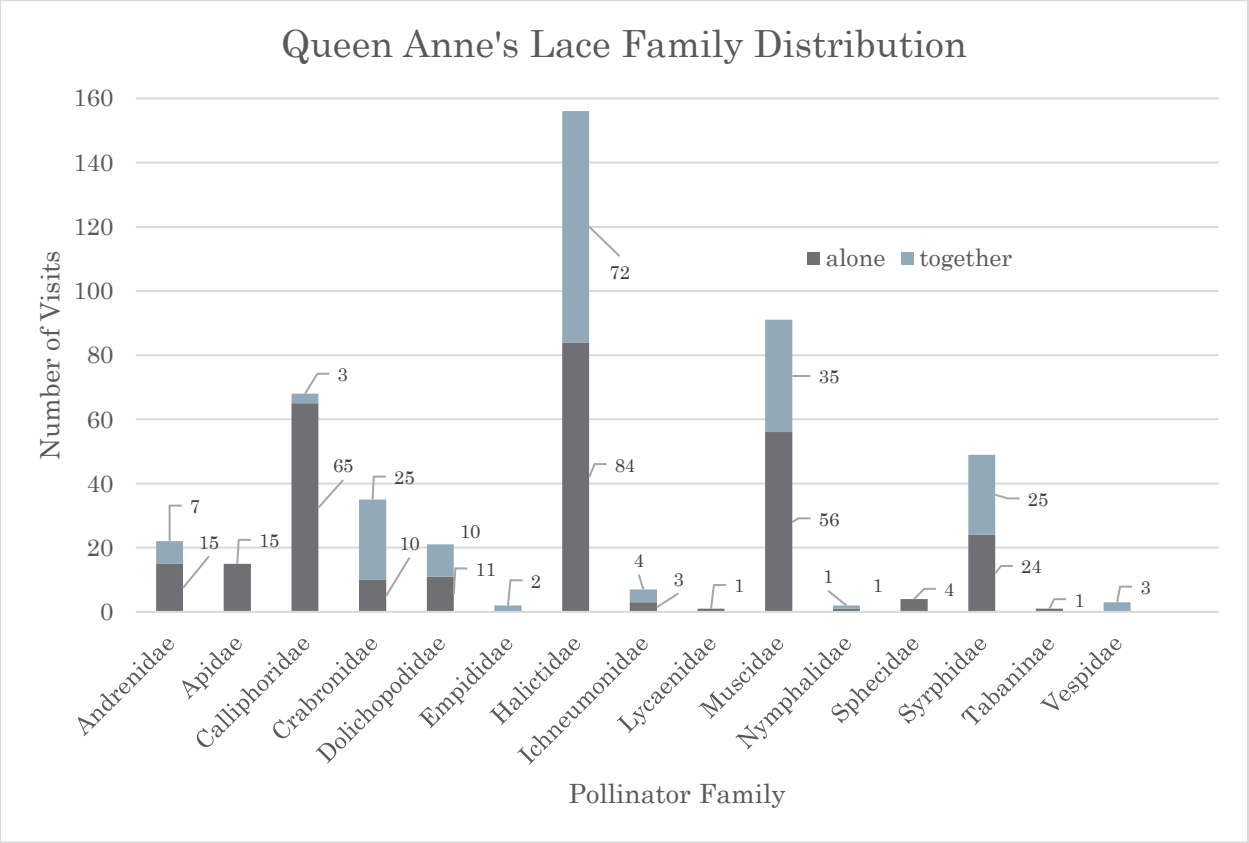


Figure 7. Toothed Whitetop Aster pollinator family distribution.

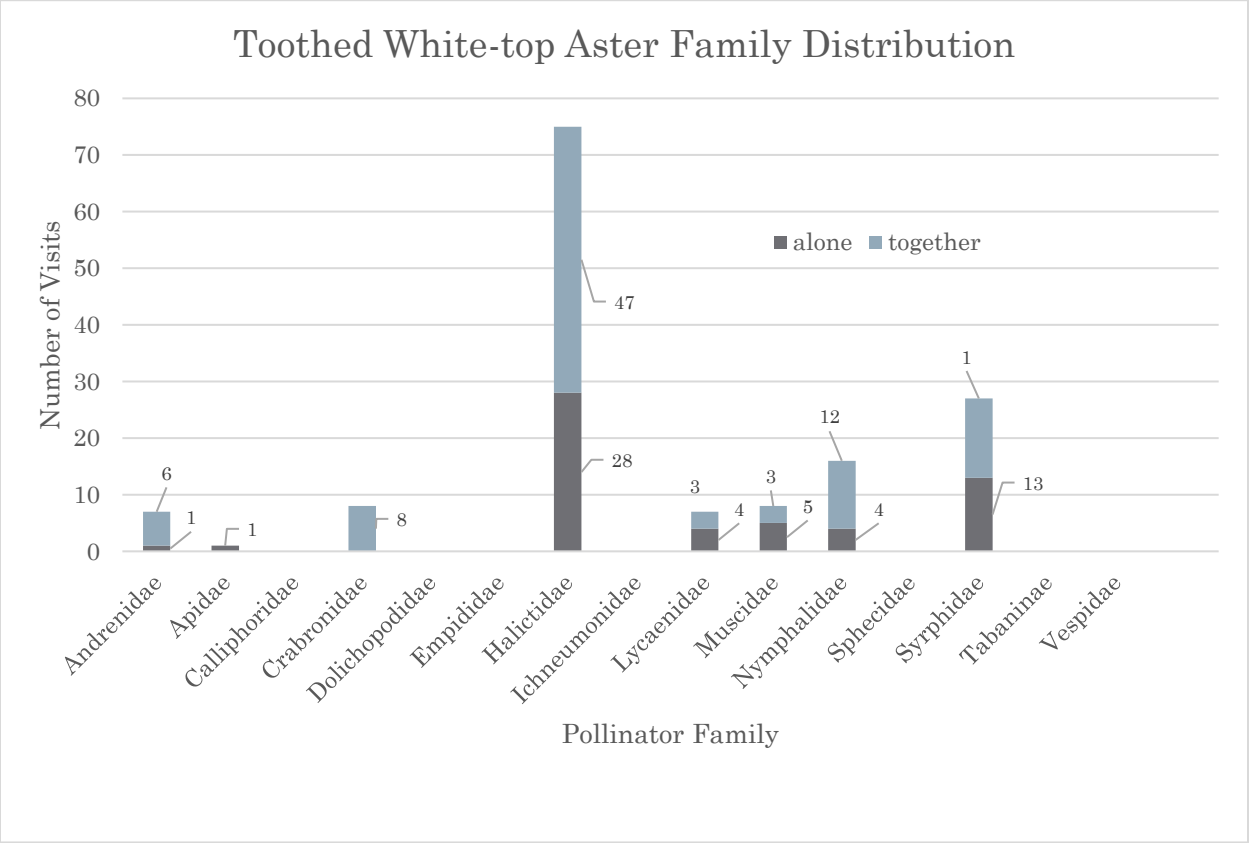


Figure 8. Number of pollinator visits standardized to inflorescence per site. Between A and B is a significant difference (p = 0.001), but between the two TWTA treatments there is no significant difference (p = 0.08).

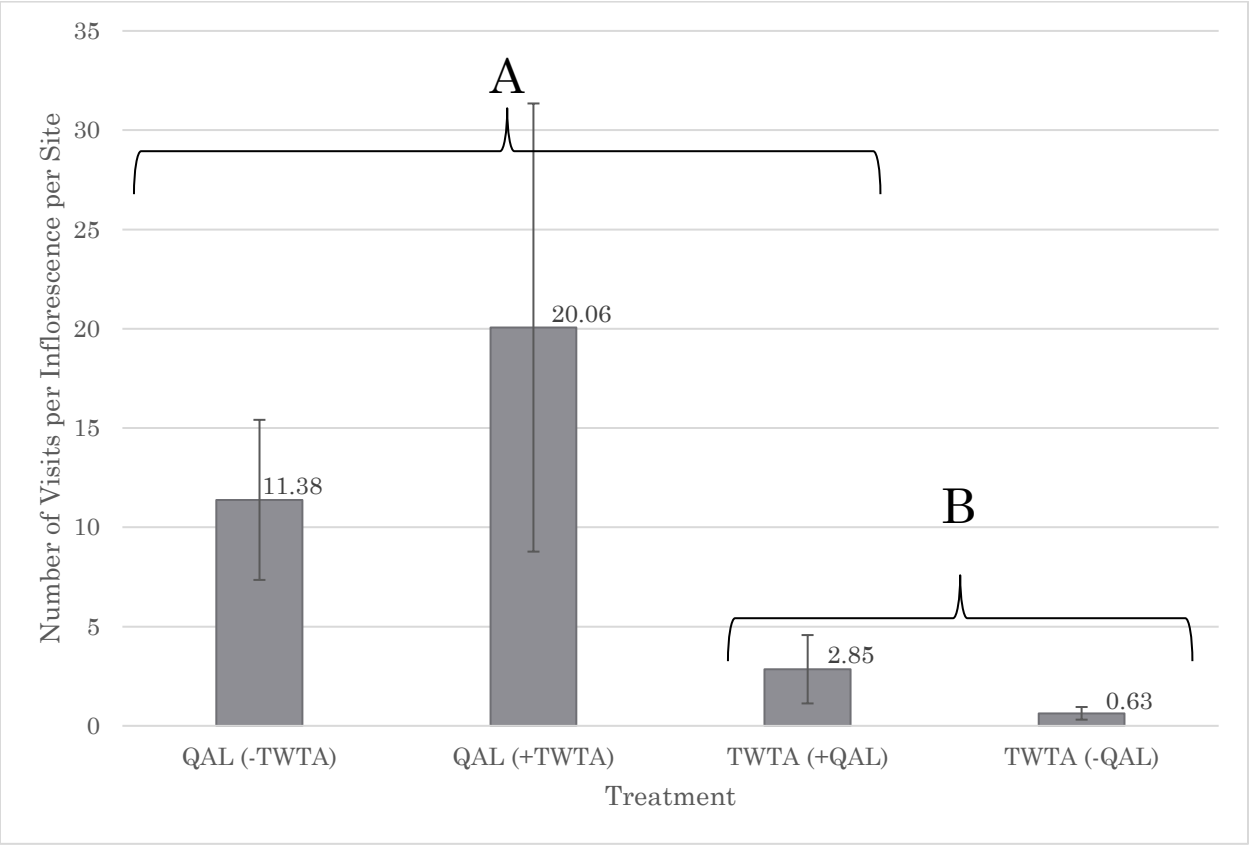


Figure 9. Number of pollinator families per site. The two species are significantly different (p = 0.0131), but there is no difference between the treatments within species.

