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Assessing the contribution of geography and host use to genetic structure in New York populations of the parasitoid wasp, Aphidius ervi

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Abstract

Host-associated differentiation (HAD) has been shown to be important in generating genetic differentiation within herbivorous insects, but the applicability of HAD to other parasitic taxonomic groups remains unclear. For example, parasitoid wasps that attack herbivorous insects share many similar life habits with their hosts, suggesting that HAD may also be a prevalent and important mechanism in this group. I tested for the genetic signature of HAD in the parasitoid wasp, *Aphidius ervi*, that attacks aphids. *Aphidius ervi* is a biocontrol agent that uses many species of pest aphids including the clover and alfalfa host-races of the pea aphid (*Acyrthospihon pisum*). The pea aphid host races differ in their defenses and resource quality as hosts for *A. ervi*. I assessed allelic variation from six microsatellite loci across sixteen *A. ervi* populations along a 200 km transect in New York State to examine genetic structure in relation to pea aphid host race use. Results from AMOVA and pairwise F_{ST} analyses indicated that there is no genetic structure in *A. ervi* due to HAD, and there was no genetic structure across the sampled range. These findings suggest that *A. ervi* populations are connected by high levels of gene flow that likely swamp out selection for specialization on the pea aphid host races of *A. ervi*. At least for *A. ervi*, the spatiotemporal distribution of hosts as well as the high dispersal rate suggest that HAD is unlikely to be a mechanism of genetic differentiation among populations.

Assessing the contribution of geography and host use to genetic structure in New York populations of the parasitoid wasp, *Aphidius ervi*

by

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B.A., Albion College, 2013

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Table of Contents

List of Illustrative Materials

TABLES:

FIGURES:

Introduction

A species' population structure depends on the interplay between genetics, ecology, and geography. These factors can interact in complex ways to lead populations to diverge evolutionarily from one another. Often, this divergence is not a discrete endpoint, but rather is a continuum that results from the interplay of many processes (Dres and Mallet 2002; Nosil 2009; Hendry 2009). Documented examples of populations at varying stages of genetic divergence have been reported for nearly all taxa (Invertebrates -- Quicke et al 1983; Li et al. 2015; fish -- Schluter 1995; birds -- Grant and Grant 2002; Benkman 2003; mammals -- Wang et al 1999), and there is also documentation of populations shifting along the continuum in response to different ecological factors (Hendry 2009; Mallet et al. 2012). Here, I seek to better understand the role of species interactions in causing populations to diverge along this continuum. Species interactions are an integral part of the biology of every organism, but it is still unclear how they influence genetic divergence among populations.

An excellent starting point to understand how species interactions can influence evolutionary differentiation is to examine an extremely diverse group of organisms: plant-feeding insects. Plant-feeding insects comprise one of the most diverse groups of organisms on the planet, and selection generated from the interaction of phytophagous insects and their host plants has been suggested as the primary reason for divergence in both groups (Ehrlich and Raven 1964; Mitter et al. 1988; Berlocher and Feder 2002; Mullen and Shaw 2014). The process by which insects adapt to host defenses and radiate along independent paths of evolutionary divergence is termed host-associated differentiation (HAD) (Diehl and Bush 1984; Bernays 1991; Carroll and Boyd 1992; Pappers et al. 2001; Dres and Mallet 2002; Antwi et al 2015). The premise of HAD is that host plant species have different physical and chemical defenses that cause their associated plant-feeding insects to adapt to distinct feeding challenges (Gatehouse 2002; Funk 2002; Poelman 2008; Lucas-Barbosa et al. 2011; Fürstenberg-Hägg et al. 2013). As adaptations to increase feeding efficiency accumulate in insect populations, the insects become specialized to a particular host plant. Specialization can then be reinforced by increased reproductive success of efficient feeding, proximity of mates on similar plants, and diverging sexual communication signals (McMillan et al. 1997; Jiggins et al. 2001; Mullen and Shaw 2014; Proffit et al. 2015). HAD has been suggested to be a critical mechanism for producing incredible diversity within herbivorous insects (e.g. Bush 1969; Berlocher and Feder 2002; examples: *Membracidae* -- Wood and Keese 1990; *Diptera* -- Craig et al. 1993; *Coleoptera* -- Funk 1998) but its importance and applicability to other taxonomic groups is still unclear.

To test the general applicability of HAD, I have chosen to examine another extremely diverse group of insects that have a close association with plant-feeding insects: the parasitoids. Parasitoids are insects that consume and kill their host during the course of their lifecycle. Similar to a parasite, a parasitoid completes development in or on a single host individual, consuming tissue for nutrients, and eventually causes the death of the host. Not unlike the selection pressures placed on plant-feeding insects by their plant hosts, parasitoids must adapt to a specific set of feeding challenges imposed by their host insects (Vinson 1990; Kraaijeveld and VanAlphen 1994; Strand and Pech 1995; Fellowes and Godfray 2000; Vorburger et al 2009). Thus, parasitoids are expected to exhibit the same level of specialization and HAD as observed in many plant-feeding insects (Price 1980). Testing the role of HAD in parasitoids will allow us to further understand the generality of HAD across different types of parasitic taxa.

Over the past 15 years, there have been a number of studies that have examined the role of HAD in parasitoids. There are a suite of papers demonstrating that HAD can occur within parasitoids (Pungerl 1984; Kankare et al. 2005; Antolin et al. 2006; Stireman et al. 2006, 2012; Henry et al. 2008; Barahoei et al. 2011; Sandrock et al. 2011; Desneux et al. 2012; Schar and Voyburger 2013; Brown and Rossi 2013). For example, Schar et al. (2012) demonstrate significant HAD in *Lysiphlebus* parasitoids attacking two syntopic thistle aphid species. They find clear evidence for genetic differentiation between parasitoids attacking the different aphid species. Moreover, there was also evidence for cascading HAD in the hyperparasitoids that attack the *Lysiphlebus* parasitoids. Other studies, however, have found that host-related factors contribute little to parasitoid genetic structure, and instead suggest geography or local adaptation to abiotic factors as the primary reason for divergence (Baer et al. 2004; Althoff 2008; Lozier et al. 2009; Dickey and Medina 2011; Simonato et al. 2012; Bilodeau et al. 2013; Mitrovic et al. 2013). Determining the general importance of HAD versus other factors in parasitoid population differentiation requires additional tests in parasitoid species.

Here, I test the potential role of HAD in parasitoid population differentiation by examining the genetic structure of the braconid parasitoid *Aphidius ervi* that is associated with two different host-races of pea aphid (*Acyrthosiphon pisum*) in New York state. *Aphidius ervi* is an agriculturally important biological control agent of aphids. In 1959, a population of 1,000 individuals was introduced from France to New Jersey in an effort to control the accidentally introduced pea aphid, and periodic re-introductions over the next decade included 11,000 individuals released into aphid-infested fields in California, Arizona, Idaho, Maine, Oregon, Washington, and Delaware (Halfhill et al. 1972; Mackauer and Campbell 1972; Hagen et al.

1976; Angalet and Fuester 1977). Since its introduction, *A. ervi* has spread across North America.

Though *A. ervi* has been documented to use ten aphid host species (Starry 1970), the most widely used host is the pea aphid (*Acyrthosiphon pisum)*. *Acyrthosiphon pisum* is divided into fourteen host-races based on plant host species used, two of which occur on alfalfa (*Medicago sativa*) and clover (*Trifolium repens, T. pratense*) (Peccoud et al. 2009, 2015). The alfalfa and clover host-races of *A. pisum* exhibit HAD and perform poorly when reciprocally transplanted to each other's host (Via 1991; Henter and Via 1995; Henter 1995; Hufbauer 1999; Bilodeau 2013). These host races also differ in the magnitude and prevalence of parasitoid defensive behaviors and as a resource for parasitoids, suggesting there are selection pressures on *A. ervi* to specialize on either host (Henter and Via 1995; Nguyen et al 2008). Moreover, *A. ervi* has significant heritable variation in the ability to parasitize aphids, and is capable of adapting to these aphid defenses in the lab (Henter 1995; Dion et al 2011). If strong enough, divergent selection pressures due to aphid defenses and resource quality could lead to genetic structure among populations using different pea aphid host races.

Previous research on the genetic structure of *A. ervi* at the global scale found significant population genetic structure between European and North American populations, indicating an important role of geography in population structure (Hufbauer 2004). Because all the parasitoids were collected from alfalfa pea aphids, Bilodeau et al. (2013) made the first comparison between host races of pea aphids and showed no host-associated genetic structure at a local scale. Further testing between host races at intermediate scales is needed to test HAD in *A. ervi.* In the present study, I expand on these previous analyses of population structure to address the following questions: i) What is the genetic structure of *A. ervi* populations at a regional scale, and ii) what are the relative roles of host use and geography in determining genetic structure? Answering these questions will bridge the gap between local and global population studies and provide further information on the population structure of this important biological control agent at intermediate geographic scales.

Materials and Methods

Study System

Adult *A. ervi* wasps follow plant volatiles to locate aphid hosts and mates (He et al. 2004; Sasso et al. 2007). When the female wasp locates an aphid on a plant, she uses her antennae to assess cuticular hydrocarbons found on the aphid body. If the aphid has not already been previously parasitized and is a suitable host, a female injects venom and a single egg using her ovipositor (Falabella et al. 2007). *Aphidius ervi* is a koinobiont, so the wasp larva develops internally for several days while the aphid is alive and feeding. After 5-6 days, the wasp induces behavioral changes in the aphid that cause it to climb to the top of the plant and the upper center of a leaf, where it perishes. The aphid's body is then transformed into a puparium, or "mummy" spun from the wasp larva's silk, which it then adheres to the leaf surface by silk strands extending through a small ventral hole. The wasp will continue to develop within the mummy for about two weeks, at which point the fully formed adult wasp will chew a dorsal hole and eclose (Sequeira and Mackauer 1992; Malina et al. 2010).

Successful reproduction by the wasp involves several stages on which selection can act to generate HAD: locating an aphid host, acceptance of the host, oviposition, and larval development (Godfray 1994). Aphids are soft bodied, and thus highly vulnerable to wasp attack; however, they have evolved defenses against attack. Behavioral defenses such as kicking with the hind limbs or falling off the plant can prevent oviposition (Dixon 1985). Furthermore, aphid populations have integrated a bacterial symbiont, *Hamiltonella defensa,* which acts as a post-oviposition defense by halting the development of the wasp at the egg stage (Oliver et al. 2010; Peccoud et al. 2015).

Sampling Design

From May-July 2015, I surveyed a 200 km longitudinal transect in New York State spanning from Pompey, NY to Alexander, NY (Figure 1, Table 1). Wherever possible, these localities included collections from both alfalfa and clover plants, mostly found at alfalfa agricultural sites that had clover interspersed or surrounding the edges of the field. Mummies were collected haphazardly from each host species and were assumed to be from the aphid host race based on the plant from which they were collected. Because aphids feed for several days before succumbing to the parasitoid, finding a mummy on a non-host is unlikely. I collected 356 aphid mummies containing female *A. ervi* larvae from both alfalfa and clover host-races of *A. pisum* at ten geographic localities.

After collection, mummies were individually placed into gel capsules (Capsuline Clear Gelatin Capsules, Size #2), and stored at room temperature until eclosion. I monitored capsules daily for eclosed wasps for three weeks after collection. Upon emergence, females were immediately placed into a -20°C freezer, and then identified to species using a dichotomous key (Pike et al. 1997). After confirmation of species identity, *A. ervi* specimens were stored in a -80°C freezer until genetic analysis. Only female wasps were used in the analysis of heterozygosity because hymenopteran males are haploid.

Microsatellite Analyses

DNA from individual female wasps was extracted using a method modified from Bender et al. (1983) in which I omitted 1% diethyl pyrocarbonate from the extraction buffer. I used the entire individual for each extraction. A total of seven previously developed microsatellite loci were used to assess the genetic structure of *A. ervi,* (Hufbauer 2001; Lozier et al. 2006) (Table 2). The forward primer for each microsatellite locus was labeled with a fluorescent dye (6-FAM, VIC, NED, PET; Life Technologies, Carlsbad, CA, USA). One µL of template DNA was combined with 4.01 µL of PCR water, 2 µL of 5x PCR buffer, 1 µL of µM BSA, 1 µL of 25 mM $MgCl_2$, 0.21 µL of 10mM dNTPs, 0.35 µL each of 10 µM forward and reverse primers and 0.08 µL (4 units) of Promega GoTaq to yield a 10 µL reaction volume. Reactions were cycled in a BioRad PTC 100 Thermal cycler programmed for 95°C for 1 min, 35 cycles of 95°C for 30 s, the optimized annealing temp (Table 2) for 1 min, 72°C for 1 min, followed by 72°C for 10 min, and held at 6°C. A separate PCR was performed for each individual and locus.

The resulting PCR products (1 µL for FAM labeled, 1 µL for VIC labeled, 3 µL for PET labeled, 3 µL for NED labeled) tagged with different fluorophores were combined in a single well with 3µL LIZ-500 bp standard and 7 µL of deionized water. Samples were analyzed by the Cornell University Biotechnology Resource Center on ABI 3730xl capillary electrophoresis DNA Analyzer. Wells were multiplexed with either three or four labeled PCR products. I scored all alleles manually in GENEMARKER 2.4.2 (Holland and Parson 2011) (SoftGenetics, State College, PA, USA).

I used FSTAT (Goudet 1995) to test whether each of the microsatellite loci were in Hardy-Weinberg equilibrium and to test for linkage disequilibrium among the loci. MICROCHECKER (Van Oosterhout et al. 2004) was used to test for null alleles. I analyzed genetic structure in several ways. First, AMOVA (Excoffier et al. 1992) was used to test for genetic structure based on pea aphid host race. Second, pairwise F_{ST} values were generated for all sites to examine levels of genetic structure among populations. Finally, a Mantel test was used to examine the role of geographic distance in pairwise F_{ST} estimates. Analyses of genetic structure were conducted in GenAlEx 6.0 (Peakall and Smouse 2006, 2012).

Results

Of the 395 *A. ervi* females that were collected, I genotyped 348 (DNA extractions failed for eight individuals and 39 individuals failed to amplify during PCR). Microsatellite locus (At14) was genotyped, but was removed from analysis due to fixation within all individuals. The remaining six surveyed microsatellite loci provided adequate allelic variation to examine population structure in *A. ervi* (Table 2). A total of 57 alleles were observed at the six loci across the 10 geographic localities, and the additional six sympatric collections of wasps from the clover pea aphid host race, along the 200 km transect. The six microsatellite markers ranged from 4-23 alleles per locus, with an average of 2.7-13 different alleles per population (Table 2). Locus Ae4 had the highest number of alleles, much more so than the other five. Tests for linkage disequilibrium between all pairwise loci were not significant, as were tests for null alleles. Tests for divergence from Hardy-Weinberg equilibrium among alleles were also not significant.

A hierarchical AMOVA (Table 3) in which wasps were grouped by pea aphid host race indicated that host use did not contribute to population structure as there was no genetic variance attributed to aphid host races. There was also little evidence of population structure among geographic locations. Only 1% of the observed variance was partitioned among populations. Due to lack of evidence for the influence of aphid host race use on population structure, I combined individuals collected from sympatric aphid host races into a single geographic location for the remaining analyses, reducing the number of sites from sixteen to ten.

The overall F_{ST} among the ten populations was 0.011 ($P < 0.001$), indicating significant, but slight genetic structuring. Pairwise F_{ST} values between some populations were significant, but values ranged from zero to 0.024 again indicating a very low level of genetic differentiation among *A. ervi* populations (Table 4). The Mantel test indicated a slightly negative but non-significant correlation ($r= -0.03$, $P=0.45$) indicating that geography does not contribute to the genetic structure of *A. ervi* at this scale (Figure 2). Thus, there does not appear to be any significant population structure among *A. ervi* from the sampled localities in New York.

Discussion

HAD has been proposed as a major mechanism of differentiation for many diverse phytophagous insects (Janz et al. 2006; Hoberg and Brooks 2008; Hardy and Otto 2014). In this group, there are myriad examples of host adaptation resulting in genetic differentiation and in many cases, speciation (e.g., Stireman et al. 2005, 2006; Brunner et al. 2004; Antwi et al. 2015). Indeed, herbivorous insects have been shown to undergo greater rates of speciation than their predatory or saprophagic counterparts (Mitter et al. 1988), which has been attributed to adaptation to different host plant defenses against herbivory that result in subsequent specialization. What has been less frequently tested is whether the large diversification of plant feeding insects has led to comparable adaptation and specialization in their parasitic natural enemies (Abrahamson and Blair 2008). In essence, is HAD a process that is applicable to natural enemies, particularly parasitoids of phytophagous insects?

Parasitoids exhibit some of the same characteristics as other parasitic taxa like plant-feeding insects. Females search for and lay eggs on or within hosts and the developing larvae feed on a single host individual to complete development. The major difference is that parasitoids kill the host individual in almost all cases (Godfray 1994). Parasitoids employ two different development strategies, idiobiont and koinobiont that may also influence the likelihood of HAD (Askew and Shaw 1986). Idiobiont parasitoid larvae stop host development and usually feed externally on the host whereas, koinobiont larvae allow hosts to continue to develop and usually feed internally (Godfray 1994). This difference makes it more likely that koinobiont parasitoid taxa such as *A. ervi* will specialize on a particular host species or set of host species (Althoff 2003). Several studies have supported HAD in parasitoids through genetic, morphological and life history trait evidence. For example, Stireman et al. (2006) found that two species of koinobiont parasitoids, *Copidosoma gelechiae* and *Platygaster variabilis* using host races of two goldenrod gall-making insect species each showed degrees of genetic differentiation based on gall-maker host-races. For *P. variabilis* parasitoid populations, genetic differences among populations using host races of the gall midge *Rhopalomyia solidaginis* were large enough to suggest host-associated cryptic sibling species. In contrast, others have found no evidence. Given the limited of number of studies testing the role of HAD in parasitoids, further studies are needed in order to determine whether HAD is a ubiquitous process for parasitoids and whether HAD has influenced large scale patterns of speciation.

I examined the potential role of HAD in population differentiation of the biocontrol agent *Aphidius ervi*, and found a distinct lack of population structure, despite previous experimental evidence that it could become specialized to specific aphid host types. Though it is widely considered a generalist that uses many aphid species (Stary 1970), *A. ervi* is a putative candidate for HAD based on evidence from a number of studies. Henter and Via (1995) and Henter 1995 documented genetic variation in pea aphid clones to vulnerability to parasitoid attack and also genetic variation among *A. ervi* families in the ability to attack pea aphids (i.e. virulence). The difference in virulence among *A. ervi* families is partly due to immune defenses in the pea aphids and interactions with bacterial endosymbionts (Oliver et al. 2012). Hufbauer (1999, 2002) further demonstrated that the pea aphid host races on clover an alfalfa differed in susceptibility to attack by *A. ervi*. Others studies have demonstrated fitness costs for *A. ervi* to exhibit when using alternate host species (i.e. hosts in which they did not develop) and selection experiments demonstrate that *A. ervi* can adapt to different host species under laboratory conditions (Daza-Bustamante et al. 2003; Henry 2008; Dion et al. 2011; Emelianov et al. 2011; Zepeda-Paulo 2013).

While laboratory studies indicate *A. ervi's* ability to become specialized to a particular host aphid, I did not find empirical evidence for host-based population structure in naturally occurring populations. Results from the AMOVA in which I grouped populations by aphid host race showed no evidence for population structure due to host use. Furthermore, there was little genetic variance associated with geography. Pairwise F_{ST} values among sites were all quite low, and there was no correlation between genetic and geographic distance. The lack of genetic structure in *A. ervi* in central New York is similar to other surveys of population structure for this species at smaller and larger geographic scales. Bilodeau et al. (2013), found that geographically proximal populations *A. ervi* using different host races of pea aphids were also not differentiated, even though the aphid host-races themselves showed clear population structure based on host plant species. Zepeda-Paulo et al. (2015) also examined the effects of intra- and inter-species host use on the population structure of introduced *A. ervi* across Chile. They detected no evidence for HAD at the aphid host race level or the aphid host species level. Similar to the results in New York, they also did not find any role of geographic distance on population structure.

The lack of population structure within *A. ervi* found in this and other studies indicates that high gene flow among populations may prevent adaptation to use a specific aphid host. Selection due to differences in aphid defense mechanisms, aphid symbiont communities, aphid host quality, and population origin of *A. ervi* (Hufbauer 1999) is well established, yet it is not reflected in the population structure in nature. For local adaptation to occur and remain prevalent, gene flow must be limited enough so that it does not counter selection within populations that use different hosts. Gene flow often correlates with mobility, and *A. ervi* is a highly mobile parasitoid wasp, capable of migrating across agricultural landscapes to find hosts and mates. Additionally, agricultural land is broken up into discrete habitats, making host availability patchy. The combination of a patchwork agricultural landscape and high mobility in the wasp could have resulted in *A. ervi's* lack of genetic structure.

In addition to high levels of gene flow, the absence of genetic structure for *A. ervi* in New York could be an artifact of small populations sizes used in the initial introduction to North America. This may have caused a bottleneck in the population, resulting in insufficient genetic variation to facilitate adaptation to host populations (Hufbauer 2002). The initial introduction from France was only 1,000 individuals, from an unknown source in France, thus we lack information on whether the founding population was a diverse group of individuals or if they were all from the same field (Hufbauer 2002). However, subsequent introductions over the next several decades from several other source populations would have enriched the genetic makeup of *A. ervi* populations. Additionally, selection experiments in laboratory stocks have shown that adaptations to a new host species can occur in as little as three to four generations (Henry 2008).

Thus, it seems unlikely that lack of genetic variation is a strong impediment to local adaptation by *A. ervi* populations.

One of the major assumption of HAD is that differences in host use among populations sets up the conditions in which local specialization will be favored. This will in part be determined by the stability of host populations in both space and time (Schellhorn et al. 2014). For *A. ervi*, however, there may be large variability in host availability. For example, aphid host races and aphid species are available in different agricultural fields and at different times throughout the growing season (personal observation). Additionally, agricultural areas are typically variable patchwork landscapes with many fields of different crops adjacent to each other and to natural and developed areas, resulting in discrete habitat types (Tscharntke et al 2007). This variability in host availability coupled with how quickly *A. ervi* colonized and migrated across North America suggests that there are many constraints that limit the formation of population structure for this parasitoid.

In conclusion, the short generation time of *A. ervi* and known differences among aphid hosts in terms of defensive abilities and resource quality suggest the potential for rapid specialization in host use. Even so, host availability across agricultural systems has likely selected for generalism in host use rather than specialization. The ability of *A. ervi* to use multiple host species has allowed *A. ervi* to outcompete other introduced aphid parasitoids (Cameron and Walker 1989) making it the numerically dominant aphid parasitoid in many agricultural systems. The results suggest that the circumstances in which host use could lead to HAD are quite limited for *A. ervi*.

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Table 1: Geographic localities for collections of *Aphidius ervi*. Site numbers correspond to those in Figure 1.

Site #	Site Names	Latitude	Longitude	Number of *A. ervi* mummies from clover	Number of *A. ervi* mummies from alfalfa
1	Jamesville	42°58'38.42"N	76°3'52.15"W	13	23
2	Lafayette	42°53'39.23"N	76°7'13.34"W	47	23
3	Otisco Lake	42°54'43.35"N	76°13'45.99"W	8	21
4	Skaneateles	42°56'8.5"N	76°21'57.65"W	0	26
5	Auburn	42°55'31.9"N	77°38'1.20"W	0	25
6	Geneva	42°51'40.50"N	77°4'38.68"W	0	24
7	Canandaigua	42°52'50.27"N	77°19'16.32"W	2	22
8	Lima	42°54'7.25"N	77°37'39.21"W	0	25
9	Bethany	42°54'15.08"N	78°6'31.17"W	38	23
10	Alexander	42°54'10.68"N	78°17'38.31"W	6	22

Table 2: Allelic diversity for the six microsatellite markers used to assess population structure of *Aphidius ervi* in central New York (bp is base pairs).

Locus name	**Number of alleles**	**Range of allele sizes (bp)**	**Average number of alleles per population**
Ae4	23	216-306	13
Ae47	6	290-293	4.6
Ae51	8	289-310	5.2
Ae74	5	123-138	2.7
Ae78	4	122-131	3.5
At17	8	165-179	5.3

Table 3. Results of AMOVA to test for population subdivision in *Aphidius ervi* associated with pea aphid host race (**= $P < 0.01$).

Source	df	Estimated variance	Percent variance
Among aphid host races	1	0	0
Among populations within races	14	0.026**	1
Within populations	340	1.89**	99

Overall $F_{ST} = 0.011$**

Table 4: Pairwise F_{ST} values for the ten geographic locations of *Aphidius ervi* in central New York. (Bolded values are statistically significant at $P < 0.05$).

	Alexander	**Auburn**	**Bethany**	**Canandaigua**	**Geneva**	**Jamesville**	**LaFayette**	**Lima**	**OtiscoLake**	**Skaneateles**
Alexander	--									
Auburn	0.004	--								
Bethany	**0.003**	**0.019**	--							
Canandaigua	0.016	0.016	0.010	--						
Geneva	**0.024**	**0.024**	**0.011**	0.000	--					
Jamesville	0.006	**0.017**	0.000	0.006	**0.011**	--				
LaFayette	0.015	**0.021**	0.010	0.000	0.000	0.009	--			
Lima	0.011	0.013	**0.010**	0.009	0.006	0.005	0.002	--		
Ostico Lake	0.008	**0.020**	0.001	0.000	0.000	0.003	0.006	0.011	--	
Skaneateles	0.011	0.019	0.011	0.002	0.006	0.016	0.000	0.008	0.001	--

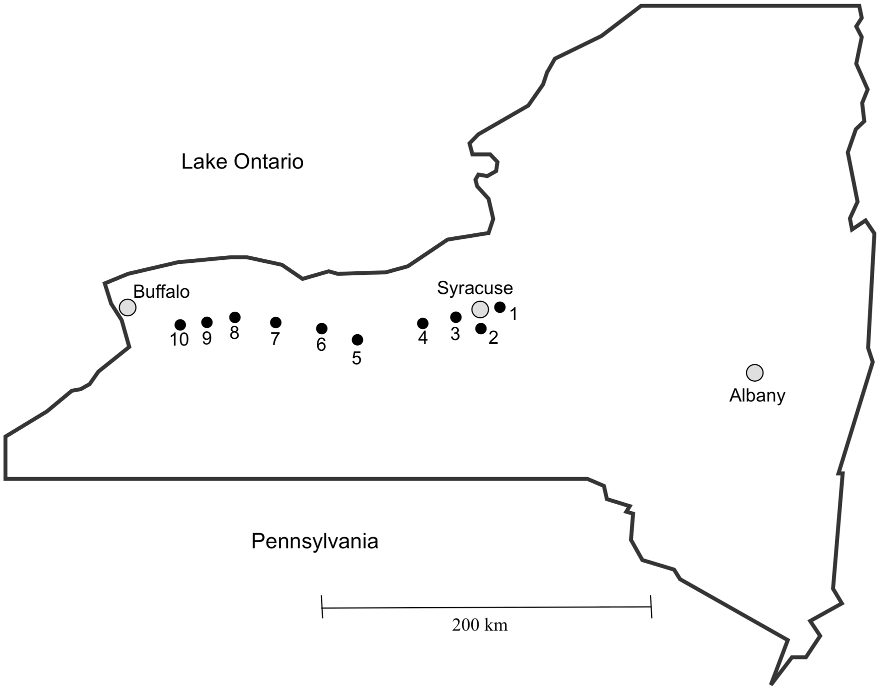

Figure 1: Map of agricultural localities for collections of *Aphidius ervi*. All sites were alfalfa fields with clover comprising 0-10% cover of the field.

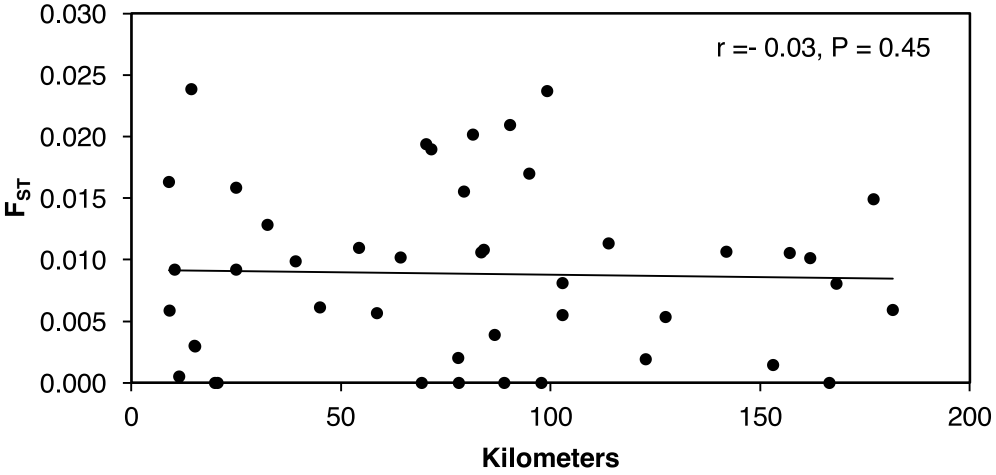

Figure 2: Isolation by Distance. Differentiation among populations of *Aphidius ervi* along a 200km transect. F_{ST} was estimated using the methods of Weir and Cockerham (1984).

Vita

Haley Plasman was born in Grand Rapids, Michigan on March 19, 1991, the daughter of Rodney and Shonnie Plasman. After graduating from Comstock Park High School in 2009, she attended Albion College where she received her Bachelor of Arts in Biology with a concentration in Environmental Science. She received her Master of Science from Syracuse University in 2016.