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# Variations in the Invertebrate Communities of Wild
# Cape Cod Cranberry Bogs

A Thesis Presented

by

BARBARA WAGNER

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
Of the requirements for the degree of

MASTER OF SCIENCE

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Plant Biology

# Variations in the invertebrate communities of wild
# Cape Cod cranberry bogs

A Thesis presented

By

BARBARA WAGNER

Approved as to style and content by:

Wesley Autio, Chair

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Programs

# DEDICATION

To my family, friends, and the women of Wake Robin Morris, who are included in the first two categories, but ought to be mentioned twice.

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# ABSTRACT

# VARIATIONS IN THE INVERTEBRATE COMMUNITIES OF WILD CAPE COD CRANBERRY BOGS

FEBRUARY 2016

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As a species domesticated only in the last century, agricultural cranberry plants (*Vaccinium macrocarpon*) remain little removed from their wild relatives. Thus, it is a potential model species for studies of the earliest stages of domestication; however, there is little available quantitative information on its wild population biology and ecology. As such information is vital to studies of the ecological changes occurring during domestication, the purpose of this study was to consolidate the relevant knowledge available and conduct a preliminary search for patterns in the invertebrate communities of wild bogs. The alpha diversity was found to be greater than the overall (gamma diversity), which is likely a result of the metric used (Simpson index, which weights common taxa more heavily than rare taxa) and the fact that there was minimal overlap in rare species between bogs. In addition, alpha diversity was found to be significantly negatively correlated with bog age ($R = -0.5782$, $p = 0.00951$), though because of the use of a single sampling method in this study, this might be indicative of a significant shift in community composition rather than a true change in diversity. Two pairs of species were found to be correlated with each other, Blunt-nosed (*Limotettix vaccinia* (Van Duzee)) and Sharp-nosed leafhopper (*Scaphytopius sp.*) ($R = 0.64$, $p = 0.001$), along with fleabeetle (*Sysena frontalis* (F.))

and firebeetle (*Cryptocephalus incertus* (Oliv.)) (R = 0.75, p = 0.00013), though the ecological meaning of these data is not clear. In addition, it was found that spiders are significantly more common in western bogs (R = -0.7658, p = 0.000132), while firebeetle is significantly more common in eastern bogs (R = 0.6634, p = 0.0014). However, this may be indicative of a correlation with bog age rather than a true correlation with geographic location. More work is needed to determine the true dynamics driving these findings, so that the information could eventually be used to improve the efficacy and decrease the environmental impact of pest management on agricultural bogs.

## TABLE OF CONTENTS

Page

CHAPTER

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER I

# INTRODUCTION

## A. Domestication studies

One of the most critical innovations of early humanity was the development of agricultural practices. It allowed for the growth of larger population centers and the beginning of the division of labor that was so crucial for the further development of art, science, and technology. This development is thought to have occurred in two primary bursts, one around the dawn of the Holocene (approximately 12,000 years ago) (Larson, G. et al 2014, Meyer, R. S., & Purugganan 2013) and the other in the mid-Holocene (approximately 7,000 years ago) (Larson, G. et al 2014). Given its importance to the course of human history, a great deal of work has gone into the study of the domestication process, from genomic, evolutionary, and cultural perspectives, but in the face of climate change and our increased understanding of many of the negative environmental impacts of current agricultural technologies, understanding domestication has become more crucial than ever. With a better understanding of the domestication process, it will be possible to improve existing agricultural crops and practices to increase sustainability, without decreasing yield (Larson, G. et al 2014).

Many studies of domestication have been performed on widely-used crops (often cereals, rice and maize) (Meyer, R. S., & Purugganan 2013, Larson, G. et al 2014), which is logical from a number of perspectives, not least of all that most of the human population on earth is dependent on these species for a large portion of their daily caloric intake. However, there are a number of characteristics these species share which present some significant difficulties when it comes to studying their transition from wild plant to economically significant domesticated species grown over large portions of the globe.

For one, the climate conditions during the early and mid-Holocene were very different than the climate of today, being 2˚C cooler and containing about 135 fewer ppm carbon dioxide (Piperno, D. R. et al nd.). This difference resulted in a long-term mystery surrounding the early origins of maize domestication (Martínez-Soriano, J. P. R., & Aviña-Padilla, K. 2009) which has only very recently been solved.

The grass teosinte (*Zea mays* spp. *parviglumis* HH Iltis & Doebley) is well known to be the wild progenitor of maize, but in modern times the plant resembles maize very little, producing small, brittle cobs which easily release their hard seeds as opposed to the large soft ears of non-dispersing, easily edible corn that so many consume today (Martínez-Soriano, J. P. R., & Aviña-Padilla, K. 2009). The question has been such a mysterious one that it had even been suggested that maize domestication occurred largely by accident, with the original focal point of cultivation being the *Ustilago maydis* fungus, a delicacy known as huitlacoche, which has been consumed in Mexico since before the arrival of Europeans to the New World (Martínez-Soriano, J. P. R., & Aviña-Padilla, K. 2009). Recently, however, researchers with the Smithsonian Tropical Research Institute have discovered that teosinte displays a dramatic level of phenotypic plasticity in response to differences in environmental conditions: when grown in $CO_2$ and temperature conditions modeled after those of the late Pleistocene and early Holocene, the plants showed many 'maize-like' traits: where teosinte grown under modern conditions shows a great deal of secondary branching and with many tassels, late-Pleistocene/early-Holocene grown teosinte shows very little secondary branching (much like a modern cornstalk) and terminates in a single apical tassel (Piperno, D. R. et al 2015).

Figure 1: Photographs of the STRI experiment. Picture A shows teosinte grown under early-Holocene climatic conditions, where the resulting plant shows a morphology similar to that of modern Maize. Picture B shows the same species grown under modern conditions. These individuals show the many lateral branches and smaller seed heads which have so confounded researchers in the past (Piperno, D. R. et al nd.).

This level of phenotypic plasticity was completely unexpected, but ought to be kept in mind when planning future studies of other long-domesticated crop species.

Part of the teosinte debate illuminates another problem with the study of early domestication in common graminoid crops: it has been asserted that teosinte was never cultivated (Martínez-Soriano, J. P. R., & Aviña-Padilla, K. 2009), but given that this is a discussion of a period of history which occurred 12,000 years ago, it is difficult to see how it would be possible to rule the possibility out so absolutely. The farther back in the historical record, the more sparse reliable information becomes. While our ability to analyze archaeological evidence has certainly advanced, it is impossible to analyze evidence that has yet to be found. Thus, given the cultural component of the domestication process, there will likely always be difficulties in studying the initiation of domestication in crops where that beginning occurred so many millennia ago.

Finally, there is a problem presented by the fact that a domesticated crop does not exist in isolation. Especially in earlier stages of cultivation, there is continued gene flow between wild and managed populations, muddying one's ability to discern when, exactly, domestication began (Larson, G. et al 2014). Similarly, many plants hybridize very readily, and thus there have been influxes of genes from wild relatives of other species related to a given crop plant, further complicating the study of domestication genetics (Greene, S. 2011). Where species have migrated to new regions and even continents with the movement of human populations, gene flow between imported plants and locally native species can even confound efforts to determine the true area of origin for a given crop (Larson, G. et al 2014).

### B. Utility of studying wild relatives for applications in agricultural science

Effective cultivation of most crops requires not only an understanding of its biology (from a natural-history perspective at least) but also an understanding of the crops' interactions with surrounding landforms and biota. Knowing the details of the biology and ecology of a crop's wild ancestors may be helpful for putting into context the plant's responses to specific cultivation practices. Similarly, with crops like cranberry, where the cultivars in use are still comparatively very close to their wild forms (Rodriguez-Saona, C. et al 2011), further understanding of the ecology of wild cranberry bogs will help inform management decisions on cultivated ones.

### C. Cranberry as an ideal model for the study of the earliest stages of domestication

Cranberry (*Vaccinium macrocarpon*) is a crop which by its nature and history would allow for the development of domestication studies unplagued by many of the issues associated with research on older crops. A Captain Henry Hall is credited with the earliest attempt at the cultivation of cranberries in 1816 in the Sandy Neck region of

Barnstable, with cuttings from the dune bogs in that part of Cape Cod, with cranberry cultivation beginning in earnest in the 1820s in eastern Massachusetts (Franklin, 1914). Having only come under conventional cultivation in the first half of the nineteenth century, and only under active domestication (i.e. targeted breeding for desired traits) since the 1920s (Rodriguez-Saona, C. et al 2011), many of the important cultivars still in use are what are known as 'Native Selections,' that is, they are a genotypes of cranberry that have been clonally grown from a cutting selected from a wild bog and re-planted in a managed setting (Rodriguez-Saona, C. et al 2011). Since cranberry bogs are started by the planting of cuttings which are then allowed to fill in clonally rather than being grown from seed (Sandler, 2008), many of the original wild genotypes of the 1800s have been preserved (Rodriguez-Saona, C. et al 2011). Active breeding has only picked up speed in the past few years. Until recently, the only 'domesticated' cultivars were no more than one or two generations removed from their wild progenitors, and even now, the most heavily domesticated genotypes in common use are no more than four generations removed from genetic wild types (Rodriguez-Saona, C. et al 2011). For the most heavily-bred varieties of cranberry, their precise records of breeding lineages and all of the cultivars used in their creation are still readily available for study. In addition, the *V. macrocarpon* genome has been sequenced, and there has already been some significant research carried out exploring the rapid loss of herbivore resistance over only a few generations of controlled breeding (Rodriguez-Saona, C. et al 2011, Georgi, L. et al 2013).

Another advantage of cranberry as a study system is that since the very beginning of its domestication and even early in its cultivation, the budding industry was remarkably well documented. Thanks to the writings of Henry J. Franklin, not only was a great deal of the cranberry-related natural history of that period recorded, but cultivation practices and potentially important events and people (such as the name of the grower responsible for introducing false blossom disease to the East coast cranberry population, and the date of its introduction) are recorded. The UMass Cranberry station has been in existence nearly as long, and has since its founding been dedicated to improving growing practices and conducting continuous cranberry research. A near-complete record of the pest management advice charts exists, as only the charts for 1942 and 1943 are missing (given historical context of this gap, it's also possible that no new charts were issued for those years). Thus, the Cranberry Station's archives may be one of the most complete records of a crop plant domestication in existence.

It is also useful to note that the majority of Massachusetts cranberry cultivation occurs within a hundred miles of the origin point of the first cultivars, and thus it is arguable that the possibility of geography confounding ecological comparison of wild and cultivated systems is greatly reduced. In cases where locally grown cultivars have parentage of, say, Midwestern origin, it is a matter of record and can be taken easily into account with a limited amount of guesswork (Rodriguez-Saona, C. et al 2011).

### D. Outer Cape dune bogs

The cranberry bogs most appropriate for comparison with cultivated cranberry bogs are those found on the dune formations of Cape Cod. There are two regions where these formations cover a large area and feature significant cranberry colonization, and both are part of the Cape Cod National Seashore. One of these is located in Barnstable County, on a spit of land colloquially referred to as Sandy Neck.  This is a naturally occurring dune formation produced by the continuous deposition of sand by the arctic

Labrador Current. This is the region from which the cuttings for the original cultivation experiments were collected (Franklin, 1914). The second region is located on the outer Cape, near Provincetown. This area also is maintained by sand deposition by the same ocean currents; however, its recent history is more complex than that of Sandy Neck.

Figure 2: Locations of dune bog regions on Cape Cod. Region A is the Provincelands area, Region B is Sandy Neck. Aerial images by the US Geological Survey.

The Outer Cape (and much of Cape Cod) was, prior to the 1600s, covered primarily in a forest of American beech trees (*Fagus americana*), a far cry from the pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*) which currently comprises the majority of forest cover of Cape Cod. However, with the establishment of European settlements on the Cape, land use in the area changed drastically.  Traditional European agricultural methods demanded widespread clearing of forest for the planting of crops. This, combined with the effects of grazing livestock on vegetation which had previously stabilized dune formations, led to the dune sand rapidly covering cleared land (Forman, S. L. et al 2008). This had an ecological effect roughly comparable to an extreme forest fire or a volcanic eruption. The soils in the area went from (presumably) being rich enough to make agriculture a reasonable endeavor in the area, to being primarily bare sand with little to no organic component (Forman, S. L. et al 2008).

Because of this history, in the Provincelands, cranberry functions as a species of the primary successional stage. It has been shown that the presence and thickness of organic peat layers in bogs is correlated with age (Smith, S. M. et al 2008). However, given the severity of the disturbance which formed the Outer Cape parabolic dunes, and their current state after approximately 400 years of recovery time, it seems likely that any succession back towards a beech forest would only happen over a period of millennia.

### E. Current understanding of cranberry biology

*Vaccinium macrocarpon* is a small perennial evergreen woody vine in the family Ericaceae, distributed through the northeastern and northwestern sections of North America (Figure 3), (USDA Plants Database). It grows in soils of pH 4.0-5.5, is aggressively clonal, and largely spreads via the growth of runners. Its two distinct growth forms are named according to this habit – where cranberry vines are densely packed, they grow in what is designated a 'phalanx' habit, with short uprights approximately three to eight inches in height. Where coverage is sparse and a clone is actively spreading, the resulting stoloniferous growth is designated 'guerrilla' physiology (Jr., C. N. S., & Nilsen, E. T. 1995).

Figure 3: Distribution of *Vaccinium macrocarpon*, according to the USDA. Green areas indicate the presence of the species. Map is produced by the USDA.

Figure 4: A patch of cranberry plants newly colonizing a portion of sand dune. Guerilla physiology is visible around the edges of the patch, while the bushier center grows in the carpet-like, upright 'phalanx' form.

Having the poricidal anthers characteristic of the family Ericaceae, flowers are predominately buzz-pollinated by native bumblebees. Uprights produce up to 12 pink flowers in spring, but have been shown in experiments to only produce 1-3 berries, regardless of pollinator efficiency (Brown, A. O., & McNeil, J. N. 2006). It is thought that this is a strategy for resource conservation, with the upper flowers acting as additional pollen sources for increased genetic dispersal, and 'insurance' in case of damage to the set of lower fruits (Brown, A. O., & McNeil, J. N. 2006). This strategy seems plausible, given that wild cranberry characteristically grows in very acidic, nutrient poor soils that are severely nitrogen limited. However, there is also evidence that fruit set is somewhat variable according to nutrient availability and pollinator efficacy (Cane, J. H., & Schiffhauer, D. 2003). Ripening occurs approximately 80 days after full bloom, depending on the genotype. Commercial harvesting takes place from mid-September through early November (Sandler, 2008), though on wild bogs berries often remain on bogs throughout the winter and into the spring, especially on highly productive bogs.

With the rapid development of new genetic techniques, there has recently been rapid advancement in our understanding of cranberry genetics. The species under cultivation, *Vaccinium macrocarpon* Ait., is self-fertile and consistently diploid, with an n of 12 chromosomes (Stewart, C. N., & Excoffier, L. 1996). By contrast, the other cranberry species present in North America, *Vaccinium oxycoccos* L., have been found in diploid, tetraploid, hexaploid, and pentaploid forms (Bruederle, L. P. et al 1996, Republic, C., & Territories, A. 2001).  In the field, the species are distinguishable by the orientation of their fruits; *V. macrocarpon* produces multiple laterally placed berries, where *V. oxycoccos* uprights produce a single apical berry. As of late 2012, a unified genomic map of *V. macrocarpon* has been published (Georgi, L. et al 2013).

Due to cranberry being both self-fertile and vigorously clonal, study of the structure of cranberry population genetics is somewhat complicated – even more so because individual clones are understood to not be visually distinguishable from each other (Stewart, C. N., & Excoffier, L. 1996). At present, nothing is known about cranberry population genetics on a local (bog) scale. While cranberry grows in very discrete patches, in some areas there are a number of bogs oriented close enough together that it seems very likely that there would be pollen transfer from one population to the next – it seems likely that in areas like the Provincelands on the Outer Cape, and Sandy Neck in Barnstable County, it would be more accurate to consider cranberry bogs in the context of metapopulations, rather than a collection of small, isolated populations. In comparison to other plant species, cranberry is considered to have very low genetic diversity, and there has been some speculation that self-pollination may be the most common source of fertilization (Stewart, C. N., & Excoffier, L. 1996). There has been some study of the clonal structure of wild bogs, but this study utilized only two bogs, one in West Virginia and one in Tennessee (Jr., C. N. Stewart, & Nilsen, E. T. 1995), and thus did not take into account any variability that might occur with variation in factors such as bog age. Differences in bog age may play a role in genetic diversity, especially in populations which seem to have a distinct development trajectory as they age. As it is, the two different sites showed differences in genetic spatial variability, with the Tennessee site seeming to consist of one dominant clone and a few very small ones, where the West Virginia site included a second clone that seems to cover a fairly significant portion of the bog's total area (Jr., C. N. Stewart, & Nilsen, E. T. 1995). It ought to also be pointed out that in the case of this study, the samples taken did were not distributed across the entirety of the bogs – it is possible that there were more clones present but were simply not picked up by the relatively coarse sampling pattern (Jr., C. N. Stewart, & Nilsen, E.

T. 1995). Likewise, these studies did not investigate possible genetic connectivity between bogs which are local to each other. Improving understanding of this in the future would be helpful for increasing our ability to predict the response of cranberry-based ecosystems to ecological pressures, as genetic diversity generally plays a significant role in a system's ability to recover from stresses such as disease, herbivore attack, or storm damage. As the dune bog systems on Cape Cod serve as habitat for endangered species (two lepidopterans and one sedge) a better understanding of the stability of those sites would have implications for species besides cranberry (Smith, S. M. et al 2008, Averill and Sylvia 1998).

As previously mentioned, *V. macrocarpon*, as is common in the family Ericaceae, grows in acidic, nutrient poor soils. The bogs of concern to this study form in what is called dune slacks: depressions between sand dunes where water collects and is retained for some period of time, and where the ground-water is frequently high enough to be accessible by cranberry plants (roughly 6-8 inches below ground, or the approximate depth of the cranberry rhizosphere) (Smith, S. M. et al 2008). Cranberry is one of the first species to colonize these depressions, along with species of sedge and rush. Eventually, the bogs will support a wider variety of species, including pines, sundews, bayberry, blueberry, bog laurel, orchids, and a plethora of graminoid species (Smith, S. M. et al 2008). Bogs often will feature an upper layer of peat over the base of sand. The presence and thickness of this layer seems to be correlated with the bog's age (Smith, S. M. et al 2008). In spite of the proximity of these bogs to the ocean, the groundwater is not noticeably saline, though this characteristic has not yet been quantified. It was, however, noted that the vegetative composition of the dune slack bogs was not affected by proximity to the ocean, which is a common proxy used to account for exposure to salt spray (Smith, S. M. et al 2008).

Cranberry has its own mycorrhizal associations which aid in survival in nutrient poor environments, but one of the other species highly characteristic of this variety of ecosystem, bayberry (*Myrica pennsylvanica* Mirbel.) is a nitrogen-fixing species, and likely its widespread colonization of the bogs has some impact on their suitability for colonization by a more diverse range of species. A previous study has quantified the soil nutrient characteristics of wild bogs, and found $NO_3$ and $NH_4$ to be present in the soil at concentrations of 1.5 and 2.4 $\mu$ $g^{-1}$ dry soil mass, respectively, while Ca was present at a concentration of 22.0 $\mu$ $g^{-1}$ dry soil mass. However, it is not clear how representative of dune slack bogs these quantities are, as water conditions are understood to change from day to day in such ecosystems (Sadler et al. 2007).

In winter, vines frost harden and turn a reddish purple color; in the spring the same leaves will re green in approximately mid-March. Also of significance to the subject of physiological adaptations of cranberries, which are geared towards prevention of frost damage during over-wintering, is the ability of the species to survive long periods of anoxia (Crawford, R., & Braendle, R. 1996). This is largely due to its ability to enter a form of stasis when submerged, and survive off the carbohydrates stored in its leaves (Crawford, R., & Braendle, R. 1996, Croft, P. J., Shulman, M. D., & Avissar, R. 1993). Additionally, in response to a prolonged period of flooding, the plant's roots will die back while the shoots undergo a period of increased growth, though whether or not this has a practical function has not been shown (Baumann, D. L. et al 2005). This tolerance of flooding provides an additional indirect benefit for cranberry plants: winter flooding in the bogs actually functions as a protection from frost damage to the vines (Sandler 2008). This is used to great advantage in cultivated bogs; however, even in years where some wild bogs do not flood, they seem significantly less prone to frost damage than cultivated bogs (Caruso, personal communication).

With regards to information on invertebrate herbivore communities present on wild bogs, the most current information available in the literature is that provided by the observation of Franklin in the early to mid-twentieth century. While his writings are an invaluable resource for historical information, how accurate a description of the state of today's wild bogs they are is unclear.

### F. A summary of current cultivation practices

When new bogs are planted, the most common method is to obtain cut uprights by mowing or pruning an existing bog, scattering the unrooted cuttings (usually 30-45 cm long) on the surface of the new bog, and disked into the substrate. Alternately, cuttings may first be inserted into soil plugs and raised in a greenhouse until they have developed roots. This is more commonly done with new varieties, as it requires a significantly greater investment, and is not necessary for established varieties (Sandler 2008).

Initially, cultivated cranberry bogs were established on converted wetland; however, with improved wetlands protection laws, commercial bogs are now constructed in upland areas. In contrast to the structure of wild bogs, which form in depressions, cultivated bogs are essentially planted on mounds – layers of substrate are laid down to construct confining layers for water and organic matter, on top of which is placed a 20 cm layer of sand which forms the bog proper. Around this layer of sand, there is a perimeter ditch to assist with drainage from the bog, and dikes surround the entire construction. Cuttings from established bogs are planted in the central sand portion, and after allowing a few years for the vines to fill in, the bog becomes productive. Bogs are periodically 'sanded' for a variety of reasons: improved aeration of bogs, increased root growth, and pest and weed control (Sandler 2008). Peculiarly, this manner of construction means that a cultivated bog is roughly the inverse of a wild bog.

The main benefit of this construction is improved water management (Franklin, 1912). Water serves multiple purposes in cranberry cultivation. It is of course necessary for the growth and wet harvesting of cranberry, but it is also used to prevent frost damage in winter, and has historically also been used as a tool for pest management, since keeping bogs flooded into early spring reduces the population sizes of some invertebrate pest species (Franklin 1927). Pests, like weeds, are otherwise generally managed in the usual way, with fairly extensive pesticide use, including those meant to soak into the bog substrate to combat species which attack cranberry roots (Sandler 2008). It is notable that these root pests have not historically been found in wild bogs (Caruso, personal communication). Other control methods involve application of various bacteria and parasitoids which attack common pests, along with other measures such as pheromone traps (Sandler 2008).

More importantly, the particular configuration of cultivated bogs allows for the bogs to be well-drained. This is of course in complete contrast to what is understood of the hydrology of wild bogs, but the problem with simply going a 'natural' route and allowing commercial bogs to remain continuously swamped is that too much flooding has a negative impact on yield (Sylvia, personal communication). Also, when cultivated bogs are not sufficiently well drained, they may become infested with phytopthera root-rot

(Polashock, J. J. et al 2005). These infestations can only be stopped by improving drainage, but oddly enough it does not seem to be possible to re-plant portions of bog that have died off as a result of phytopthera infection. The only real way to repair the resulting bare patches is to renovate the bog, which requires complete removal and re-laying of the bog substrate, followed by replanting (Sandler 2008). Phytopthera is another problem which does not seem to plague wild bogs, though its presence has been reported, where it seems to only damage small patches before disappearing. After such damage, the bare areas are once again filled in by runners from neighboring clones (Caruso, personal communication).

Otherwise, bogs are fertilized to maximize growth and fruit production, since one of the limiting factors for yield is nitrogen availability (Davenport, J. R. 1999). As with many other crops, pollination is ensured via the importation of captive honey bee hives, which, though less effective pollinators of cranberry on an individual level, can effectively pollinate a bog due to the sheer number of bees per hive. However, more recently there has been an increased move toward the use of broods of captive bumblebees, in an effort to mimic more closely the effectiveness of native bee pollination (Sandler 2008).

### G. Cranberry pests

Discussions of cranberry pests and their control have made up a sizeable portion of cranberry agricultural research since its earliest documentation. Franklin writes extensively on the subject in his personal writings and pamphlets, produced as part of earliest efforts of the UMass Cranberry station, most of which are now only available in a single copy of a printed book currently held by the station. The UMass Cranberry Station has published management protocols for growers since as early as 1933: the date of the earliest charts still held by the Station. These charts grew progressively longer, until the late 90s, when the number of species included became so long that yearly pest-control advice began to be published in full-sized booklets. In light of this, it would be excessive to discuss in detail each pest species appearing on cultivated bogs.

Of greater interest in the context of this study is the fact that very little is formally known about the pests found on wild bogs – the majority of existing knowledge was either recorded nearly a century ago by Franklin, or in observational notes made by Frank Caruso, who visited a small subset of the wild dune slack bogs annually between 1990 and 2012. These existing observations seem to indicate the presence of a disparity between the pests found on wild bogs and those that are major pests on cultivated bogs. As such, it seems most relevant to discuss those species which exhibit the most noticeable overlap between cultivated and wild settings.

One of the most significant cranberry pests both currently and historically is the blackheaded fireworm (*Rhopobota naevana* (Hübner)), which is mentioned on the very first pest control chart, issued in 1933. It is a Lepidopteran which whose larvae feed on the leaves of cranberry plants, binding the tip leaves of the uprights (or the tips of multiple uprights) together with silk. The insect produces two generations per year, with the second generation often having a more severe impact than the first. In addition to damaging the leaves, blackheaded fireworm will frequently feed on the berries as well (Averill and Sylvia, 1998). Late flooding is known to reduce infestations of this pest in agricultural settings, and it has been observed that in the wild, blackheaded fireworm population sizes fluctuate on multi-year cycles with increases and decreases in precipitation. Frank Caruso observed that heavily infested bogs which were flooded through most of one growing season (easily survivable for the majority of cranberry plants, due to their ability to enter a form of stasis and survive off of carbohydrates stored in their leaf tissue) experienced an apparent total loss of their fireworm populations, which took several years to recover or re-colonize (Caruso, personal communication). However, if cranberry bogs are flooded too late into the growing season, they also do not produce fruit. As cranberries are perennial, this is not much of a disadvantage for wild populations, but limits the utility of very long-term flooding in an agricultural setting.

One pest of previous (and likely future) significance on cultivated bogs is the Blunt-nosed cranberry leafhopper, *Limotettix vaccinia* (Van Duzee), a sucking insect which attaches to the stem of a cranberry plant to consume its phloem. However, its main threat to cranberry plants is the transmission vector of False Blossom disease, a phytoplasma which was introduced to Cape Cod bogs by the import of infected cranberry vines from Wisconsin, at least as early as 1914, when Franklin first recorded that infected vines exhibiting the symptoms of the disease had been brought to the UMass Cranberry Station for identification. For many years, False Blossom disease was controlled by spraying against its carrier (blunt-nosed cranberry leafhopper) and by destroying infected areas of vines. Now, blunt-nosed leafhopper is not considered to be a significant cranberry pest, and is generally discussed as one of the invertebrate pests that are present on wild bogs but not cultivated ones; however, this is almost certainly due to the fact that, according to the UMass Cranberry Station pest management chart, DDT began to be recommended as a control measure for this particular pest in 1947. While the recommended control measure for leafhopper varied from year to year, the pest is dropped off of control charts entirely after 1980. Thus, it seems likely that the lack of blunt-nosed leafhopper on cultivated bogs is due to eradication, rather than ecological differences between wild and cultivated bogs. However, variability in its presence on wild bogs may still provide insight into wild bog ecology, and as it has begun to re-colonize bogs in New Jersey (Frank Caruso, personal communication) it may prove to be of future interest to cranberry agriculture.

Another invertebrate found on wild bogs which was previously a pest of concern on cultivated bogs is the Cranberry Spittle insect (*Clastoptera saint-cyri* Provancher). Producing one generation per year, both nymphs and adults feed on the phloem of cranberry plants, though it is the nymphs that produce the spittle-like froth shelters which give the species its common name (Averill and Sylvia 1998). The adults exhibit polymorphism, with the form apparently most commonly found on wild bogs being that with yellow and black striped coloration, and the less commonly found morph being entirely black (personal observation). According to Franklin (1950) the majority of yellow-striped adults are female, while the majority of black adults are male, though a small proportion of black adults are female; however, this observation has not yet been verified (Averill and Sylivia 1998). Franklin also indicates that this species is damaging to cranberry bogs when present in high numbers, and describes populations large enough that “they thoroughly wet the shoes of one walking among infested vines” (1919). This level of infestation is not currently observed on wild bogs, though this may be due to multi-year flooding patterns, as a 24 hour flooding treatment at the start of blooming is an effective method of clearing this pest from cultivated bogs for two or three years (Averill and Sylvia 1998).

The Red-headed flea beetle, *Sysena frontalis* (F.), is present in large numbers on wild bogs, and primarily feed on the undersides of cranberry leaves, but will also gouge out berries. Feeding by flea beetles has been shown to impact the development of the following year's buds (Averill and Sylvia 1998). While the larvae in other areas (such as Wisconsin) are reported to be root-feeders, no root damage due to flea beetle larvae has been documented in Massachusetts. Flea beetles produce one generation annually, with adults emerging on the bogs in July and persisting until September, when they deposit eggs in the surface soil.

During the early part of the 20th century, the Fire Beetle (*Cryptocephalus incertus* (Oliv.)) was an occasional serious pest on cultivated bogs that had been subjected to winter flooding. Now, however, it is only found on wild bogs. It is not specific to cranberry, but feeds on a number of ericaceous and rosaceous plants in and around cranberry bogs. The beetle goes through one generation annually, with an overwintering egg stage, with hatching occurring in late May, and while larval feeding habits are as yet unknown, the adults will consume the outer layer of leaves, in a manner similar to that of the flea beetle, but on both the upper and undersides of the leaves (Averill and Sylvia 1998).

The Chain-spotted geometer (*Cingilia catenaria* (Drury)) is a locally endangered moth species which is found on some wild bogs. Where it occurs, it often occurs in large numbers and can have a large impact on cranberry vegetation, as it feeds heavily on the leaves. However, it is not specific to cranberry, feeding on a wide variety of tree, shrub, vine, and herbaceous species (Averill and Sylvia 1998). In the early part of the 20th century, it was occasionally an important pest in blueberry cultivation. The eggs of this species overwinter, after which the larvae exhibit slow growth until early to mid-August, when pupation occurs, followed by emergence in early to mid-September (Averill and Sylvia 1998).

One type of pest that is common on cultivated bogs but rarely if ever seen on wild bogs, is soil insects that attack the roots of cranberry plants. Pests such as cranberry root grub (*Lichnanthe vulpina* Hentz) and scarab grubs have not been observed to affect wild bogs (Caruso, personal communication). A likely reason for this is the tendency for wild bogs to experience long-term flooding on a semi-regular basis (every few years), and the general tendency for wild bogs to retain water much later into the year than cultivated bogs. As the grub larvae require access to oxygen, long-term flooding of the time that cranberry is well adapted to surviving likely drowns them, preventing populations from ever reaching sizes large enough to cause noticeable damage.

Given the lack of any basic characterizations of the invertebrate communities currently present on wild bogs, a logical preliminary step in the process towards gaining an understanding of the invertebrate communities inhabiting wild dune slack cranberry bogs is to investigate the diversity found at the local, individual bog scale (i.e., the alpha diversity, or mean diversity per bog). In addition, the beta diversity, which is indicative of the differentiation among the individual wild bog communities, could provide an indication of the level of spatial heterogeneity present in that diversity, and thus be an indicator of the value of further investigation into the ecosystem dynamics of wild cranberry bog invertebrates.

### H. Genetics of cultivated cranberry varieties

The previously described method of bog construction means that commercial bogs are constructed with the intent of having each bog comprised of only one genotype. This is helpful for production, because the phenology of a bog is internally synchronized, increasing the effectiveness of specifically-timed pesticide application and helping to ensure that the flowering and fruiting will happen roughly at the same time. Whether bogs are, at this point, true genetic monocultures is difficult to say, since it is not known whether stray berries in commercial bogs clipped for re-planting of new bogs might have cryptically increased the number of genotypes representing a given cultivar (Sandler 2008). At the very least, spring time leaf color changes on commercial bogs are visibly patchy where, in theory, this should also happen uniformly.

Figure 5: Photograph of a cultivated bog in March 2012, showing uneven timing of spring re-greening.

It has been found that some native selections previously considered different are, in fact, genetically identical (Novy, R. G. et al 1994).

Due to its vigorous clonal growth and the relative newness of cranberry breeding, many of the varieties in cultivation are referred to as 'native selections.' They have undergone no selective breeding whatsoever and are effectively representatives of a wild-type genome (Rodriguez-Saona, C. et al 2011, Sandler 2008). These cultivars were simply established by taking new cuttings from wild sites and planting them in an agricultural one. It is from these native selections that more 'domesticated' cultivars were produced, though crosses did also involve native selections from other states (Rodriguez-Saona, C. et al 2011, Sandler 2008). For instance, the popular 'Stevens' cultivar is a cross of the Massachusetts 'McFarlin' variety and the Wisconsin 'Potter' variety. The most heavily-bred cultivars are the product of no more than three crosses (Rodriguez-Saona, C. et al 2011).

In spite of this, there is evidence that even this minimal breeding has had a negative impact on the innate defense capacity of cultivated cranberry varieties. Specifically, this has been studied with respect to defense genes associated with resistance to fruit rot (Georgi, L. et al 2013).

## I. Specific aims

1.) Perform a preliminary survey of the invertebrate community found on the wild cranberry bogs of the Outer Cape.

2.) Determine whether there is a significant degree of variability in herbivorous insect communities between individual wild bogs (beta diversity), and compare this to the level of diversity within individual bogs (alpha diversity), to provide a preliminary view of the invertebrate diversity found in wild cranberry bogs.

3.) Determine whether within-bog diversity is correlated with bog age.

4.) Determine if the occurrences of certain species are correlated.

5.) To map the geographic distribution of common species.

# CHAPTER II

# METHODS

## A. Field site selection

To pick field sites, the coordinates of candidate sites were initially obtained via perusal of aerial imagery on Google Earth, because cranberry bogs are usually visible from above as reddish patches in coastal dune regions. However, since this method is not entirely accurate, final site determination also required individually locating each site and determining its suitability. Some sites were not suitable for reasons including complete inaccessibility due to being completely surrounded by dense thickets of pitch pine. In addition, some sites which appeared to be cranberry bogs in aerial photos were determined to be blueberry or bayberry shrub thicket, with minimal cranberry ground cover that would have been physically impossible to sample with sweep nets. An additional factor constraining site selection was the significant rainfall that occurred in June 2013, which flooded all potential Sandy Neck sites and some Provincelands sites under several feet of water well into August. While a late August visit confirmed that the cranberry vines in the majority of the flooded sites survived the flooding, and that the sites had drained by the end of the summer, it was not possible to include these bogs in this study.

Of the remaining candidate sites, twenty were selected in a relatively even geographical distribution along the Cape Cod National Seashore of the outer Cape. Locations of confirmed sites were recorded on a Garmin Oregon 250 handheld GPS unit.

## B. Sampling methods

Sampling methods were based on those used annually in commercial bogs.

Cranberry sweep nets were used to collect invertebrates inhabiting the cranberry uprights. Sweeping was carried out in rough transects along the longest axis of each bog, as possible. The lengths of these transects varied greatly because of the irregular shapes and orientations of the wild bogs, and thus standardized North-South or East-West transects would have resulted in some bogs being sampled with fewer than ten sweeps. Three collections were made, in July, August, and September of 2013.

Invertebrates captured by sweep net were killed with chloroform, bagged, and then frozen upon return to the UMass Cranberry Station. Specimens were then identified where possible.

### C. Statistical analyses

Data for each sampling of each site were standardized by dividing the raw count data by the total number of sweeps used to sample the site on that day, giving an approximate density metric of individuals per sweep. For analysis of total samplings across the summer, the standardized data for each sampling was totaled.

To analyze gamma, alpha, and beta diversity, the overall richness (number of invertebrate types collected) was determined, and the diversity was measured using the Simpson index (which describes the probability that any two individuals selected at random will belong to the same type). The alpha diversity was determined by calculating the mean Simpson value of the individual bogs, and the beta diversity was calculated using the following equation:

$$\beta = \gamma / \alpha$$

Where “$\beta$” represents the true beta diversity, “$\gamma$” represents the overall (gamma) diversity, and “$\alpha$” represents the mean within-bog (alpha) diversity. Diversities were calculated using both the Simpson index results and the overall richness data.

Information about the ages of the bogs surveyed was obtained from data collected by a previous study conducted by Stephen Smith et al. at the Cape Cod National Seashore (2008). In this previous study, age categories were determined by examining historical aerial photographs to determine whether current cranberry bogs had been established by that year. Thus, bogs were placed in the following categories: pre-38, pre-47, pre-60, pre-86, pre-94, and pre-01, indicating that the bog had been established by 1938, 1947, 1960, 1986, 1994, or 2001, with “CBD” indicating bogs whose age could not be reliably determined. The Simpson indices of the bogs in each age group were plotted in order to conduct a preliminary assessment of whether within-bog diversity is linked to bog age. The Pearson correlation between bog age and Simpson index value was then generated, in order to further investigate whether diversity changes with bog age.

Table 1: Bogs, in order of East to West, along with their coordinates and ages. *Numbers in this column indicate the bogs' corresponding Smith, S. M. et al 2008 designations. Bogs with two numbers in the second column are those which were two different bogs at the time of the previous study and have since merged. †Indicates that the age of one of the two bogs was listed as CBD (could not be determined), so the known age was used.

| **Bog** | **2008 Number*** | **Longitude** | **Latitude** | **Age** |
|---|---|---|---|---|
| PL4 | 291 | 70° 07'4.45"W | 42° 3'54.74"N | pre86 |
| PL2 | 254 | 70° 07'8.97"W | 42° 3'44.80"N | pre86 |
| PL7 | 246 | 70° 07'33.87"W | 42° 3'57.42"N | pre47 |
| PL26 | 231 | 70° 07'55.34"W | 42° 3'53.04"N | pre86 |
| PL8 | 228 | 70° 08'13.83"W | 42° 3'58.45"N | pre86 |
| PL9 | 223 | 70° 08'25.40"W | 42° 4'07.84"N | pre47 |
| PL10 | 221 | 70° 08'42.54"W | 42° 4'14.87"N | pre86 |
| PL11 | 187 | 70° 08'58.06"W | 42° 4'21.25"N | pre86 |
| PL27 | 199 | 70° 09'10.17"W | 42° 4'14.11"N | pre38 |
| PL14 | 164 | 70° 09'46.90"W | 42° 4'24.70"N | pre60 |
| PL13 | 160,156 | 70° 09'50.09"W | 42° 4'08.54"N | pre60† |
| PL16 | 123,122 | 70°10'29.87"W | 42° 4'37.05"N | pre94† |
| PL15 | 118 | 70°10'35.00"W | 42° 4'29.70"N | pre86 |
| PL17 | 88 | 70°11'10.33"W | 42° 4'38.35"N | pre38 |
| PL18 | 87 | 70°11'13.94"W | 42° 4'44.78"N | pre60 |
| PL20 | 331 | 70°12'03.98"W | 42° 4'33.64"N | pre38 |
| PL21 | 33 | 70°12'32.54"W | 42° 4'31.22"N | pre47 |
| PL24 | 32 | 70°12'33.68"W | 42° 3'59.74"N | pre38 |
| PL23 | 29 | 70°12'41.41"W | 42° 4'14.70"N | pre38 |
| PL25 | 30 | 70°12'42.81"W | 42° 3'57.69"N | pre38 |

Finally, the most common taxa were subjected to correlation analyses (both within sampling dates and overall), and the among-sites distribution of each of the most common species was visualized using LibreOffice. All analyses were conducted either in LibreOffice, Microsoft Excel, or the statistics program R.

# CHAPTER III

# RESULTS

Thirty-nine different taxa of invertebrate where collected during sampling, with all spiders counted as one taxa, because this investigation is primarily concerned with herbivores. Of these, only twelve sites produced collections of more than fifteen taxa total, over all sites and all samplings. The most abundant species were primarily ones which are also considered pests on cultivated bogs, with the exception of Chain-spotted Geometer (the endangered moth *Cingilia catenaria*), and an unidentified Hemipteran. (For a list of species names and abbreviations along with density data, see Appendix.)

## A. Diversity analyses

The density data was used to determine the Simpson index of the overall dataset ($\gamma_{\text{Simpson}}$ diversity), as well as that of each individual bog. The former was found to be 0.8117, while a list of the latter can be found in Table 2. The mean of the within-bog diversity results ($\alpha_{\text{Simpson}} = 0.6147$) was used to determine the $\beta_{\text{Simpson}}$ diversity, which was found to be 1.320. Similarly, the diversity results based on richness were as follows: $\alpha_{\text{richness}} = 8.75$, $\gamma_{\text{richness}} = 39$, and $\beta_{\text{richness}} = 4.457$.

Table 2: List of bogs, ordered East to West, and their Simpson index values as calculated using density data.

| **Bog** | **Simpson Index** |
|---|---|
| PL4 | 0.557130461 |
| PL2 | 0.823592912 |
| PL7 | 0.617283951 |
| PL26 | 0.823384428 |
| PL8 | 0.805232558 |
| PL9 | 0.716934042 |
| PL10 | 0.694967841 |
| PL11 | 0.479990399 |
| PL27 | 0.720075532 |
| PL14 | 0.844606707 |
| PL13 | 0.742966684 |
| PL16 | 0.409364588 |
| PL15 | 0.832120001 |
| PL17 | 0.376842211 |
| PL18 | 0.75134193 |
| PL20 | 0.396208213 |
| PL21 | 0.442238608 |
| PL24 | 0.305916661 |
| PL23 | 0.401616557 |
| PL25 | 0.552786401 |
| **Mean** | **0.614730034** |

To explore the relationship between bog age and diversity, the Simpson indices were plotted by bog age, after omitting PL16, as it was the only bog in the pre-94 group (Figure 6).

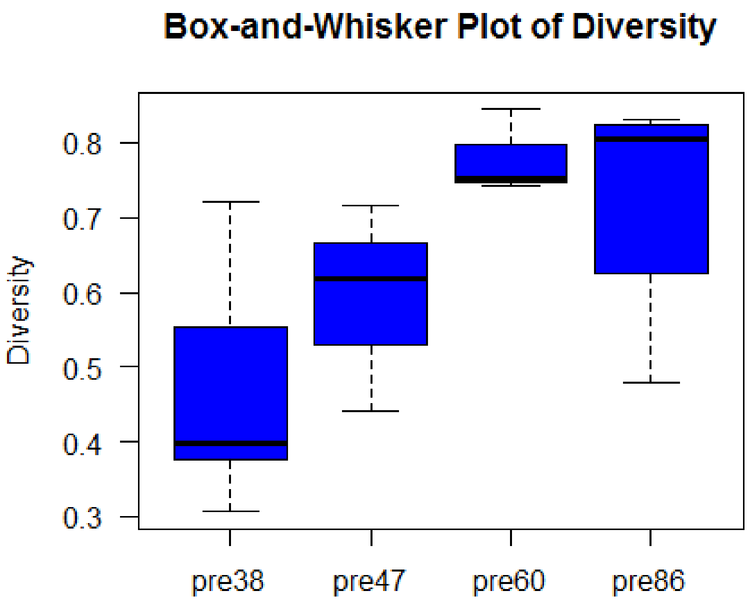


Figure 6: A box and whisker plot of the Simpson indices of the individual bogs, by age.

According to the box-and-whisker plots in Figure 6, the diversity of the pre60 group appears to be significantly different from those of the pre38 and pre47 groups. However, the pre60 group included data from only three bogs, so whether this result is ecologically relevant is not clear. An additional analysis of the Pearson correlation between age and diversity resulted in an R score of -0.5782 and a very significant p-value of 0.00951 ($p < 0.01$). Thus, bog age and diversity appear to have a significant positive correlation.

**B. Species correlations**

A scatterplot matrix of the Spearman's correlations of those species of present and historical agricultural interest show two pairs of interest: Blunt-nosed and Sharp-nosed leafhopper are significantly correlated ($p = 0.001$), as are Firebeetle and Fleabeetle ($p = 0.0003$) (Figure 7).

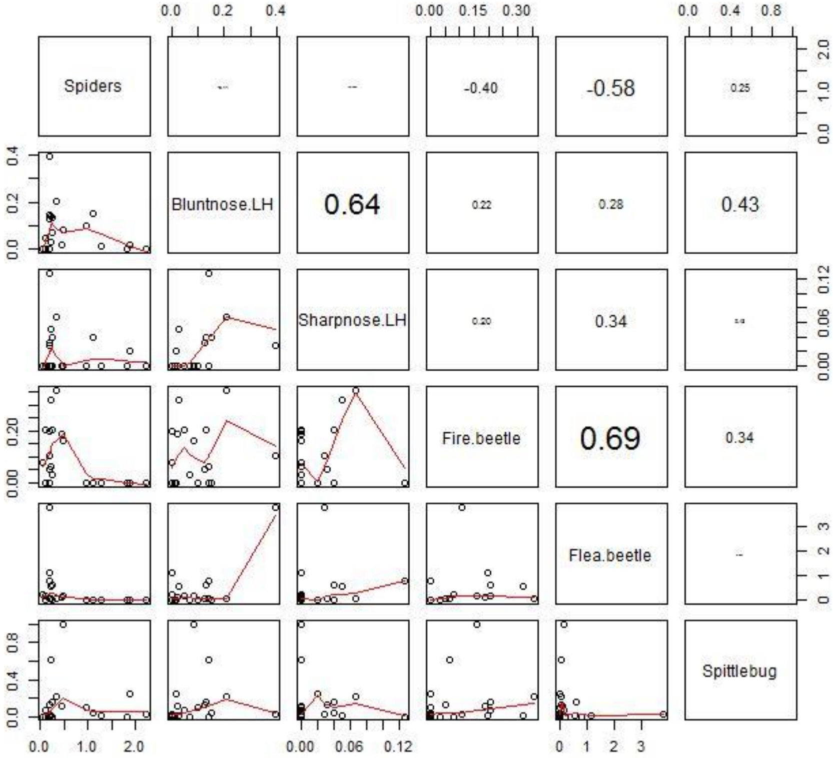


Figure 7: A scatterplot matrix with Spearman correlation coefficients. The above figure shows a correlation between blunt-nosed leafhopper (*Limotettix vaccinii*) and its sharp nosed counterpart (*Scaphytopius sp.*), and between flea beetle (*Systena frontalis*) and firebeetle (*Cryptocephalus incertus*), and a small negative correlation between spider presence and flea beetle. Also shown is the scatterplot for cranberry spittlebug, *Clastroptera saint-cyri*.

This correlation between leafhopper species (p = 0.001) only holds over the course of the entire summer's sampling – at the bog-level scale, the correlation between the two falls to a coefficient of 0.09 (p = 0.705).

However, this is not the case with flea and fire beetle – in 76.92% of sites where one of the two occurs, the other is also present. A Spearman's rho correlation was run on the standardized counts of the two species, on the assumption that the relationship between the two was monotonic, but not necessarily linear. At this level, the correlation coefficient of the two species was found to be 0.7510089 (p = 0.00013), which highly significant.

The correlation between spiders and non-spiders sampled was also calculated, but found to be only -0.17 (p = .473) at its strongest, during the September collection period, and thus cannot be deemed significant given the available data.

### C. Geographical distributions of species of interest

The following graphs are representations of the geographical distributions of various invertebrates sampled. The size of the blue points is determined by the sample size at each site. The axis coordinates of each point were developed from the longitude and latitude coordinates in order to simplify subsequent analyses. Orange points represent sites in which the invertebrate was not found. Based on visual representations of distributions, for some taxa, analyses using Pearson's rho do support this impression.

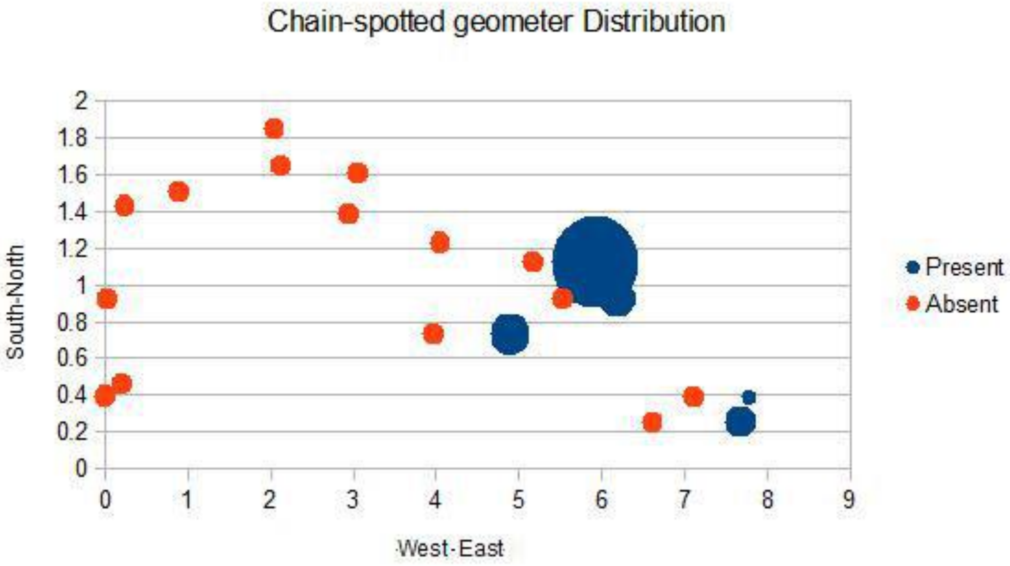
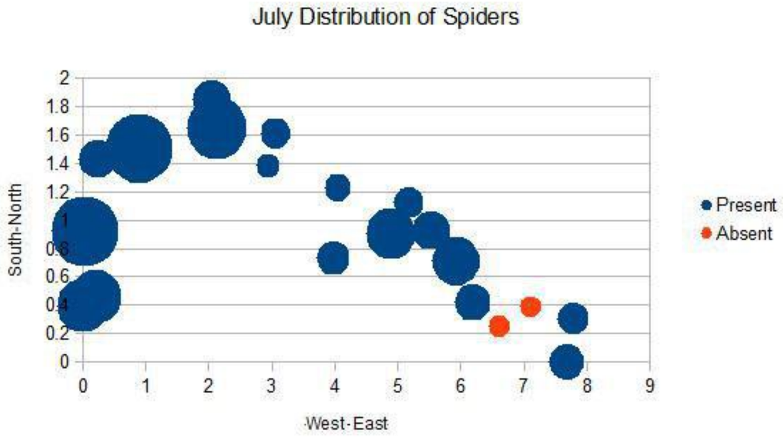
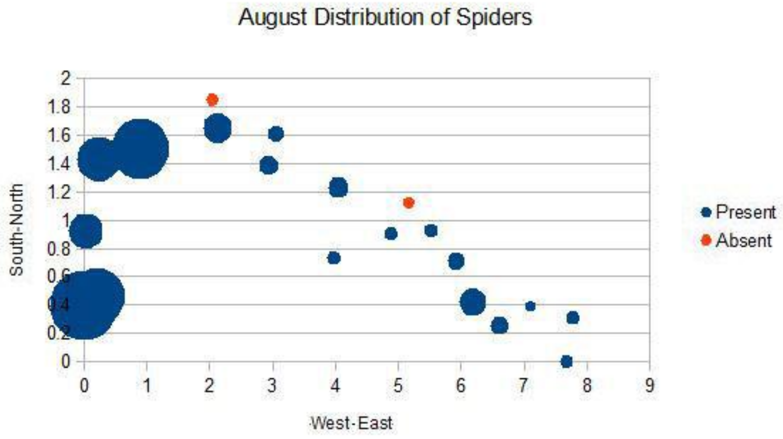


Figure 8: Chain-spotted geometer, an endangered moth, is relegated to a few bogs in the less wooded, eastern portion of the National Seashore preserve. Pearson's rho of east-west distribution is 0.2906 (p = 0.213), and insignificant.





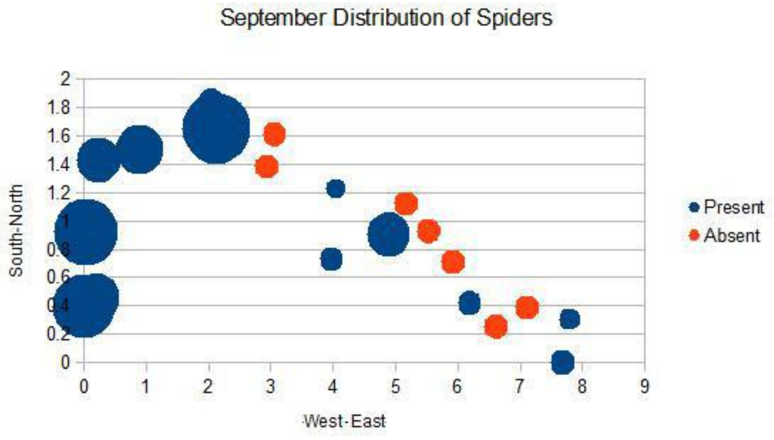
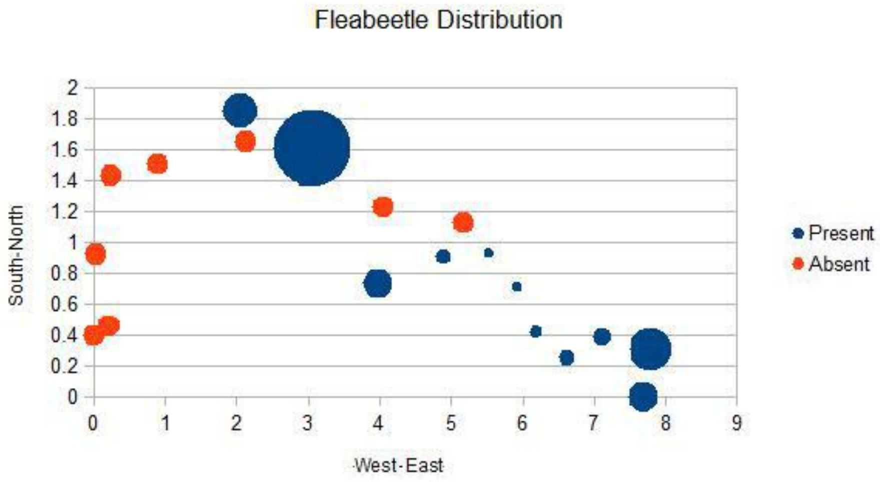


Figure 9: Change in distribution of spiders over three months. Pearson's rho of east-west distribution for July, August, and September are -0.6243 (p = 0.003*), -0.6983 (p = 0.0006**), and -0.6891 (p = 0.0007**), respectively, indicating that spiders are significantly more likely to be present in western bogs than at eastern sites. The overall rho was -0.7658 (p = 0.000132**). (* indicates significance, ** indicates a value is highly significant.)



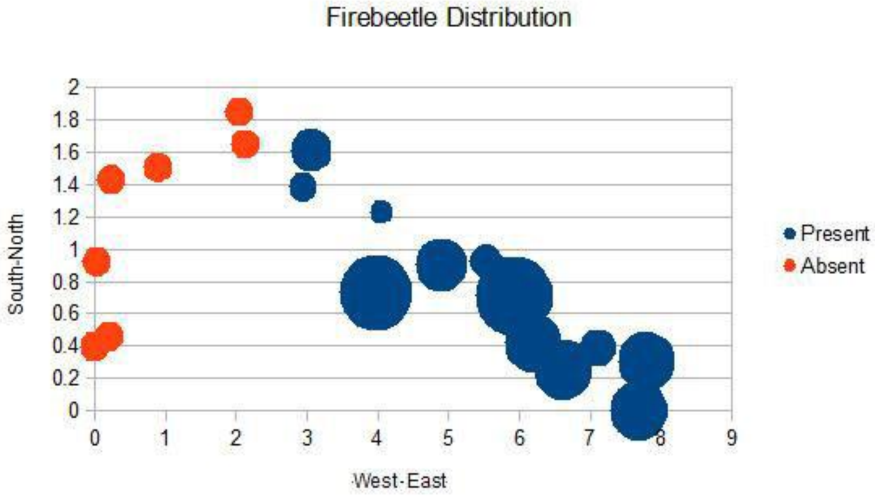


Figure 10: Fleabeetle and Firebeetle distribution. Pearson's rho values of the east-west distribution of Fleabeetle and Firebeetle presence were 0.0967 (p = 0.685 n.s.) and 0.6634 (p = 0.0014**), respectively. This indicates that while Fleabeetle presence is not significantly correlated with position on an East-West axis, Firebeetle is significantly more likely to be found in eastern bogs.

Finally, the Pearson's rho of East-West distribution and bog age was 0.5988 (p = 0.005), indicating that within this dataset, younger bogs are significantly more likely to be located in eastern bogs.

## D. Observations of bog characteristics

From an observational standpoint, there are some bogs can be split into a few general categories based on their characteristics:

*Grown-in:* These bogs were clearly at one point open cranberry bogs, but have become nearly overgrown by shrub plants such as bayberry and various blueberry species.

*Open, sandy:* These bogs often have a great deal of ericaceous shrub growth in the center, and seem, observationally, to be some of the dryer bogs.

*Open, peaty:* These bogs seem to be characteristically wetter than the above bogs, and often feature a greater apparent diversity of associated plant species, including in at least one case, two species of orchid (*Pogonia ophoglossoides* and *Calopogon tuberosus*). In these bogs, shrubs are often mostly relegated to margins, or else there is evidence that there once was greater shrub cover which was flooded out. (This is evidenced by their being full of the 'skeletons' of dead bayberry shrubs.)

In addition, in some bogs it is readily apparent that they were at one point flooded long enough to kill off a large area of cranberry vines. This change is visible on aerial imagery, but is also very obvious on the ground. In these bogs, there is a border of cranberry plants and bayberry shrubs ringing what was clearly the former margin of the bog, with large bare sections in the middle which are in the process of being re-colonized by the marginal cranberry plants, which send runners in from the edges.

Frost damage seems to not be much of an issue in wild bogs, whereas in cultivated bogs a significant portion of the effort that goes into water distribution is for the purpose of frost protection (Sandler 2008). The only areas on wild bogs where any frost damage is noticeable is on uprights directly adjacent to bayberry shrubs. Given that bayberry is a nitrogen-fixing plant, it is probable that the increased nutrient levels in the substrate interfere with the cranberry plant's natural frost-hardening mechanisms (Frank Caruso, personal communication.) This would also explain why heavily-fertilized agricultural bogs are so vulnerable to cold where unmanaged plants are not.

# CHAPTER IV

# DISCUSSION

Given that cultivated cranberry plants are so little removed from their wild relatives, both genetically and spatially, it's reasonable to hypothesize that the majority of differences between the invertebrate community composition of wild and agricultural bogs is due to the particular cultivation practices used in agricultural ecosystems, which produce conditions fundamentally different from those found in wild systems. Though agricultural fields are not commonly referred to as ecosystems, the organisms in question still exist in a form of ecosystem, no matter how artificially managed. Especially in contexts like this one, it's helpful to approach both types of system from an ecosystem perspective; however, given that agricultural systems are generally not closed systems, they are still subject to environmental and ecological interactions with surrounding ecosystems, and thus it seems reasonable to treat agricultural systems as artificial ecosystems. Approaching agricultural systems from an ecological perspective can only expand our understanding of our agricultural crops and allow for the development of more efficient agricultural practices.

## A. Invertebrate diversity

Given that the Simpson index produces a probability (the probability that any two individuals selected will belong to the same type), the fact that using the Simpson index to calculate the beta diversity of the study area produces a number greater than one (1.320) is an obvious issue. This result is produced by the fact that the Simpson index of the entire dataset is larger (indicating lower diversity) than the mean within-bog diversity. However, this is not the case when simple richness data is used ($\alpha_{richness}$ = 8.75, $\gamma_{richness}$ =

39, and $\beta_{\text{richness}}$ = 4.457). Because the Simpson index is a metric that places greater weight on common species than rare species, these results are likely caused by the large number of rare species (found in only a few bogs, sometimes in only a single bog, and usually in small numbers) present in the overall dataset. Given that there is little bog-to-bog overlap of rare species, it is probable that the lower diversity index of the overall dataset is a result of the effect of rare species becoming even smaller at the larger scale than it is at the smaller within-bog scale. The issue of obtaining a probability metric greater than one can at least be resolved by using the Gini-Simpson index (1 – Simpson index value = Gini-Simpson index value, or the probability that any two randomly selected individuals will belong to different types), which produces the following results: $\alpha_{\text{Gini-Simpson}}$ = 0.3852, $\gamma_{\text{Gini-Simpson}}$ = 0.1882, and $\beta_{\text{Gini-Simpson}}$ = 0.4885.

Given the minimal bog-to-bog overlap of rare species, the above diversity results indicate that rare invertebrate types may be better indicator species candidates than common ones in future studies of the ecological factors affecting wild cranberry bogs, especially if presence/absence data are to be used. Given that the common species are largely those which are found on both wild and cultivated bogs, it seems likely that these species represent a cohort of environmental generalists (relative to other cranberry bog invertebrates) that have greater tolerance for a wide range of conditions (including the more extreme conditions found in agricultural environments) than rare species.

With respect to the potential relationship between diversity and bog age, the dataset collected during this study indicate that there is a strong negative correlation between bog age and diversity. Given that only one sampling method (sweeping) was used, this could be indicative of a true decrease in overall diversity, or it may be that over time, the diversity of taxa likely to be caught in sweep nets decreases and the diversity of taxa more likely to be caught via other methods increases. In addition, the small number of sampled bogs in the pre60 group (three), means that there is a high likelihood that the apparent significance is due to the small sample size rather than a true effect. Greater clarity could be achieved by conducting an additional study that sampled a larger number of bogs and measured an array of environmental variables, then utilized multivariate analyses such as a principal component analysis to determine which factors have the greatest relationship with the invertebrate community composition of wild cranberry bogs.

### B. Correlating species

Although a perusal of pesticide recommendation charts would indicate that leafhoppers have not been a problem on agricultural bogs since the use of DDT, blunt-nosed leafhopper has begun to creep its way back into commercial bogs in New Jersey. While *Limotettix vaccinii* (Blunt-nosed leafhopper, hereafter BNLH, in contrast to *Scaphytopius sp.,* SNLH) does feed on cranberry directly, its primary importance as a pest is as a vector for cranberry false blossom disea se, which has historically been a significant threat to the cranberry industry (Franklin 1927). Contrary to previous observations, this disease is commonly observed on wild cranberry bogs in both the Sandy Neck and Provincelands regions, and on some bogs the associated stunted flowers make up a fairly sizable portion of blooms. Therefore, it is reasonable to assume that if BNLH once again becomes a pest on commercial bogs, false blossom disease is likely to return as well. Like BNLH, SNLH is also a vector for plant disease, though not one affecting cranberry: SNLH vectors a blueberry stunt disease. Thus, while the fine-scale correlation between BNLH and SNLH is very weak, it does seem that bogs with one leafhopper are likely to have the other present, and so it may be that SNLH hopper could have an agricultural impact in the future, if blueberry crops are grown near cranberry bogs.

The strong positive correlation between flea and firebeetles on wild bogs is also potentially ecologically significant. While firebeetle is not much of a pest currently (it has historically shown up sporadically on bogs that had been flooded for the winter), fleabeetle can have an impact on cranberry production, especially the development of the following year's buds (Averill, Sylvia 1998). It is interesting that fire and fleabeetle presences are so strongly correlated, since their feeding habits are very similar, and one might expect competition. Also, fleabeetle larvae develop in the soil; the eggs, which overwinter in the soil, must not be susceptible to water damage. It's possible that a better understanding of what causes these two species' presences to be correlated on wild bogs would provide clues about what cultivation practice causes this correlation to apparently not be mirrored in agricultural ecosystems. It might also allow for fleabeetle to be fully controlled by an adjustment of existing management practices.

### C. Geographic distribution of species

Though spiders were correlated with western sites and firebeetles with eastern sites, the ecological significance of these findings is unclear. Within this dataset, the longitudinal location of a bog is also significantly correlated with age, which is significantly correlated with changes in diversity. In addition, other conditions that likely vary among sites (e.g., hydrological dynamics) may be the true drivers of firebeetle or spider presence, and may be correlated with geography by proxy due to their association with bog age. Further sampling and more detailed multivariate analyses would be needed in order to conclusively identify the factors affecting the geographical distribution of the above species.

### D. Endangered insect species in Provincelands bogs

Chain-spotted geometer (*Cingilia catenaria*) is present on wild bogs in the Provincelands, but only a few, though there is one bog where they are locally very abundant (Site PL9, with 1.634 individuals per sweep.) Franklin writes about them being so abundant that occasionally infestations would invade cultivated bogs from wooded areas, and do dramatic damage to the edges of bogs. Now, however, the moths are considered rare. Curiously, though Franklin describes these infestations as coming from wooded areas, the current populations of geometer are not centered on sites which have any particular association with tree cover (PL9 is devoid of the pitch pine border which often edges wild cranberry bogs.) It may be that dryness of a site is a more important factor affecting site suitability, though why the geometer is not present on wetter bogs surrounded by upland tree cover is difficult to determine.

### E. Further research

It seems likely, based on observations of the varying characteristics of wild bogs, that hydrology is a major driving factor affecting the bogs' ecosystem dynamics. Historically, one of the methods of pest control on commercial bogs has involved maintaining winter flooding into the spring. This flooded out many of the pest larvae, but also puts bogs at risk for decreased yield (Franklin 1927.) This method is still in use on some organic cranberry bogs (Sandler 2008).

In wild ecosystems, long-term observations by Frank Caruso of a small number of bogs have indicated that some bogs will periodically experience heavy-flooding years, after which populations of damaging insects such as blackheaded fireworm (*Rhopobota naevana*) take several years to recover to pre-flood levels. This, combined with the fact that many of the invertebrates present on cranberry bogs have year-long life cycles, means that further studies on the ecological drivers of invertebrate community composition on cranberry bogs would need to be long-term projects, and cover a large number of sites, since these extreme flooding events are probably highly irregular, and depend as much on the vagaries of large-scale climate patterns as local landscape features.

Flooding patterns also seem to have a significant effect on whether bogs remain open and cranberry dominated or become overgrown with shrub species. As previously described, some bogs were obviously much more overgrown at one time, before being flooded for a period of time longer than bayberry can tolerate, and now are inhabited mainly by cranberry plants, and skeletal dead or near-dead bayberry shrubs, occasionally with a small number of growing leaves at their very top. Wetter bogs also seem more likely to have a peat layer present, which benefits cranberry plants in that provides a substrate for the plants to root which floats on the surface of mucky soils, preventing the vines from being permanently submerged in perpetually anoxic bogs.

### F. The difficulties of studying dune bog hydrology

A preliminary study of the hydrology of the Provincelands bogs has been attempted before (Smith, S. M. et al. 2008) but abandoned due to its complexity. It has been joked that the hydrological patterns “follow no known rules of physics” (Frank Caruso, personal communication), but at least one thing is apparent: due to the bogs' proximity to the shoreline, water level fluctuations in the bogs seem to have a heavy tidal influence (Stephen Smith, personal communication.) As a result, measuring the fluctuations would require the development of a synchronous system of water level sensors capable of recording and storing timed data, so that water level measurements could later by synchronized and compared in a meaningful manner. The other alternative would require a very large workforce capable of taking measurements close to simultaneously over a long period of time.

Another odd characteristic of the dune slack bogs is that there is no readily apparent hard pan layer aiding water retention. It's possible that the cranberry bogs may be unusual wetlands by being directly connected to the groundwater. Alternately, the hard pan layer could be present, in the form of whatever historic topography was present before the arrival of the colonial agricultural practices that so drastically transformed the outer Cape. Perhaps part of the reason why the hydrology of these systems seems so incomprehensible is because the now-underground historical landforms were irregular, and so have a variable influence on below-ground water movement in today's landscape. Other than trying to survey what the historical landforms may have looked like via the use of geological equipment, it's not clear how one would investigate this potential factor. Topographic maps of the late 17th century are unreliable, when available at all.

# CHAPTER V

# CONCLUSIONS

Wild cranberry bogs are an ecosystem type with enough individual variability that, were a longer study to be conducted, larger patterns in invertebrate community composition would likely become apparent. As it is, bog diversity seems to be negatively correlated with bog age, and at least two of the taxa detectable by the chosen sampling method display a strong correlation in an ecological context. In addition, some taxa seem to exhibit a distinct geographical distribution, though this may simply be indicative of a correlation with bog age, as most of the western bogs selected as sites for this study belong to older age groups. In the future, the current data could be compared to that collected yearly on commercial bogs. This, in combination with an extended study of the drivers of wild bog invertebrate ecology, could help improve our understanding of what conditions make individual agricultural bogs vulnerable to infestation by different pest species.

This increased understanding would also be a benefit to our understanding of the early stages of the domestication process of crop species, since the earliest stages of domestication involve the creation of artificial, controlled ecosystems for crop plants – controlled ecosystems which by nature differ from (but mimic to some extent) the wild environment the crop species originally evolved with. Factors such as climate change and colonization by invasive species alter the dynamics of wild ecosystems and affect the composition of their zoological communities, and many studies are conducted to understand how changing environmental factors will impact natural ecosystems and how these impacts might be mitigated. It seems logical that, by extension, a better understanding of the impact of cultivation on the ecology associated with cranberry plants might allow for the development of pest control techniques based in an understanding of the wild ecosystem dynamics.

# APPENDIX

# SPECIES AND POPULATION DATA

Appendix Table 1: List of invertebrate types collected, including four-letter abbreviation, scientific name, and common name.

| **Code** | **Scientific Classification** | **Common Name** |
|---|---|---|
| SPID | Arachnid | Spider |
| BNLH | *Limotettix vaccinia* | Blunt-nosed leaf hopper |
| SNLH | *Scaphytopius* sp. | Sharp-nosed leaf hopper |
| FIBE | *Cryptocephalus incertus* | Firebeetle |
| FLEA | *Systena frontalis* | Read-headed flea beetle |
| SPBG | *Clastoptera saint-cyri* | Cranberry spittlebug |
| PHTI | *Fulgoromorpha* | Unknown Plant Hopper |
| KATY | *Neoconocephalus* sp. | Common cone-headed katydid |
| DAFL | Odonata | Damselfly |
| MANT | Mantodea | Praying mantis |
| GRHP | Caelifera | Grasshopper (immature) |
| SPTL | Collembola | Springtail |
| CRIC | Gryllinae | Field cricket |
| WPCA | Sphecidae | Unknown wasp (pupa casing) |
| REDB | Coleoptera (red) | Unknown red beetle |
| SPAN | *Itame sulphurea* | Green spanworm |
| BHFW | *Rhopobota naevana* | Blackheaded fireworm |
| FLIS | Diptera 1 | Fly |
| SAWF | *Pristiphora idiota* | Cranberry sawfly |
| WASP | *Sceliphron caementarium* | Black and yellow mud dauber (wasp) |
| DRAG | Anisoptera | Dragonfly |
| OBN | Unknown | Unknown black nymph |
| BEET | Coleoptera | Beetle |
| FGTI | *Gyponana* sp. | Leafhopper (nymph) |
| CSGE | *Cingilia catenaria* | Chain spotted geometer |
| TICK | *Dermacentor variabilis* | Dog tick |
| BRSW | *Ematurga amitaria* | Brown spanworm |
| CRAN | *Anthonomus musculus* | Cranberry weevil |
| MOSQ | *Tipula* sp. | Cranefly |
| BEEN | Anthophila | Bee |
| ANTS | Formicidae | Ant |
| STINK | *Holcostethus*sp. | Shield bug |
| ARMW | *Xylena nupera* | False armyworm |
| SGTH | Unknown | Unknown green insect |
| BRBE | Coleoptera (brown) | Beetle (brown) |
| FLYT | Diptera 2 | Fly 2 |
| GRFY | Diptera 3 | Fly (green) |
| LADY | *Harmonia axyridis* | Multicolored Asian ladybeetle |
| MITE | *Oligonychus ilicis* | Southern red mite |

Appendix Table 2: Population density (individuals per sweep) by type, collected in each bog (ordered East to West).

| **Bog** | **SPID** | **BNLH** | **SNLH** | **FIBE** | **FLEA** | **SPBG** | **PHTI** | **KATY** | **DAFL** | **MANT** | **GRHP** | **SPTL** | **CRIC** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PL4 | 0.2071 | 0 | 0 | 0.19785 | 1.1271 | 0.01785 | 0.01785 | 0.03785 | 0 | 0.01785 | 0.03571 | 0 | 0 |
| PL2 | 0.25273 | 0.13322 | 0.04 | 0.20571 | 0.57989 | 0.158644 | 0.08847 | 0.00847 | 0 | 0 | 0 | 0 | 0 |
| PL7 | 0.04 | 0 | 0 | 0.08 | 0.2 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 |
| PL26 | 0.10909 | 0.04615 | 0 | 0.20675 | 0.16403 | 0.0769 | 0 | 0 | 0 | 0 | 0.0181 | 0.0181 | 0.03333 |
| PL8 | 0.44 | 0.02 | 0 | 0.19 | 0.09 | 0.12 | 0.48 | 0 | 0 | 0 | 0 | 0 | 0.04 |
| PL9 | 0.3473 | 0.20607 | 0.06666 | 0.3571 | 0.07142 | 0.214857 | 0 | 0.0645 | 0 | 0 | 0 | 0 | 0 |
| PL10 | 0.21451 | 0.13951 | 0 | 0.06451 | 0.057258 | 0.62177 | 0.06451 | 0 | 0 | 0 | 0.05 | 0 | 0 |
| PL11 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL27 | 0.4925 | 0.08333 | 0 | 0.16 | 0.1425 | 1 | 0 | 0 | 0 | 0.02083 | 0 | 0 | 0 |
| PL14 | 0.26333 | 0.07 | 0 | 0.03333 | 0 | 0 | 0.1 | 0.09 | 0.05333 | 0 | 0.07 | 0 | 0.03333 |
| PL13 | 0.23666 | 0.02666 | 0.05 | 0.31832 | 0.54663 | 0.01333 | 0 | 0 | 0 | 0 | 0.07333 | 0 | 0.075 |
| PL16 | 0.18571 | 0.394047 | 0.02857 | 0.10666 | 3.79038 | 0.02666 | 0 | 0.025 | 0.05 | 0 | 0.0952 | 0 | 0 |
| PL15 | 0.1825 | 0.125 | 0.0312 | 0.05 | 0.05 | 0.125 | 0 | 0 | 0.0312 | 0 | 0 | 0 | 0 |
| PL17 | 1.1 | 0.15 | 0.04 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL18 | 0.2038 | 0.14356 | 0.12692 | 0 | 0.7715 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL20 | 1.8875 | 0.01538 | 0.02 | 0 | 0 | 0.242307 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL21 | 0.96666 | 0.1 | 0 | 0 | 0 | 0.1 | 0.1 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL24 | 1.8312 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.01923 | 0 | 0 | 0.13461 | 0 |
| PL23 | 1.27923 | 0.0125 | 0 | 0 | 0 | 0.00689 | 0 | 0.0375 | 0.01379 | 0 | 0 | 0 | 0 |
| PL25 | 2.2242 | 0 | 0 | 0 | 0 | 0.03333 | 0.18476 | 0 | 0.0363 | 0 | 0 | 0 | 0 |

Appendix Table 2 (cont): Population density (individuals per sweep) by type, collected in each bog (ordered East to West).

| Bog | WPCA | REDB | SPAN | BHFW | FLIS | SAWF | WASP | DRAG | OBN | BEET | FGT | CSGE | TICK |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PL4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.05357 | 0 |
| PL2 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.20333 | 0 |
| PL7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0.3 | 0 |
| PL9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.06435 | 1.634 | 0.01075 |
| PL10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL11 | 0.06666 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.3541 | 0 |
| PL14 | 0 | 0 | 0 | 0.02 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 |
| PL13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL16 | 0 | 0 | 0 | 0.08452 | 0.02857 | 0 | 0 | 0 | 0 | 0 | 0.00952 | 0 | 0 |
| PL15 | 0 | 0 | 0 | 0.29875 | 0.05 | 0.05 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL18 | 0 | 0 | 0 | 0 | 0.25 | 0.0192 | 0.0192 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL20 | 0 | 0 | 0 | 0.175 | 0.030769 | 0.01538 | 0 | 0.0125 | 0.0625 | 0 | 0 | 0 | 0 |
| PL21 | 0 | 0.05 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL24 | 0 | 0 | 0 | 0.11428 | 0.01428 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL23 | 0 | 0 | 0 | 0.0685 | 0.112 | 0 | 0 | 0 | 0 | 0 | 0.00689 | 0 | 0 |
| PL25 | 0 | 0 | 0.01666 | 0.18636 | 0.6666 | 0 | 0.11666 | 0 | 0 | 0.0181 | 0 | 0 | 0 |

Appendix Table 2 (cont): Population density (individuals per sweep) by type, collected in each bog (ordered East to West).

| Bog | BRSW | CRAN | MOSQ | BEEN | ANTS | STINK | ARMW | SGTH | BRBE | FLYT | GRFY | LADY | MITE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PL4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 |
| PL2 | 0 | 0.00847 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.02857 | 0 |
| PL7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL26 | 0 | 0 | 0 | 0 | 0 | 0.06153 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.27142 | 0 | 0 | 0 |
| PL10 | 0 | 0 | 0 | 0 | 0.025 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL14 | 0 | 0 | 0 | 0 | 0 | 0.06 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL13 | 0 | 0 | 0 | 0.01333 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL16 | 0 | 0 | 0 | 0.0875 | 0 | 0.00952 | 0 | 0.05 | 0 | 0 | 0 | 0 | 0 |
| PL15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL17 | 0 | 0.04 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL18 | 0.1346 | 0.03846 | 0.03846 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| PL24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.05769 | 0.0192 | 0.01923 | 0 | 0 |
| PL23 | 0 | 0 | 0 | 0 | 0 | 0.01333 | 0 | 0 | 0 | 0.12 | 0 | 0 | 0 |
| PL25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.01666 |

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