2016

Host Densities and Parasitism Rates in a Forest Defoliator Across a Rural-Urban Landscape

Abigail J. Nelson
Virginia Commonwealth University

Host densities and parasitism rates in a forest defoliator across a rural-urban landscape

A thesis submitted in partial fulfillment of the requirements for the degrees of Master of Science at Virginia Commonwealth University.

by

Abigail J. Nelson,
B.A., Hartwick College, 2014

Director: Dr. Derek M. Johnson, Assistant Professor, Department of Biology

Virginia Commonwealth University
Richmond, Virginia
August, 2016

Acknowledgement

Table of Contents

Abstract

HOST DENSITIES AND PARASITISM RATES IN A FOREST DEFOLIATOR ACROSS A
RURAL-URBAN LANDSCAPE

By Abigail J. Nelson, M.S.

A thesis submitted in partial fulfillment of the requirements for the degrees of Master of Science
at Virginia Commonwealth University.

Virginia Commonwealth University, 2016

Major Director: Dr. Derek M. Johnson, Assistant Professor, Department of Biology

Fall cankerworm (FCW) outbreaks have recently increased in frequency and intensity in
the mid-Atlantic region of the United States, especially around cities of Charlotte, NC and
Richmond, VA. This study evaluated the effects of two landscape features associated with
urbanization, impervious surface and forest cover, on population patterns of FCW and its
parasitoids across eastern Virginia. Forest cover was positively related to parasitism rates while
impervious surface was positively related to FCW abundance, suggesting that FCW outbreaks
may be amplified in urban areas. FCW abundance declined over the two-year period of this
study, but parasitism rate increased at most sites. Parasitism was highest at sites that experienced
FCW outbreaks first, indicating that parasitoid populations are responding to moth abundances.
It remains to be seen whether this outbreak was an aberrant occurrence, or represents a regime
shift to more frequent defoliation in Virginia, similar to that in North Carolina urban areas.

Introduction

Insect outbreaks are the primary cause of natural disturbance in North American forests (Logan et al. 2003). Defoliation by insects has been shown to decrease tree growth, decrease nitrate and ammonium uptake in trees, and increase the rate of tree crown dieback (Kosola et al. 2001). Successive years of defoliation can cause tree mortality, or increased susceptibility to other natural enemies (Kuhlman 1971, Kegg 1973). Insect outbreaks have similar effects in urban areas as in forests and not only impact the urban ecosystem, but often the aesthetics and economics of urban forests as well. A single species of defoliator insect could cost between $5 million and $63 million a year in damages in a single city (Bigsby et al. 2014). An understanding of what factors drive the timing, frequency, and extent of outbreaks in urban areas is essential to the management of these environments.

The fall cankerworm (*Alsophila pometaria*, Lepidoptera: Geometridae) is a forest defoliator native to much of North America and until recent years, has been particularly understudied, in spite of the fact that its populations commonly undergo local to regional outbreaks in parts of its range. The fall cankerworm is polyphagous, feeding on a broad range of deciduous tree species, and is commonly found on oaks (*Quercus spp.*). Fall cankerworms have a univoltine life-cycle; the adults emerge from pupation from November-February to lay their eggs on tree branches, which will then overwinter and hatch in the spring in synchrony with the bud burst of their hosts (Schneider 1980). The larvae feed for about six weeks and then drop to the soil to pupate. In Virginia, prior to 1981, recorded defoliation from the fall cankerworm never exceeded 4,046 hectares in a year, and was concentrated in the Bull Run Mountains of northeastern Virginia and along ridgetops in western Virginia. However, since then there have been several years in which the annual defoliation exceeded 40,468 hectares, suggesting that fall

cankerworm population dynamics have changed in the last 30 years. In 2012-2014, the fall cankerworm had the largest documented outbreak in Virginia, affecting over 800,000 hectares (Asaro & Chamberlain, 2015). For the first time, the urban areas of Richmond, Fredericksburg, and Fairfax County have records of severe defoliation, bringing the fall cankerworm to the attention of the public. The metropolitan area of Charlotte, NC has been largely affected by the fall cankerworm for the last 20 years with defoliation so severe that the city has implemented a spray program using *Btk* (*Bacillus thuringiensis* var. *kurstaki*) to reduce the effect of defoliation on the environment (Ciesla & Asaro 2013). The recent increase in the frequency and severity of fall cankerworm defoliation in and around the areas of Richmond and Fairfax County, VA begs the question of whether urban landscapes play a role in the outbreaks.

Hairston et al. (1960) proposed the natural enemies hypothesis, stating that populations are regulated and controlled by their natural enemies, including predators and parasitoids. Urbanization may reduce the abundance and diversity of natural enemies, including parasitoids, thus increasing herbivore abundances (Denys & Schmidt 1998, Frankie et al. 1987). Insects that attack the egg stage of the fall cankerworm seem to be a major mortality factor and, thus, could potentially be an important factor in outbreak patterns (Fedde et al. 1973). A guild of egg parasitoids suppresses fall cankerworm populations, the most common being a tiny wasp, *Telenomus alsophilae* (Fedde et al. 1973), which utilizes various lepidopteran hosts (Fedde 1977). Parasitism of fall cankerworm eggs by *T. alsophilae* is more common in the spring, but also has been recorded in the fall (Fedde 1980).

The majority of studies in urban ecology focus on the responses of single taxa or community assemblages, with fewer looking specifically at the effects on trophic interactions. Trophic structure is likely affected by anthropogenic alterations to the environment associated

3

with urbanization, with higher trophic levels being the most affected, as they rely on lower trophic levels for survival. This is evidenced by reduced parasitoid biodiversity and parasitism rates with increasing urbanization (Kruess & Tscharntke 2000). However, parasitoid biodiversity has also been shown to be higher in suburban areas due to an increase in flowering plants in ornamental gardens (Bennet & Gratton 2012), thus the effect of urban and suburban environments on host-parasitoid interactions may be complex. How urbanization affects parasitism rates in forest defoliating insects has received less attention, despite the important role parasitoids play in regulating some hosts (Fedde 1973, Turchin et al. 2003). Changes in the frequency of insect outbreaks are predicted under global change scenarios (Stireman et al. 2005, Ims et al. 2008); therefore, understanding how urbanization may alter these interactions is important to the management of insect pests.

Urbanization is the process whereby natural areas are replaced by human development, resulting in habitat loss and fragmentation (McDonnell et al. 1997). This conversion to anthropogenic land use can decrease the amount of suitable area available to an organism, alter the structure of the vegetation, and create barriers to movement, in turn altering the animal species composition and abundances (McKinney 2008). This new community assemblage often differs drastically from undeveloped adjacent areas (McKinney 2006) because the area of habitat has not only been reduced, but also altered as vegetative cover is replaced with non-biologically active surfaces, such as concrete and asphalt, resulting in high levels of impervious surface cover (Niemela 2001). This increased level of impervious surface alters geomorphological, biogeochemical, and hydrological processes (Arnold & Gibbons 1996). The urban ecosystem often has increased pollutants (Abensperg-Truan & Smith 1999, McDonnell et al. 1997, Niemela

2001), a high proportion of non-native species (Rebele 1994), and elevated temperatures (Kim 1992, Oke 1973) as compared to rural environments.

Urban areas can be up to 10°C warmer than surrounding natural areas (Oke 1973, Kim 1992). This increased temperature, known as an urban heat island, results largely from a reduction in canopy cover (Hart & Sailor 2009) and increased impervious surface (Dale & Frank 2014). Herbivorous pests are often more abundant in urban areas as compared to their rural counterparts (Hanks and Denno 1993, Speight et al. 1998). Urban heat may increase the fecundity of herbivores (Raupp et at. 2010; Dale & Frank 2014), therefore increasing their population growth rate in urban areas. Urban heat islands may affect defoliators and their natural enemies differently. Elevated temperatures and CO_2 have been shown to cause asynchrony between caterpillar and parasitoid development (Dyer et al. 2013, Meineke et al. 2014) and climatic variability decreases parasitoid abundances (Stireman et al. 2005).

Reduced forest cover and increased fragmentation affects insect diversity, abundance, and survival (Kruess & Tsharnkte 2000, Wood et al. 2010, Rotham & Roland 1998) and can alter both the severity and length of insect outbreaks (Swetnam & Lynch 1993, Roland 1993). It has been hypothesized that forest fragmentation disrupts the interactions between herbivores and their natural enemies (Roland 1993). Parasitoids often need larger areas of habitat than their hosts (Kruess & Tsharnkte 2000) and fragmentation may reduce the ability of parasitoids to disperse, thus reducing their efficiency at suppressing host populations (Roland 1993).

In this study, I address whether landscape characteristics associated with urbanization affect host-parasitoid interactions of the fall cankerworm in eastern Virginia. I examined the effects of both forest cover and impervious surface cover on populations of the fall cankerworm and rates of parasitism. I hypothesized that fall cankerworm abundance would be greater, and the

rate of parasitism would be less, in urban areas with low forest cover and high impervious surface cover. I expect these characteristics of urbanization to reduce the rate of parasitism, therefore freeing fall cankerworm populations from suppression, resulting in higher abundances and facilitating more widespread defoliation.

Methods

Study Area

During 2014-2015, 18 study sites were established in mixed hardwood forests in eastern Virginia (Fig. 1) to monitor the abundance of the fall cankerworm. The sites were established in areas of varying urbanization and included state parks, wildlife management areas, city parks, and residential properties, and were divided into four geographical classifications within the eastern part of the state: Richmond, Eastern, Northern, and Western (Table 1).

Field Study Design

To estimate fall cankerworm density, I applied sticky banding material, Tanglefoot™ Insect Barrier, around trunks of oak trees (*Quercus spp.*) at breast height, which trap wingless females as they ascend the trunks to mate and lay eggs. Tree banding was done in the winters of 2014-15 and 2015-16. Four to five trees were banded at each site in each year. Each tree was first wrapped with pipe insulation or cotton batting to prevent the cankerworms from crawling through crevices in the bark under the bands, and then overlaid with roofing felt. A 15 cm wide band of Tanglefoot™ Insect Barrier was applied to the roofing felt to capture crawling females. Females trapped on the bands were counted weekly from December 2014 to March 2015 to ensure that the maximum counts were recorded, and to ensure that our data were not

6

substantially affected by the possible removal of moths from the sticky bands by predators. After finding in 2014-15 that predators rarely removed moths and that peak counts took place in late February, in 2016 I counted females on sticky bands in late February. Fall cankerworm females laid eggs on the roofing felt below the sticky band. The eggs were collected in early spring before either the fall cankerworm or its parasitoids emerged. The eggs were then allowed to hatch in the lab where, under a dissecting scope, I counted the total number of eggs in a mass as well as the number of fall cankerworm larvae and parasitoids that emerged. Parasitoids were sent to the Insect Identification Lab at Virginia Tech for identification. Different *Quercus* trees were sampled in 2015 and 2016 to avoid any effect of trapping females on the second year's abundance. Certain sites were not sampled in the second year because of the logistics of working with private landowners and a limited number of trees on their properties, so new sites were sampled in the same geographical region in order to represent all regions.

In order to quantify herbivory in the year prior to sampling, I collected ~25 fallen oak leaves from around each sample tree haphazardly in December of both years. These leaves were taken back to the lab where the percentage of leaf missing due to herbivory was visually estimated as 0%, 5%, 10%, 20%, 30%, 40% or 50%. Fall cankerworm damage is identifiable as 'shotgun holes' in the leaves. While other herbivore species can make similar damage patterns, fall cankerworms were the primary forest pest in Eastern Virginia during these years, thus, likely caused most of the observed leaf damage. Only oak leaves were analyzed because they are a preferred host tree for the fall cankerworm.

To investigate the effects of landscape characteristics on fall cankerworm abundance and parasitoid attack rate, I used ArcMap GIS to calculate the percentage of different land cover types in the area surrounding each sample tree. GIS land cover data were obtained from the 2011

National Land Cover Database and were used to calculate land cover percentages for impervious surface and forest cover (deciduous and mixed). Land cover was assessed at buffers of 50m, 100m, and 500m around each sample tree. In the spring of 2015, I took field measurements to characterize the forest habitat at each site by identifying species and measuring the distance from each sample tree to the 10 closest neighboring trees with a diameter at breast height $\geq$ 5.0cm (Fig. 4).

Data Analysis

I used generalized linear mixed-effects models (GLMM) to determine the relative effects of forest cover and impervious surface cover on fall cankerworm abundance and the number of parasitoids from an egg mass (Table 5). I used the glmmPQL function in the MASS package R 3.2.4 (for negative binomial GLMMs). Model assumptions were checked by examining the model deviance residuals on the response distribution.

Results

The Richmond sites had the highest impervious surface cover (Fig. 2) and the lowest forest cover (Fig. 3) and these landscape features were weakly negatively correlated ($r^2 = -0.19$) The eastern, western, and northern sites all had very low impervious surface ($< 5\%$, Fig. 2). All geographic regions had similar forest composition in terms of tree density (Fig. 4). Herbivory was quite varied among sites, but was overall greater in the Richmond and northern sites (Fig. 5). The distance to neighboring trees was more variable in the Richmond and northern sites than in the eastern and western sites, which is attributable to the fact that these were the only regions that contained residential properties. The proportion of oaks and conifers around each sample tree

had no effect on fall cankerworm or parasitism and was not included in either model. Herbivory from the previous year was also not predictive of either fall cankerworm abundance or parasitism and was therefore not included in the models.

Fall cankerworm abundance varied across sites with counts on a single tree ranging from 0 to 1,234 females (Fig. 6). The best fit model for fall cankerworm abundance included year, impervious surface, region, and diameter at breast height (DBH) as fixed effects and site as a random effect. The best fit model for parasitism rate included year, mixed forest cover, impervious surface, region, and number of fall cankerworm females as fixed effects and site as a random effect. Forest cover was not included in the model because it did not have an effect on fall cankerworm abundance at a radius of 50m, 100m, or 500m around each sample tree (Table 1). From 2015 to 2016, fall cankerworm abundance decreased at every site sampled (Fig. 6, $p <$ 0.001). Abundance was positively correlated with DBH ($p < 0.001$). Impervious surface cover at a radius of 500m around the sample tree was positively related to fall cankerworm abundance ($p = 0.09$), and a better fit than at 50m or 100m radii. Fall cankerworm abundance was highest in the northern sites than the eastern sites ($p = 0.05$), western sites ($p = 0.04$), and Richmond sites ($p = 0.23$).

The number of egg masses collected from each site ranged from 0-76 and contained 2-268 eggs per egg mass (Table 4). More egg masses were laid in 2014-15, 430 containing a total of 13,854 eggs, compared to 2015-16, 27 containing 1,111 eggs. Parasitoids were confirmed to be *Telenomus alsophilae.* The number of parasitoids that emerged from an egg mass ranged from 0 to 80, and the parasitoid attack rate ranged from 0-100% (Fig. 7). The number of parasitoids in each egg mass was predictably related to the number of eggs in a mass ($p < 0.001$, Table 2). Parasitism rates were greater in 2016 than in 2015 ($p = 0.08$). Impervious surface cover did not

have an effect on the number of parasitoids at a radius of 50m, 100m, or 500m around each sample tree and was therefore not included in the model. Mixed forest cover at a radius of 500m was the best predictor of the number of parasitoids ($p < 0.001$). Parasitism rates were lower in the northern sites than in Richmond ($p < 0.001$), the eastern sites ($p = 0.15$), and the western sites ($p = 0.16$). Parasitism rates were higher in Richmond than in the western sites ($p = 0.06$) and the eastern sites ($p = 0.25$).

Discussion

Landscape features have been shown to affect insect outbreaks (Swetnam & Lynch 1993, Roland 1993, Speight et al. 1998), with an increase in forest cover increasing outbreak duration of forest insects (Roland 1993) and reducing parasitism rates (Roland & Taylor 1997, Kruess & Tscharntke 1994). Fragmentation can uncouple the host population from its natural enemies, allowing them to escape population collapse (Kareiva 1987). In this study, I found no relationship between forest cover and fall cankerworm abundance; however, parasitoid abundance was positively related to forest cover. Parasitoids are often more affected by forest fragmentation and need larger areas of habitat than their hosts (Kreuss & Tsharnkte 2000). In particular, small parasitoids, such as those that attack the egg stage of the fall cankerworm, may be more vulnerable to habitat loss than those that attack the larval and pupal stages of their host (Roland 1993). Forest fragmentation may reduce dispersal ability of parasitoids, thus affecting their ability to aggregate in response to host density (Roland 1993, Roland & Taylor 1997).

Increased impervious surface has been shown to increase forest insect abundance in the scale insect *Melanaspis tenebricosa* (Dale & Frank 2014). In my study, impervious surface was positively related to fall cankerworm abundance. Impervious surface cover causes increased

temperatures and it has been hypothesized that the resulting urban heat island has direct effects on herbivores including increasing their fecundity (Raupp et at. 2010; Dale & Frank 2014), larval development (Meineke et al. 2014), and survival (Meineke et al. 2013). Another hypothesis is that increased temperatures mediate species interactions, including the relationship between herbivores and host plants, and between herbivores and natural enemies. Increased air and surface temperatures can alter timing of phenophases of trees, both advancing spring budburst (Fu et al. 2012, Menzel et al. 2006) and delaying autumn senescence, thus, increasing the growing season (Menzel et al. 2006) and allowing the herbivore more time to feed. This shift in timing has been linked to urban heat (Luo et al. 2007). Fall cankerworm populations are sensitive to timing with bud-burst; if they hatch too early in the spring they will starve, but if they hatch too late the nutritional quality of the leaves has deteriorated (Schneider 1980). While I detected no effect of impervious surface on parasitism rates in this study, others have shown that increased temperatures associated with impervious surface cover may disrupt interactions between herbivores and their natural enemies by disproportionally affecting their development (Dyer et al. 2013, Meineke et al. 2014).

Defoliation patterns show that recent fall cankerworm outbreaks began in Richmond in earlier years than in other areas of the state. Fall cankerworm outbreaks reached their peak in the Richmond area in 2012, and progressed northward over the next two years. Defoliation was not classified as heavy or severe in the northern sites of this study until the spring of 2014 (Chris Asaro, Virginia Department of Forestry, *unpublished*). This is consistent with my finding that fall cankerworm abundance was highest in the northern sites in 2015 and 2016; the population cycle started later there than in Richmond. Natural enemy population densities often lag behind that of their prey/host and do not peak in abundance until their prey/host population is in decline

(Turchin et al. 1999, Turchin et al. 2003), which is consistent with my finding of lower parasitism in the northern sites in this study. The Richmond sites had the highest parasitism rates, likely because this region experienced fall cankerworm outbreaks beginning in 2012, therefore allowing parasitoid populations to increase by 2015 and 2016. Thus, this regional effect of parasitoid abundance may be related to timing of outbreak rather than to urbanization.

Vegetation structure has been shown to affect the frequency and intensity of forest insect outbreaks (Dalin et al. 2009, Dale & Frank 2014); for example, vegetation diversity and structural complexity are negatively related to outbreaks in scale insects (Dale & Frank 2014). Urban environments often have lower vegetative diversity and complexity, thus, may also be a driving factor in fall cankerworm outbreaks – as in Charlotte and Raleigh NC, and more recently in Richmond and Fairfax County, VA. The intense defoliation experienced in Charlotte, NC may be a product of an abundance of willow oaks, a preferred host of the fall cankerworm, combined with a lack of vegetation complexity (Ciesla & Asaro 2013). In contrast, my simple measures of forest composition did not explain the differences in fall cankerworm abundance nor parasitism rates across eastern Virginia in this study. The proportion of oaks and conifers around each sample tree had no effect on fall cankerworm or parasitism rates, and the mean distance to neighboring trees was similar for each region.

Fall cankerworm outbreaks have increased in severity across the mid-Atlantic over the last 20-30 years, causing large amounts of defoliation in metropolitan areas of North Carolina (Nounkoun et al. 2014) and more recently in Virginia (Asaro & Chamberlayne 2015). The outbreaks around Charlotte, NC have caused annual defoliation for the last 20 years (Ciesla & Asaro 2013). Whether Virginia is experiencing a similar regime shift is unclear. Fall cankerworm abundance declined from 2014-15 to 2015-16 in this study, with no more than 300

female moths on a single tree in 2016, as compared to a maximum of 1,234 in 2015. This decline is synchronized with an observed reduction in fall cankerworm counts in 2015-16 compared to previous years in North Carolina (Steven Frank, North Carolina State University, *pers. comm.*), suggesting the decline is a geographic pattern. Whether it is part of a normal host-parasitoid cycle or is attributable to unfavorable weather is unclear. My study showed that annual effects on fall cankerworm abundance were much greater than effects of landscape characteristics. This may be due to unusual weather patterns in 2015-16. The winter of 2015-16 was unusually warm, with mean December temperatures reaching record highs across the eastern United States. Both Virginia and North Carolina experienced mean temperatures 5.5°C over the monthly average (NOAA National Centers for Environmental Information). Little is known about how temperature affects the fall cankerworm lifecycle, but if this moth is like some other temperate univoltine insects, deviations in weather can create phenotypic mismatches with available food (Visser & Holleman 2001, Dewar & Watt 1992) and increase mortality rates in pupae (Mercader & Scriber 2008). The late onset of cold weather may have interrupted their normal lifecycle, resulting in an increase in mortality. Fall cankerworm eggs may be more susceptible to parasitism during warm winters since parasitism occurs in both the winter and spring, but is more common in spring when temperatures are warmer (Fedde 1980).

The increase in the severity of fall cankerworm outbreaks in and around urban areas of the mid-Atlantic begs the question: is urbanization playing a role? This study suggests that impervious surface cover affects fall cankerworm populations while forest cover affects populations of their parasitoids. How these combine to affect fall cankerworm outbreaks across an urban gradient is unknown, and is perhaps complex. This study showed that annual effects were more important than landscape features, and although this could be part of a natural

outbreak cycle, it may also be that the fall cankerworm is sensitive to changes in weather patterns. It remains to be seen whether the fall cankerworm outbreaks in eastern Virginia were an anomaly or represent a regime shift in population patterns more similar to those in North Carolina. Regardless, increasing global change, including increasing temperatures and increasing forest fragmentation, may play a role in the frequency and intensity of future fall cankerworm outbreaks in the region.

Literature Cited

Abensperg-Truam, M. and G.T. Smith. How small is too small for small animals? Four terrestrial arthropod species in different-sized remnant woodlands in agricultural Western Australia. *Biodiversity and Conservation.* 8:709-726.

Arnold, C. L. Jr. and C. J. Gibbons. 1996. Impervious surface coverage: The emergence of a key environmental indicator. *Journal of American Planning Association.* 62(2):243-258.

Asaro, C. and L.A. Chamberlain. 2015. Outbreak history (1953-2014) of spring defoliators impacting oak-dominated forests in Virginia, with emphasis on gypsy moth (*Lymantria dispar* L.) and fall cankerworm (*Alsophila pometaria* Harris). *American Entomologist.* 61(3):174-185.

Bennet, A.B. and C. Gratton. 2012. Local and landscape scale variables impact parasitoid assemblages across an urbanization gradient. *Landscape and Urban Planning*. 104:26-33.

Bigsby, K. M., M. J. Ambrose, P. C. Tobin and E. O. Sills. 2014. The cost of gypsy moth sex in the city. *Urban Forestry & Urban Greening.* 13:459-468.

Ciesla, W.M. and C. Asaro. 2013. Fall cankerworm. *USDA Forest Service, Forest Insect and Disease Leaflet*. 182:8.

Dale, A.G. and S. D. Frank. 2014. Urban warming trumps natural enemy regulation of herbivorous pests. *Ecological Applications.* 24(7):1596-1607.

Dalin, P., O. Kindvall, and C. Björkman. 2009. Reduced population control of an insect pest in managed willow monocultures. *PLoS One.* 4(5): e5487.

Denys, C. and H. Schmidt. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. *Oecologia,* 113:269-277.

Dewar, R.C. and A.D. Watt. 1992. Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia*. 89:557-559.

Dyer, L. A., L. A. Richards, S. A. Short, and C. D. Dodson. 2013. Effects of CO_2 and temperature on tritrophic interactions. *PLoS ONE*. 8(4): e62528.

Fedde, G. F., C. L. Morris, and A. T. Drooz. 1973. Delayed parasitism of fall cankerworm eggs in Virginia. *Environmental Entomology.* 2(6):1123-1125.

Fedde, G. F. 1977. A laboratory study of egg parasitization capabilities of *Telenomus*

alsophilae. Environmental Entomology. 6(6):773-776.

Fedde, G.F. 1980. Spring parasitism of fall cankerworm eggs in northern Georgia by *Telenomus alsophilae* (Hymenoptera: Scelionidae). *Journal of the Georgia Entomological Society.* 15(2):199-206

Frankie, G. W., J. W. Brewer, W. Cranshaw, and J. F. Barthell. 1987. Abundance and natural enemies of the spindle gall midge, *Pinyonia edulicola* Gagné, in natural and urban stands of pinyon pine in Colorado (Diptera: Cecidomyiidae). *Journal of the Kansas Entomological Society,* 60(1): 133-144.

Fu, Y.H., M. Campioli, G. Deckmyn, and I.A. Janssens. 2012. The impact of winter and spring temperatures on temperate tree budburst dates: Results from an experimental climate manipulation. *PLoS One.* 7(10): e47324.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist*, 94:421-425.

Hart, M. A. and D. J. Sailor. 2009. Quantifying the influence of land-use and surface characteristics on spatial variability in the urban heat island. *Theoretical and Applied Climatology.* 95: 397-406.

Hanks, L. M. and R. F. Denno. 1993. Natural enemies and plant water relations influence the disturbance of an armored scale insect. *Ecology,* 74(4): 1081-1091.

Ims, R.A., J. Henden, and S.T. Killengreen. 2008. Collapsing population cycles. *Trends in Ecology and Evolution.* 23(2):79-86.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature.* 326:388-390.

Kegg, J. D. 1973. Oak mortality caused by repeated gypsy moth defoliations in New Jersey. *Entomological Soceity of America,* 66(3): 639-641.

Kim, H.H. 1992. Urban heat island. *International Journal of Remote Sensing.* 13(12):2319-2336.

Kosola, K. R., D. I. Dickmann, E. A. Paul and D. Parry. 2001. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. *Oecologia* 129:65-74.

Kruess, A. and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. *Science.* 264: 1581-1584.

Kruess, A. and T. Tscharntke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium. Oecologia.* 122:129-137.

Kuhlman, H. M. 1971 Effects of insect defoliation on growth and mortality of trees. *Annual Review of Entomology.* 16:289-324.

Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment.* 1(3):130-137.

Luo, Z., O.J. Sun, Q. Ge, W. Xu, and J. Zheng. 2007. Phenological responses of plants to climate change in an urban environment. *Ecological Research.* 22(3): 507-514.

McDonnell, M. J., S. T. A. Pickett, P. Groffman, P. Bohlen, R. V. Pouyat, W. C. Zipperer, R. W. Parmelee, M. M. Carreiro, and K. Medley. 1997. Ecosystem processes along an urban-rural gradient. *Urban Ecosystems.* 1:21-36.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation.* 127:247-260.

McKinney, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* 11:161-176.

Meineke, E.K., R.R. Dunn, J.O. Sexton, and S.D. Frank. 2013. Urban warming drives insect pest abundance on street trees. *PLoS ONE.* 8(3): e59687.

Meineke, E.K., R.R. Dunn, and S.D. Frank. 2014. Early pest development and loss of biological control are associated with urban warming. *Biology Letters.* 10:10-13.

Menzel A., T.H. Sparks, N. Estrella, E. Kosh, A. Asa, R. Ahas, K. Alm-Kübler, P. Bissoli, O. Braslavská, A. Briede, F.M Chmielewski, Z. Crepinsek, Y. Curnel, Å. Dahl, C. Deflia, A. Donnelly, Y. Filella, K. Jatczak, F. Mage, A. Mestre, Ø. Nordli, J. Peñuelas, P. Pirinen, V. Remišová, H. Scheifinger, M. Striz, A. Susnik, A.J.H, Van Vliet, F. Wielgolaski, S. Zach, and A. Zust. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology.* 12:1969-1976.

Mercader, R.J. and J.M. Scriber. 2008. Asymmetrical thermal constraints on the parapatric species boundaries of two widespread generalist butterflies. *Ecological Entomology.* 33(4):537-545.

Niemela, J. 2001. *Urban Ecology: Patterns, Processes, and Applications*. (ed. J. Niemela, J. H. Breuste, G. Guntenspergen, N. E. McIntyre, T. Elmqvist and P. James). Oxford University Press.

NOAA National Centers for Environmental Information, State of the Climate: National Overview for December 2015, published online January 2016, retrieved on July 17, 2016 fromhttp://www.ncdc.noaa.gov/sotc/national/201512.

Nounkoun, C., G. Bryant, and S.D. Frank. 2014. The effect of sticky bands on cankerworm abundance and defoliation in urban tress. *Arboriculture and Urban Forestry.* 40:135-142.

Oke, T. 1973. City size and urban hear island. *Atmospheric Environment.* 7:769-779.

Raupp M.J., P.M. Shrewsbury, D.A. Herms. 2010. Ecology of herbivorous arthropods in urban landscapes. *Annual Review of Entomology* 55:19–38.

Rebele, F. 1994. Urban ecology and special features of urban ecosystems. *Global Ecology and Biogeography Letters.* 4(6):163-187.

Roland, J. 1993. Large-scale forest fragmentation increases duration of tent caterpillar outbreak. *Oecologia.* 93:25-30.

Roland, J. and P.D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature.* 386 (6626):710-713.

Rotham, L.D. and J. Roland. 1998. Forest fragmentation and colony performance of forest tent caterpillar. *Ecography.* 21:383-391.

Schneider, J. C. 1980. The role of parthenogenesis and female aptery in microgeographic, ecological adaptation in the fall cankerworm, *Alsophila pometaria* Harris. *Ecology,* 61(5): 1082-1090.

Speight, M. R., R. S. Hails, M. Gilbert and A. Foggo. 1998. Horse chestnut scale (*Pulvinaria regalis)* (Homoptera: Coccidae) and urban host tree environment. *Ecology,* 79(5): 1503-1513.

Stireman, J. O. III, L. A. Dyer, D. H. Janzen, M. S. Singer, J. T. Lill, R. J. Marquis, R. E. Ricklefs, G. L. Gentry, W. Hallwachs, P. D. Coley, J. A. Barone, H. F. Greeney, H. Connahs, P. Barbosa, H. C. Morais, and I. R. Diniz. 2005. Climatic unpredictability and parasitism of caterpillars: Implications of global warming. *Proceedings of the National Academy of Sciences.* 102(48): 17384-17387

Swetnam, T.W. and A.M. Lynch. 1993. Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*. 63(4):339-424.

Turchin, P., A.D. Taylor, and J.D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science.* 285:1068-1071.

Turchin, P., S.N. Wood, S.P Ellner, B.E. Kendall, W.W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C.J. Briggs. 2003. Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. *Ecology.* 84(5):1207-1214.

Visser, M.E. and J.M. Holleman. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society B:Biological Sciences.* 268:289-294.

Wood, D.M., D. Parry, R.D. Yanai, and N.E. Pitel. 2010. Forest fragmentation and duration of forest tent caterpillar (*Malacosoma disstria* Hüber) outbreaks in northern hardwood forests. *Forest Ecology and Management.* 260(7):1193-1197.

Tables

Table 1. Geographic coordinates of each sampling sites classified into their geographical regions. WMA stands for Wildlife Management Area.

Site	Region	Latitude	Longitude
Bryan Park	Richmond	37.5889N	77.4777W
Forest Hill Park	Richmond	37.5175N	77.4722W
Pocahontas State Park	Richmond	37.3406N	77.5794W
Bon Air Residence	Richmond	37.5285N	77.5743W
James River Park	Richmond	37.5236N	77.4712W
Mechanicsville Residence	Richmond	37.6577N	77.2353W
Chickahominy WMA	Eastern	37.3156N	76.8902W
York River State Park	Eastern	37.4026N	76.7183W
VCU Rice Rivers Center	Eastern	37.3306N	77.2085W
Caledon State Park	Northern	38.3313N	77.1453W
Pettigrew WMA	Northern	38.2104N	77.2754W
Woodford Residence	Northern	38.2239N	77.3557W
Mattaponi WMA	Northern	38.0600N	77.3881W
Bear Creek Lake State Park	Western	37.5312N	78.2774W
Amelia WMA	Western	37.4653N	77.9135W
Powhatan State Park	Western	37.6738N	77.9305W
Powhatan WMA	Western	37.5601N	77.9627W
Hardware River WMA	Western	37.7583N	78.4119W

Table 2. Results of the best fit generalized linear mixed model explaining fall cankerworm abundance.

	Estimate	SE	t	P
Intercept	1.03388	1.0638	0.972	0.333
Year	-1.25025	0.2482	-5.037	**< 0.001**
DBH	0.04595	0.0093	4.966	**< 0.001**
Impervious Surface	0.01698	0.0098	1.736	0.085
East	-1.48084	1.1974	-1.237	0.237
North	1.49310	1.2008	1.243	0.234
West	-1.20823	0.9966	-1.212	0.246

Table 3. Results of the best fit generalized linear mixed model explaining parasitism rates.

	Estimate	SE	t	P
Intercept	-0.56621	0.3599	-1.573	0.117
Eggs	0.02799	0.0019	14.637	**< 0.001**
Year	0.68005	0.3840	1.771	0.077
Females	0.00091	0.0006	1.622	0.106
Forest Cover	0.02238	0.0052	4.279	**< 0.001**
East	-0.75477	0.6246	-1.208	0.250
North	-1.90788	0.5231	-3.647	**< 0.001**
West	-1.04664	0.4982	-2.101	0.058

Table 4. The total number of eggs and egg masses collected from each site over the two-year sample period from 2015 to 2016. Each site is classified by geographic region. Sites with no data were not sampled for one year, due to a limited availability of sample trees.

Site	Region	2015 Eggs Masses (Total Eggs)	2016 Eggs Masses (Total Eggs)
Bryan Park	Richmond	76 (2687)	5 (93)
Forest Hill Park	Richmond	37 (1050)	5 (295)
Pocahontas State Park	Richmond	–	0 (0)
Bon Air Residence	Richmond	5 (270)	–
James River Park	Richmond	52 (2969)	0 (0)
Mechanicsville Residence	Richmond	64 (1376)	–
Chickahominy WMA	Eastern	0 (0)	2 (35)
York River State Park	Eastern	0 (0)	1 (26)
VCU Rice Rivers Center	Eastern	12 (477)	2 (100)
Caledon State Park	Northern	10 (312)	7 (281)
Pettigrew WMA	Northern	22 (468)	1 (24)
Woodford Residence	Northern	42 (1744)	–
Mattaponi WMA	Northern	–	4 (257)
Bear Creek Lake State Park	Western	0 (0)	0 (0)
Amelia WMA	Western	36 (1482)	0 (0)
Powhatan State Park	Western	22 (551)	0 (0)
Powhatan WMA	Western	22 (468)	0 (0)
Hardware River WMA	Western	–	0 (0)

Table 5. A complete list of predictors for the generalized linear models explaining fall cankerworm abundance and parasitism rates. Only predictors with a p-value > 0.15 were used in the best fit model. Predictors denoted with * were only used in the model used to explain parasitism rates. Proportion of *Quercus spp.* and the proportion of conifers was out of the ten closest neighboring trees around each sample tree.

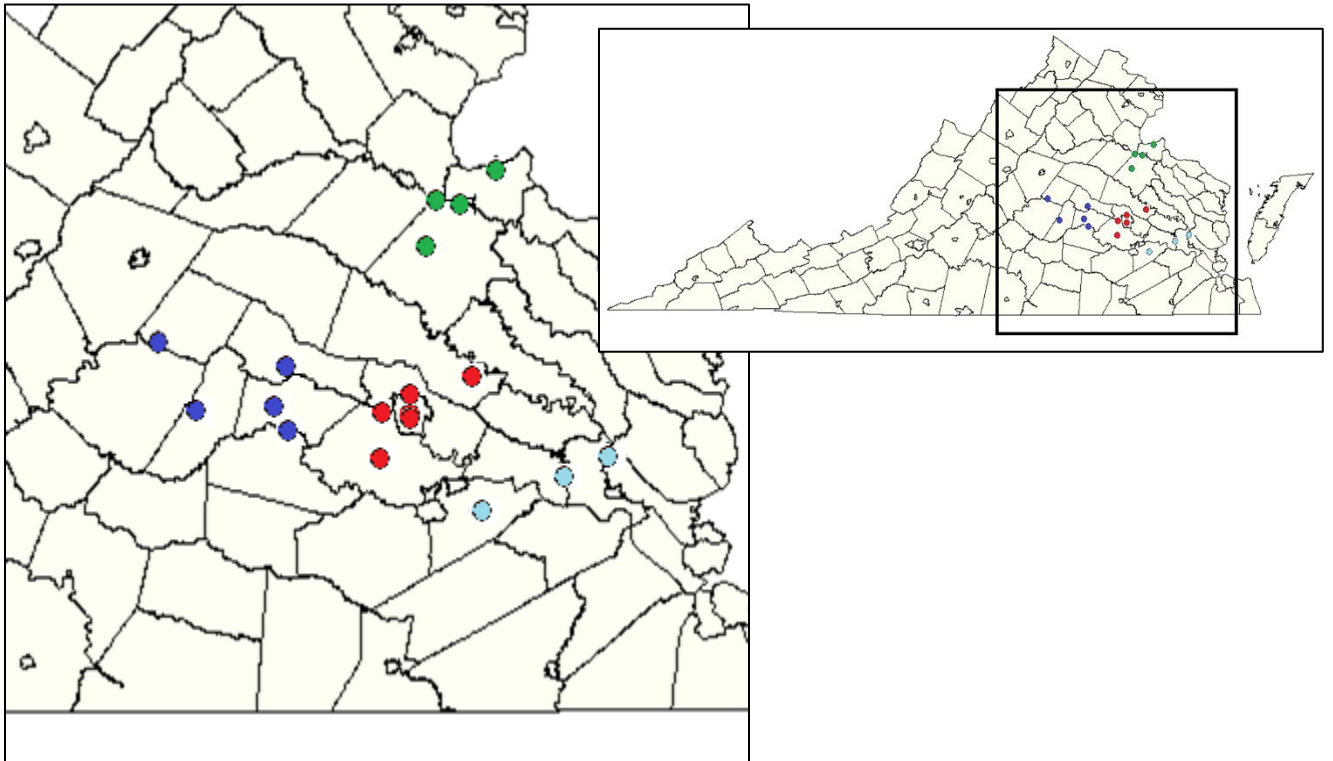| Predictor |
|---|
| Year |
| DBH |
| Impervious Surface |
| Forest Cover |
| Region |
| Site (random effect) |
| Herbivory of previous year |
| Proportion of *Quercus spp.* |
| Proportion of conifers |
| Eggs per mass* |
| Fall cankerworm females* |

Figures

Figure 1. A map of Virginia displaying the locations of the 18 sample sites. The five Western sites are dark blue, the six Richmond sites are red, the four Northern sites are green, and three Eastern sites are light blue.
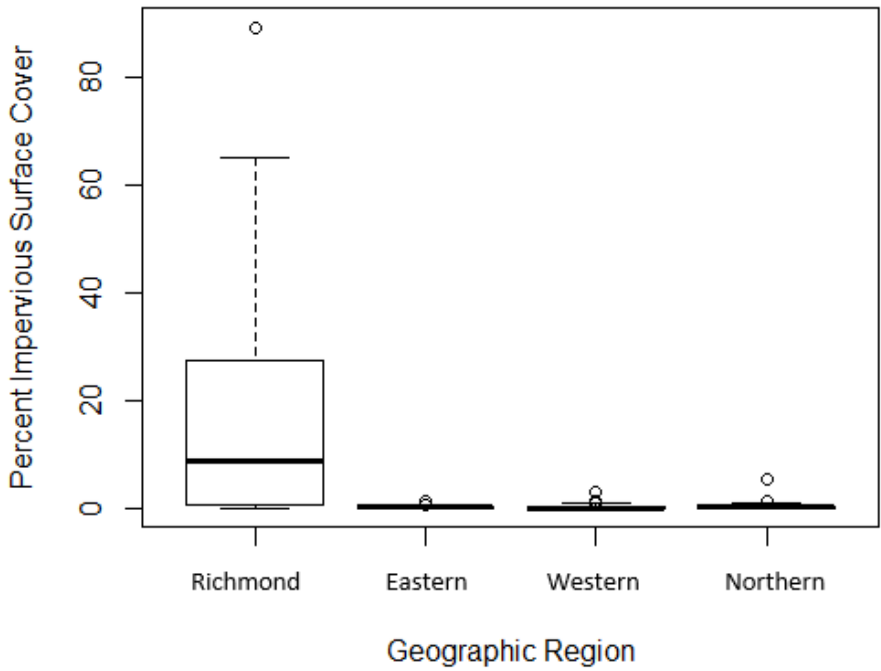
Figure 2. Median (± 1 sd) percent impervious surface cover within a radius of 500m around each sample tree at each geographical region, calculated in ArcMap GIS.
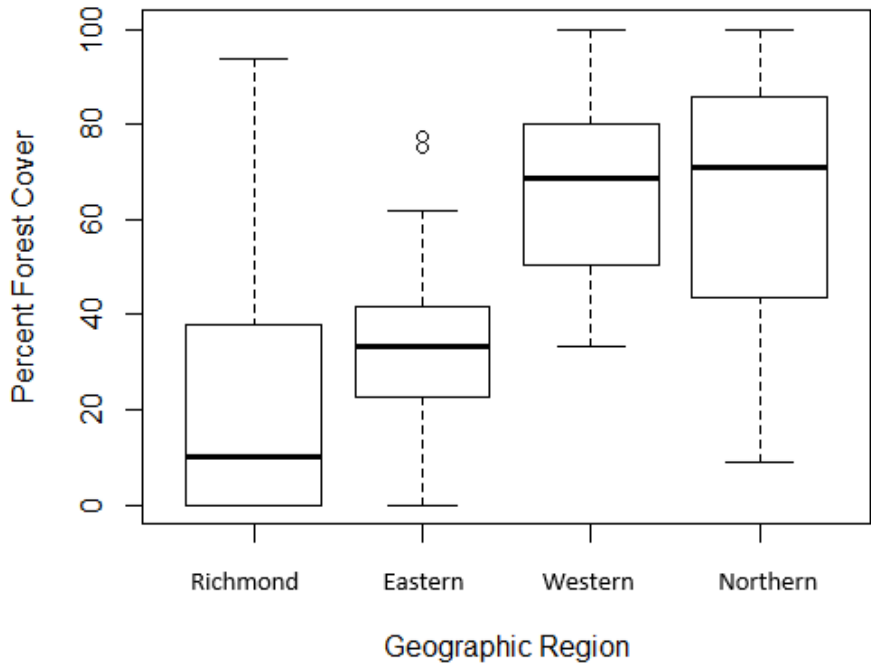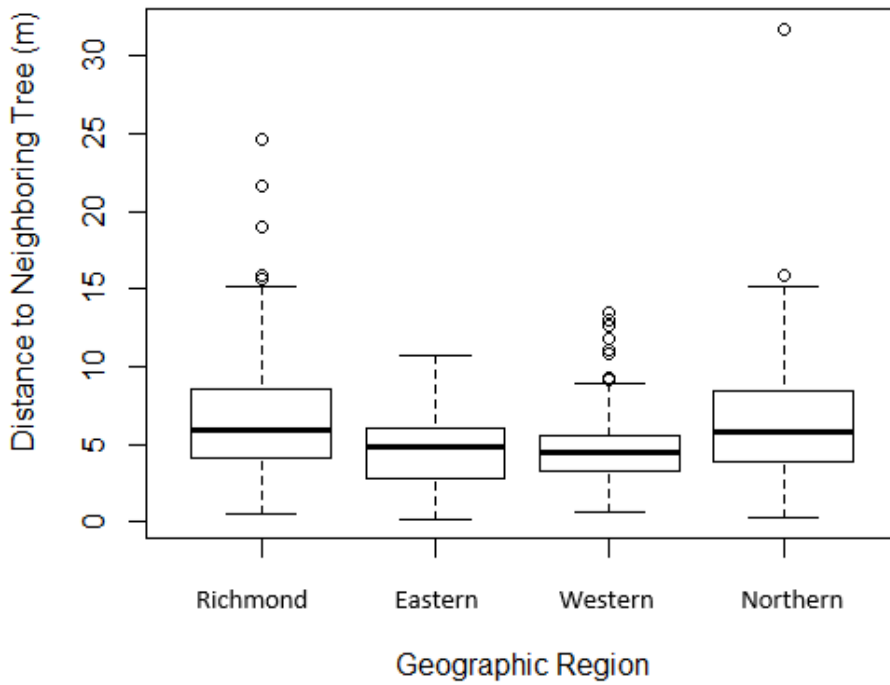

Figure 3. Median (± 1 sd) percent forest cover within a radius of 500m around each sample tree at each geographical region, calculated in ArcMap GIS.

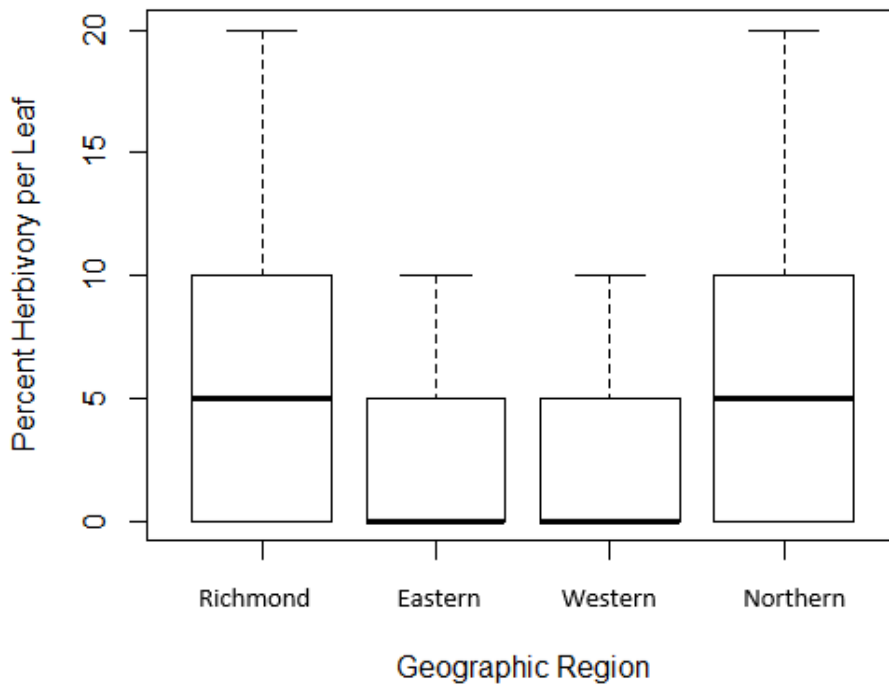Figure 4. Median (± 1 sd) distance to neighboring tree ≥ 5.0cm DBH from sample tree at each geographical region.

Figure 5. Median (± 1 sd) percent herbivory from the previous year of fallen oak leaves around each sample tree at each geographical region.
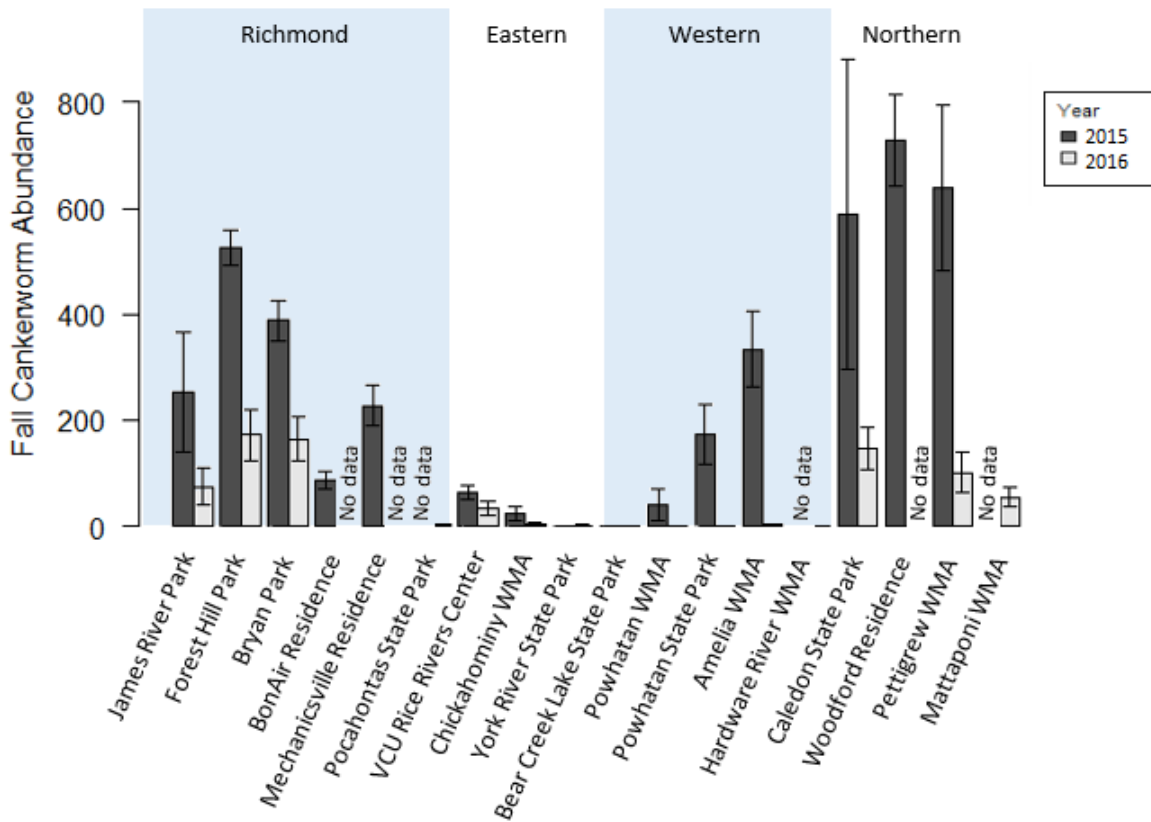
Figure 6. Mean (± 1 se) number of female fall cankerworms caught per tree at each site. Bars are ordered by region from left to right as follows: Richmond, Eastern, Western and Northern. Different *Quercus* trees were sampled in 2015 and 2016 to avoid any effect of trapping females on the second year's abundance, so due to a limited availability of trees, some sites were not sampled. 'No data' refers to these sites that were not sampled for one year.
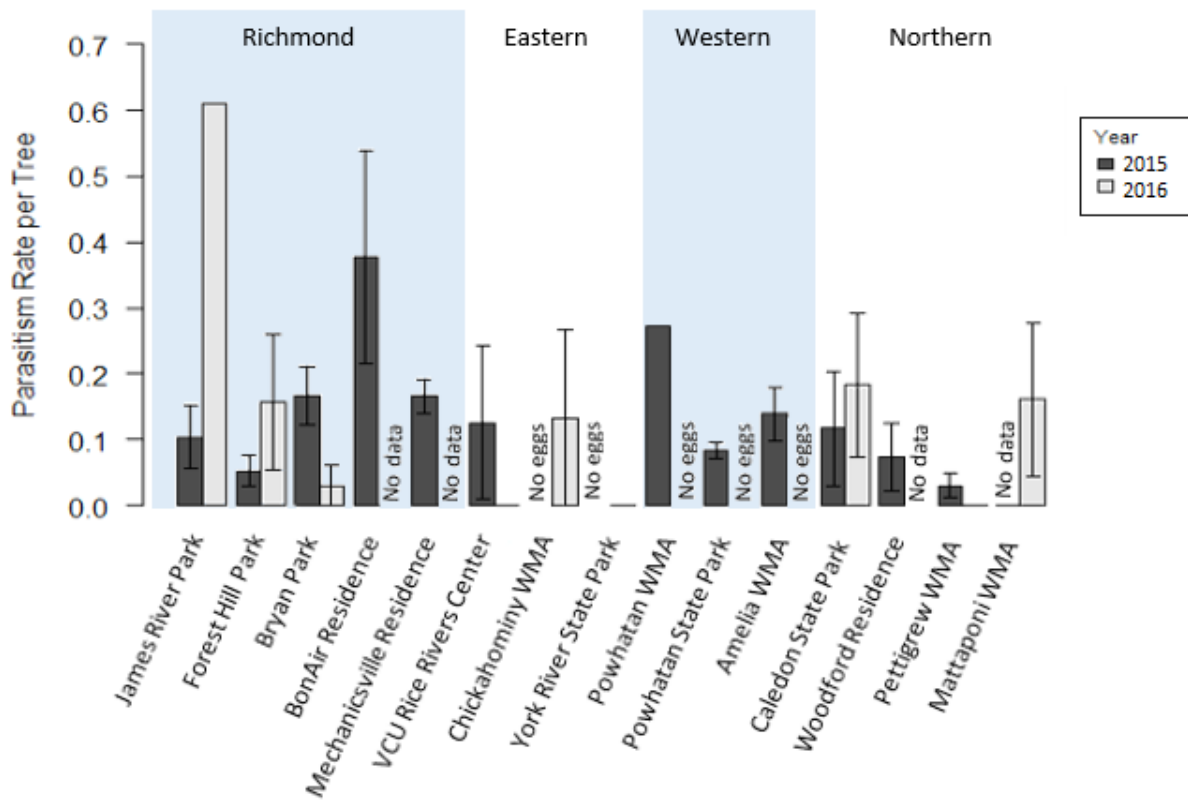
Figure 7. Mean (± 1 se) proportion of eggs parasitized at each tree at each site. Bars are ordered by region from left to right as follows: Richmond, Eastern, Western and Northern. 'No data' refers to sites that were not sampled for one year, whereas 'No eggs' refers to sites that did not have any fall cankerworm eggs available for collection.