

GARDENING FOR WILDLIFE: A COMPARISON OF NATIVE PLANT CULTIVARS AND WILD-  
PROPAGATED PLANTS AS FOOD SOURCES FOR HERBIVOROUS INSECTS

by

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(Under the Direction of J. M. AFFOLTER)

ABSTRACT

Concerns over declining biodiversity in suburban areas have prompted some homeowners to incorporate more native plants into their landscapes. However, it is unknown whether the native plants that are commercially available, typically cultivated varieties (cultivars) of a single genotype, are the ecological equivalents of the local, wild-type plants. We compared the hemipteran communities supported by cultivars and wild-type plants for four species of native ornamental plants. Insect community composition, but not overall diversity, differed between cultivars and wild-type plants for each of the plant species. Other parameters, such as total insect abundance and insect biomass, also differed between cultivars and wild-type plants, but the direction of the difference changed over time and was not consistent among plant species. These data suggest that the source of plant material can affect organisms that depend on the plants for food, but overall, cultivars fulfill similar ecological roles as wild-type plants.

INDEX WORDS: Native plants, Cultivars, Wildlife value, Biodiversity, Insect communities, Hemiptera, Plant-insect interactions, Leafhoppers, Herbivorous insects

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## CHAPTER 1

### INTRODUCTION AND LITERATURE REVIEW

As the population of the United States expands, more and more land is converted for residential use. As of 2007, approximately 61 million acres were classified as urban use, and 103 million acres were classified as rural residential use in the United States (Nickerson et al. 2011). Landscaping in residential areas typically does not reflect the natural plant community that would exist in that area before development; in fact, urban areas are associated with a replacement of native flora by exotic species (McKinney 2006), many of which also invade surrounding areas (Gavier-Pizarro et al. 2010). Most of the exotics that replace natives in landscapes are purchased through the plant trade industry for their aesthetic value (Mack and Lonsdale 2001). This prevalence of non-native vegetation in residential landscapes has recently been cited as a cause for the loss of biodiversity in suburban areas. Tallamy (2004) suggested that exotic plants might support fewer native herbivorous insects and insect species than native plants; because insects are an important component in food webs, a decline in the amount of insect biomass available within an ecosystem could cause a corresponding decline in organisms in higher trophic levels. If this is true, exotics could be considered inferior to natives in providing one of the most important ecosystem functions of plants – transferring energy from the sun to higher trophic levels (Tallamy 2004; Tallamy and Shropshire 2009; Burghardt et al. 2010).

This chapter reviews the literature that provides the theoretical basis for predicting that exotic plants are inferior food plants for native insects, summarizes empirical research supporting this prediction, and introduces the primary research question of this thesis – are cultivated varieties (cultivars) of native plants effective food plants for native insects? Chapter 2 summarizes preliminary data that were collected in 2013, Chapter 3 presents the results of the entire experiment that was conducted in 2014, and Chapter 4 provides concluding remarks.

## **Natives vs. Exotics: Theory and Empirical Evidence**

What characteristics of exotic plants might predict their ability (or inability) to host herbivorous insects in regions where they are introduced for ornamental use? All other considerations aside, the exotic plants used ornamentally in residential landscapes are part of a subset of plants potentially predisposed to deterring herbivory. That is, ornamental plants and other plants used in landscaping (including exotics) are plant species that have been selected by humans specifically because they have few disease or insect problems (Dirr 1998). The insects that cause problems are pest species that become very abundant and either defoliate or cause other types of unsightly damage to plants. However, most herbivorous insect species do not cause noticeable feeding damage and are not considered major pests, so this alone does not explain why exotic plants are expected to host fewer insect species than natives.

A more compelling explanation for why exotic ornamentals do not host as many herbivorous insects as native plants comes from plant-insect interaction theory. Most insect herbivores have evolved as specialists on a narrow group of plants (Bernays and Graham 1988). Here, a specialist is defined as an insect species feeding on plants in three or fewer families. One theory predicts this specialization is a result of the variable leaf chemistry among plant groups. The variation in leaf chemistry is expressed through different assemblages of secondary metabolites, which are known to deter herbivory by insects (Fraenkel 1959). Specialized herbivorous insects have co-evolved with groups of plants that contain similar leaf chemistry by developing physiological adaptations to deal with the secondary metabolites that are toxic to most other herbivores (Ehrlich and Raven 1964). Even generalist insect species, which may have many different species of plants recorded as hosts across their entire geographic ranges, appear to feed on a small subset of these species at the local scale (e.g. Tallamy et al. 2010). This suggests that a given population of a generalist species may have feeding habits similar to that of a specialist species. Because of the co-evolutionary history between herbivorous insects and their host plants, exotic plants are expected to escape the herbivores of their native range and support few insect species in the introduced range. This process is often used to explain how exotics become invasive and is referred to as the enemy release hypothesis (Keane and Crawley 2002).



A substantial amount of empirical evidence has accumulated that supports the prediction that exotic plants support fewer native herbivorous insects than do native plants. Much of this work compared woody ornamental plants with native woody plants. The exotic woody plants used ornamentally in suburban landscapes fall into two categories: those with a close native relative (in the same genus) and those without a close native relative. Several studies have compared these two groups with natives, using parameters such as total insect abundance, total species richness, etc. to measure a plant's value as a food plant for herbivorous insects. Some focused on many orders of herbivorous insects and others focused on a narrow taxonomic group. Zuefle et al. (2008) compared 15 species of native woody plants with congeneric and non-congeneric exotics in terms of the insect biomass and species richness supported. Pooled across plant species, native plants supported more insect biomass than exotic congeners and non-congeners. However, there were no differences in insect species richness among the three groups. Pairwise comparisons of insect biomass were also made between natives and exotics from the same genus. Despite the overall difference between natives and exotic congeners, differences for individual genera were not consistently in favor of natives. In the first year of the study, seven native species supported more insect biomass than their corresponding exotic relatives, but for four other species, the exotics actually supported more insect biomass; there were no differences for the remaining four species. The results during the second year were similar.

A subsequent study using many of the same plant species and a similar design (natives vs. exotic congeners vs. exotic non-congeners) built on the initial results of Zuefle et al. (2008). In this case, 17 plant species were used in the congeneric comparisons and 13 plant species were used in the non-congeneric comparisons, and these were divided into separate experiments (i.e. spatially distinct). Part of the study focused exclusively on lepidopteran larvae and measured abundance, species richness, and the composition of the insect community (Burghardt et al. 2010). In addition to measuring the total abundance and species richness of lepidopterans, the authors also divided the insects into specialists and generalists and analyzed those groups separately. During the first year of the study, native plants supported more species and higher biomass of both specialists and generalists in the non-congeneric

comparisons, but only the abundance and species richness of specialists were higher in the congeneric comparisons; there were no differences in species richness or abundance of generalists between natives and their exotic congeners. However, by the second year of the study, native plants supported higher abundance and richness of both specialists and generalists in both the congeneric and non-congeneric comparisons. Rarefaction curves revealed that the difference in the number of insect species supported between native plants and exotics was much larger in the non-congeneric comparisons than in the congeneric comparisons. Analyses of the composition of the insect community showed that natives and their exotic relatives (i.e. congeners) harbored similar species of insects. In the non-congeneric comparisons, however, the insect community composition was not related to plant phylogenetic relationships; that is, the dendrogram of the plant species based on their insect communities did not match the dendrogram of the plant species based on their phylogenies. Counter to expectations, very few specialists were found in either study. In Zuefle et al. (2008), only 6 of the 57 most abundant species were specialists, and in Burghardt et al. (2010), specialists made up a much smaller proportion of the insect species found and overall abundance than did generalists.

The other part of the study focused not just on lepidopteran larvae, but on all of the different orders of herbivorous insects (Burghardt and Tallamy 2013). The analyses were broken up by feeding guild and life stage of the insects and measured insect abundance (eggs and adults) and diversity (immatures and adults). Number of eggs laid and abundance of internal feeders (leaf miners and gallers) were pooled across all three sampling dates, and abundance of chewing insects and phloem-, mesophyll-, and xylem-feeding insects was analyzed separately by sampling date. More eggs were laid on native plants than on exotic plants, but the difference between natives and congeners was not as large as the difference between natives and non-congeners. Similarly, more internal feeders were found on native plants than on exotic congeners or non-congeners. The results for the other feeding guilds were not as consistent. The abundance of chewing insects was higher on native plants than non-congeners on all three sampling dates, but was higher on natives versus congeners on only one sampling date; there were no differences between natives and congeners on the other two sampling dates. For the abundances of

phloem-, mesophyll-, and xylem-feeding insects, the only difference that was observed was for phloem-feeding insects, and this difference was observed on only one of the three sampling dates. In this instance, native plants supported more phloem-feeders than did exotic congeners or non-congeners. The analyses of insect diversity revealed several patterns. Species accumulation curves showed that native plants consistently supported more insect species than exotic plants in both congeneric and non-congeneric comparisons. The difference between natives and exotics was larger in the non-congeneric comparisons, and immature insects were affected more than adults. Renyi diversity plots (a type of analysis that considers several levels of diversity simultaneously, from species richness to species evenness) showed a somewhat similar pattern. For immature insects in the congeneric and non-congeneric comparisons and adult insects in the non-congeneric comparisons, natives supported higher insect diversity (across all levels) than exotics. For adult insects in the congeneric comparisons, however, only species richness was higher on native plants; there were no differences between natives and exotic congeners at the other levels of diversity. In both the congeneric and non-congeneric comparisons, the immature insects had a more even community structure than the adult insects, and the adult insect community of the exotic non-congeners was strongly dominated by just a few insect species. As with the species accumulation curves, the diversity of immature insects was more affected by plant origin than was the diversity of adults, and there was a larger difference between natives and non-congeners than natives and congeners.

Although most of the studies examined insect use of woody plants, one study compared native and exotic herbaceous plants (Ballard et al. 2013). Rather than ornamentals, the exotic plant species chosen for this study were those that often invade disturbed sites in the northeastern United States. The authors measured total abundance, biomass, species richness, and community composition of herbivorous insects (many different orders) and their natural enemies (predators and parasitoids, including insects and other arthropods). Pooled across all arthropods (herbivores and natural enemies), native plants supported higher abundance and higher biomass of arthropods than exotic plants on all four sampling dates. When herbivores were analyzed separately, native plants supported higher biomass on two sampling dates and higher abundance on three sampling dates, with no differences between natives and exotics on the other

dates. For natural enemies, arthropod abundance was higher on native plants on one sampling date and biomass was higher on three sampling dates, with no differences on the other dates. Species accumulation curves showed arthropod richness (pooled across herbivores and natural enemies and pooled across sampling date) was much higher on native plants than exotics. The community of insects associated with native plants was very distinct from the community associated with exotic plants, with several species of leafhoppers and leaf beetles contributing most to the overall differences. Of the arthropods collected, 83 species were found only on native plants, but just 8 were found only on exotics.

All of these studies involved sampling herbivorous insects from plants in the field. When more insects were observed on natives than exotics, it was implied that this difference was caused by an inability of the insects to feed on the exotics. However, insects are able to choose which plants they feed on in the field. Given a mix of natives and exotics, they may choose to feed on natives because these are the plants they are adapted to eat. Given a different composition of plants, all exotics for example, insects would have no choice. In this case, either the insects would die from lack of food resources, or they would be forced to feed on the exotics. If they were in fact able to feed on the exotics, this would indicate that the results from these studies were due to discrimination against exotics rather than complete toxicity/unpalatability of the exotics. An additional study using generalist insect species was designed to address this aspect of the research (Tallamy et al. 2010). Four species of highly polyphagous lepidopteran larvae were fed a suite of different exotics (15-20 species) in no-choice experiments. One species was also chosen to test whether it could feed on all the native plants that have been recorded as hosts; i.e. they tested whether the local populations of the species could feed on all the plants recorded as hosts across the entire geographic range of the species. For the insects fed exotic plants, all of the larvae died on many of the exotics tested. In other instances, larvae were able to eat some of the exotic species, but the larvae grew more slowly than larvae fed their native host plant. The results of the other part of the experiment were similar. The larvae of the insect species fed all of its recorded native hosts died on many of the plant species tested, and grew quickly on only a few plant species. The authors suggested that generalist insect species may have a more specialized diet breadth at the local scale than across their entire geographic

ranges, and thus will be as sensitive to replacement of native vegetation with exotic vegetation as specialist species are.

Together, these studies provide strong evidence that replacing native plants with exotics on a massive scale, as is happening with the expansion of suburban areas, will create major negative consequences for herbivorous insect communities. Insect herbivores play a critical role in food webs; in fact, their role is so critical that most other living things couldn't get along without them (Wilson 1987). The effects of reduced insect herbivore biomass and diversity could cascade up trophic levels, resulting in extensive losses of biodiversity (Tallamy 2004; Burghardt et al. 2009). Birds are a good example to illustrate how important insects are in supporting higher trophic levels. Many adult birds in temperate climates subsist on both arthropods and the fruits and seeds of plants; however, they rear their young during the growing season, and many depend exclusively on arthropods as food for their young. Therefore, the reproductive success of some birds is highly dependent on the availability of arthropod biomass (Martin 1987). If the biomass of herbivorous insects declined as a result of exotics replacing their native host plants, then the biomass of predacious arthropods would also decline. Because birds depend directly on herbivorous insects and predacious arthropods as food for their young, one would also expect a concomitant decline in bird abundance or diversity. Indeed, available data suggest that bird diversity is strongly correlated with insect diversity in urban areas (Kim et al. 2007), and that both lepidopteran diversity and bird diversity are positively correlated with the percentage of native plant cover in residential areas (Burghardt et al. 2009).

Increasing concern for the loss of biodiversity associated with decreasing native vegetation in residential areas has generated an interest in "gardening for wildlife." The underlying premise is that we must replace exotic plants in our landscape with native plants, and increase the area of residential properties landscaped in native plants. This trend gained momentum with the publication and subsequent popularity of *Bringing Nature Home* (Tallamy 2007). Tallamy proposes that expanding urban development and preventing further losses in biodiversity are not mutually exclusive; his message is a call to action for people to learn to live with nature to prevent an impending mass extinction, and it starts with

providing suitable habitat for insects in our landscapes. One question that has been asked relative to this proposal is: are all native plants equal in providing suitable habitat for insects? It is certainly clear that some plant species host far more species of herbivorous insects than others (Tallamy and Shropshire 2009). What is not clear is whether the native plants that are available to gardeners through the nursery trade are equivalent to wild-type plants in supporting insect biomass and diversity. Most of the native plants available through the nursery trade are cultivated varieties, better known by the portmanteau ‘cultivars.’ Cultivars contain less genetic diversity than plants propagated from wild material and usually have been selected for some exaggerated characteristic that is atypical of the wild form.

### **Cultivars vs. Wild-type Plants**

There are several lines of evidence to suggest that the characteristics that distinguish cultivars from wild-type plants could cause cultivars to support relatively fewer herbivorous insects. The most obvious of these is that pest resistance is often viewed as a desirable trait when selecting new cultivars. Although resistance against disease and insects that cause major feeding damage certainly are desirable traits, a general resistance to all herbivores may not be desirable from an ecological perspective. If a cultivar successfully resists herbivory, it follows that the cultivar should support less insect biomass, and this biomass is in turn not available to organisms in higher trophic levels. Many studies have evaluated native cultivars for herbivore resistance (Klingeman 2002; Tenczar and Krischik 2007; Mphosi and Foster 2010), or the potential for developing herbivore resistance in native plants with breeding (Klingentan et al. 2007), but relatively few studies have evaluated cultivars for their ability to support insects. Those that have evaluated cultivars from the perspective of encouraging insects were concerned primarily with evaluating the cultivar’s ability to support pollinators (Comba et al. 1999; Corbet et al. 2001). Until there is a demand from consumers for plants that don’t discourage herbivory, it is unlikely this predilection for developing pest-resistant cultivars will decline.

Although pest resistance is often a consideration when developing new cultivars, it is usually a secondary concern. The primary goal of plant breeders is usually to select varieties for some novel trait relating to flower color, plant form, leaf color, flower density and abundance, etc. These traits appear

unrelated to the plant's palatability to insects, but selection for a trait may inadvertently reduce herbivory. For example, a common trait selected for by the horticulture trade is novel leaf color, such as purple, yellow, or variegated leaves. Purple leaves represent an increase in anthocyanins, a class of flavonoids that produces red and purple pigments. Flavonoids in plant tissue are thought to act as defense compounds against herbivory (Harborne and Williams 2000; Simmonds 2003). Tenczar and Krischik (2007) found reduced herbivory in a purple-leafed *Physocarpus* cultivar presumably as a result of increased anthocyanins in the leaves. Genetic modification can also result in reduced herbivory, even when the altered genes are apparently unrelated to plant palatability. For example, aspens (*Populus tremula* x *tremuloides*) were genetically modified to increase yield by manipulation of the sucrose phosphate synthase gene. Although the gene controls mesophyll sucrose content, concentrations of secondary metabolites known to influence herbivory also changed, and these trees experienced reduced herbivory by a leaf beetle (Hjalten et al. 2007).

The reduced genetic diversity of cultivars relative to the wild-type is another reason to suspect that cultivars may not support as many insects as the wild-type plants. Cultivars are often clones of a single genotype mass-produced by the nursery industry via tissue culture, cuttings, or division. The species diversity of insects in an area has been found to correlate with the genetic diversity of the plants they use as hosts (Wimp et al. 2004; Johnson et al. 2006). The driving force behind this correlation is the variation in leaf chemistry among individuals reflecting genetic variation within the population. Insects respond to this variation in leaf chemistry (Donaldson and Lindroth 2004; Bangert et al. 2006; Poelman et al. 2009), and the responses vary by insect species (Johnson and Agrawal 2007). The result is that each plant genotype can have a unique insect community associated with it (Wimp et al. 2007); in extreme cases, a particular genotype may even support unique host races (i.e. cryptic species) of arthropods (Evans et al. 2008). Therefore, differences in the composition of the insect communities across multiple genotypes can additively result in a more diverse community overall, suggesting that increasing the genetic diversity of the host plant material will translate to higher overall insect biodiversity (Ferrier et al. 2012). Conversely, one might expect the widespread use of a single genotype or cultivar to support fewer

unique insect communities and cause a decline in insect biodiversity. Although insects can be quite adaptable to the available plant material, one could use an argument analogous to Tallamy's (2004) to explain why insects would not adapt to cultivars. Insects that co-evolved with their local hosts may not be able to adapt within an ecological timeframe to a cultivar with a genotype significantly different from the genotypes of their local hosts.

### **Research Objectives**

This research used native cultivars selected for a variety of horticulturally-appealing characteristics to determine whether, in some instances, the selection for these characteristics could cause a decline in herbivorous insects relative to the insects supported by the wild-type plants. It also investigated whether certain characteristics of the plants were more prone to deterring herbivores than others. The purpose of this study was not to make generalizations about how widely applicable the results are to native plant species that are available in the trade as cultivars or about the impact of cultivars on the insects within an entire ecosystem. There is too much variation in insect communities geographically and among insect communities on different plant species to make such generalizations. The purpose also was not to draw definitive conclusions about the mechanisms by which a cultivar becomes less palatable to insects. The purpose was merely to compare the insect communities on cultivars and plant material propagated from wild-type plants to question the merit of using native cultivars in the garden to support insect biodiversity and biomass. If our results do show that cultivars support fewer insects or less insect diversity than plants propagated from local, wild populations, it would provide the impetus for further investigation into the mechanisms driving the differences and encourage research to determine how applicable the conclusions are to other regions and other plant species.

### **Literature Cited**

Ballard, M., J. Hough-Goldstein, and D.W. Tallamy. 2013. Arthropod communities on native and nonnative early successional plants. *Environmental Entomology* 42:851-859.



- Bangert, R. K., R. J. Turek, B. Rehill, G. M. Wimp, J. A. Schweitzer, G. J. Allan, J. K. Bailey, G. D. Martinsen, P. Keim, R. L. Lindroth, and T. G. Whitham. 2006. A genetic similarity rule determines arthropod community structure. *Molecular Ecology* 15:1379-1391.
- Bernays, E., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886-892.
- Burghardt, K. T., and D. W. Tallamy. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. *Diversity and Distributions* 19:1553-1565.
- Burghardt, K. T., D. W. Tallamy, C. Philips, and K. J. Shropshire. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1(5):art11. doi:10.1890/ES10-00032.1
- Burghardt, K. T., D. W. Tallamy, and W. G. Shriver. 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology* 23:219-224.
- Comba, L., S. A. Corbet, A. Barron, A. Bird, S. Collinge, N. Miyazaki, and M. Powell. 1999. Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* 83:73-86.
- Corbet, S. A., J. Bee, K. Dasmahapatra, S. Gale, E. Gorringer, B. La Ferla, T. Moorhouse, A. Trevail, Y. Van Bergen, and M. Vorontsova. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Annals of Botany* 87:219-232.
- Dirr, M. 1998. *Manual of woody landscape plants*. Stipes, Champaign, Illinois.
- Donaldson, J. R., and R. L. Lindroth. 2004. Cottonwood leaf beetle (Coleoptera : Chrysomelidae) performance in relation to variable phytochemistry in juvenile aspen (*Populus tremuloides* Michx.). *Environmental Entomology* 33:1505-1511.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586-608.

- Evans, L. M., G. J. Allan, S. M. Shuster, S. A. Woolbright, and T. G. Whitham. 2008. Tree hybridization and genotypic variation drive cryptic speciation of a specialist mite herbivore. *Evolution* 62:3027-3040.
- Ferrier, S. M., R. K. Bangert, E. I. Hersch-Green, J. K. Bailey, G. J. Allan, and T. G. Whitham. 2012. Unique arthropod communities on different host-plant genotypes results in greater arthropod diversity. *Arthropod-Plant Interactions* 6:187-195.
- Fraenkel, G. S. 1959. The raison d' être of secondary plant substances. *Science* 129:1466-1470.
- Gavier-Pizarro, G. I., V. C. Radeloff, S. I. Stewart, C. D. Huebner, and N. S. Keuler. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20:1913-1925.
- Harborne, J. B., and C. A. Williams. 2000. Advances in flavonoid research since 1992. *Phytochemistry* 55:481-504.
- Hjalten, J., A. Lindau, A. Wennstrom, P. Blomberg, J. Witzell, V. Hurry, and L. Ericson. 2007. Unintentional changes of defence traits in GM trees can influence plant-herbivore interactions. *Basic and Applied Ecology* 8:434-443.
- Johnson, M. T. J., and A. A. Agrawal. 2007. Covariation and composition of arthropod species across plant genotypes of evening primrose (*Oenothera biennis*). *Oikos* 116:941-956.
- Johnson, M. T. J., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24-34.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17:164-170.
- Kim, J., J. Chae, and T.-H. Koo. 2007. Variation in bird diversity in relation to habitat size in the urban landscape of Seoul, South Korea. *Acta Ornithologica* 42:39-44.
- Klingeman, W. E. 2002. Bagworm survival and feeding preferences as indicators of resistance among maples. *Journal of Environmental Horticulture* 20:138-142.

- Klingentan, W. E., F. Chen, H. J. Kim, and P. C. Flanagan. 2007. Feeding preferences of dogwood sawfly larvae indicate resistance in *Cornus*. *Journal of Environmental Horticulture* 25:134-138.
- Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: Getting more than we bargained for. *Bioscience* 51:95-102.
- Martin, T. E. 1987. Food as a limit on breeding birds - a life-history perspective. *Annual Review of Ecology and Systematics* 18:453-487.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247-260.
- Mphosi, M. S., and S. P. Foster. 2010. Female preference and larval performance of sunflower moth, *Homoeosoma electellum*, on sunflower pre-breeding lines. *Entomologia Experimentalis Et Applicata* 134:182-190.
- Nickerson C., R. Ebel, A. Borchers, and F. Carriazo. 2011. Major uses of land in the United States, 2007. EIB-89. U.S. Department of Agriculture, Economic Research Service.
- Poelman, E. H., N. M. van Dam, J. J. A. van Loon, L. E. M. Vet, and M. Dicke. 2009. Chemical diversity in *Brassica oleracea* affects biodiversity of insect herbivores. *Ecology* 90:1863-1877.
- Simmonds, M. S. J. 2003. Flavonoid-insect interactions: recent advances in our knowledge. *Phytochemistry* 64:21-30.
- Tallamy, D. W. 2004. Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692.
- Tallamy, D. W. 2007. Bringing nature home: how you can sustain wildlife with native plants. Timber Press, Portland, Oregon.
- Tallamy, D. W., M. Ballard, and V. D'Amico. 2010. Can alien plants support generalist insect herbivores? *Biological Invasions* 12:2285-2292.
- Tallamy, D. W., and K. J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941-947.

- Tenczar, E. G., and V. A. Krischik. 2007. Effects of new cultivars of ninebark on feeding and ovipositional behavior of the specialist ninebark beetle, *Calligrapha spiraeae* (Coleoptera : Chrysomelidae). Hortscience 42:1396-1399.
- Wilson, E. O. 1987. The little things that run the world. (The importance and conservation of invertebrates). Conservation Biology 1:344-346.
- Wimp, G. M., S. Wooley, R. K. Bangert, W. P. Young, G. D. Martinsen, P. Keim, B. Rehill, R. L. Lindroth, and T. G. Whitham. 2007. Plant genetics predicts intra-annual variation in phytochemistry and arthropod community structure. Molecular Ecology 16:5057-5069.
- Wimp, G. M., W. P. Young, S. A. Woolbright, G. D. Martinsen, P. Keim, T. G. Whitham, and T. Meagher. 2004. Conserving plant genetic diversity for dependent animal communities. Ecology Letters 7:776-780.
- Zuefle, M.E., W.P. Brown, and D.W. Tallamy. 2008. Effects of non-native plants on the native insect community of Delaware. Biological Invasions 10:1159-1169.

## CHAPTER 2

# GARDENING FOR WILDLIFE: ARE NATIVE PLANT CULTIVARS AS EFFECTIVE AS NATIVE PLANTS PROPAGATED FROM LOCAL, WILD POPULATIONS FOR PROMOTING NATIVE INSECT DIVERSITY?<sup>1</sup>

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<sup>1</sup> Poythress, J.C., and J.M. Affolter. 2014. *International Plant Propagators' Combined Proceedings*. 64:487-492. Reprinted here with permission of the publisher.

## **Abstract**

Many gardeners concerned over recent declines in biodiversity in suburban areas are attempting to improve the ecological functioning of their landscapes by incorporating native plants. Native plants are important food sources for native herbivorous insects, and insects are in turn important food sources for animals in higher trophic levels. But do the native plants available in nurseries, typically cultivated varieties (cultivars) of a single genotype fill an equivalent ecological role as the local, wild-type plants? For two herbaceous perennials, we observed significant differences in both total insect abundance and total number of insect species. However, there was a significant interaction between plant species and plant origin, suggesting that insect abundance and diversity does not depend on the source of the plant material per se, but rather on the particular characteristics of the cultivar that distinguish it from the wild form. We also observed significant differences in the insect communities among treatments, though only a small proportion of the total insect species collected contributed to these differences. Identifying which characteristics of cultivars might predict a loss of ecological function will not only help gardeners make the best choices of plants for their landscapes, but also will enable horticulturalists to select varieties that potentially outperform the wild-type plants in terms of the ecological services they provide.

## **Introduction**

Recent research suggests that the exotic species planted ornamentally in our suburban landscapes are inferior to natives in providing food for native herbivorous insects (Tallamy 2004; Tallamy & Shropshire 2009; Burghardt et al. 2010). Because herbivorous insects are important food sources for organisms in higher trophic levels, there is concern that a decline in abundance or diversity of insects in suburban areas could cause a concomitant decline in animals such as birds. This concern has spurred an interest in “gardening for wildlife” by replacing exotics with native ornamental plants in suburban landscapes. But are the native plants available in nurseries, typically cultivated varieties (cultivars) of a single genotype, equally effective as the local, wild-type plants in providing food for native herbivorous insects?

There are at least two reasons supported by research that suggest cultivars may differ from wild plants in their ability to support native insects. First, cultivars are usually asexually-propagated, and therefore contain less genetic diversity than wild-propagated plants for a given species. Because insect diversity is correlated with the genetic diversity of the host plants (Wimp et al. 2004; Johnson et al. 2006), several clones of a single genotype of a plant might support fewer insect species than multiple genotypes. Second, plant leaf chemistry determines which insect species are able to feed on a particular plant (Ehrlich & Raven 1964), and some cultivars are selected for traits that alter leaf chemistry. For example, some plants are selected to have purple-colored leaves. The purple color is a result of increased concentrations of anthocyanins, a type of flavonoid known to function as a feeding deterrent in leaves (Harborne & Williams 2000; Simmonds 2003). In theory, this sort of change in leaf chemistry could affect the insects that normally feed on the plant, reducing the abundance or number of species of insects supported.

This research investigated whether these theoretical consequences of selecting cultivars actually affect herbivorous insects in a garden setting. We chose several native herbaceous perennials that occur locally in natural areas near the study site and have cultivars available commercially. We determined whether the cultivars differed from plants grown from wild-collected seed in their ability to serve as a food source for native hemipterans (the true bugs), the dominant group of insects that feed on herbaceous plants.

## **Materials and Methods**

The experiment was set up following a fully-randomized two-way ANOVA design at the Mimsie Lanier Center for Native Plant Studies at the State Botanical Garden of Georgia in Athens, Georgia. The first factor was Plant Species and included five levels: *Amsonia tabernaemontana*, *Coreopsis grandiflora*, *Monarda fistulosa*, *Oenothera fruticosa*, and *Schizachyrium scoparium*. The second factor was plant origin and included two levels: cultivar and wild-type. There were five replicates for each treatment, giving a total of 50 experimental units. Each experimental unit was a 2 meter x 2 meter plot containing 16 plants evenly spaced, and plots were placed 1.5 meters apart. All wild-type plants were grown from seed

collected from wild populations occurring within a five-mile radius of the study site. All cultivars were purchased as liners from North Creek Nurseries in Landenberg, Pennsylvania. The cultivars were *Amsonia* ‘Blue Ice,’ *Coreopsis* ‘Tequila Sunrise,’ *Monarda fistulosa* ‘Claire Grace,’ *Oenothera* ‘Cold Crick,’ and *Schizachyrium scoparium* ‘Prairie Blues.’ Wild-type plants and cultivars were planted in April 2013.

We collected preliminary data from a subset of the plant species on August 25, 2013. Insects were vacuumed from plots in the *Coreopsis*-Wild (CW), *Coreopsis*-Cultivar (CC), *Oenothera*-Wild (OW), and *Oenothera*-Cultivar (OC) treatments with a modified leaf vacuum. The order in which the plots were sampled was randomized to reduce any systematic bias caused by insects that escaped the vacuum and moved to other plots. Sampling began at 11 a.m. and ended at 2 p.m. to coincide with peak xylem flow. The insects were killed with ethyl acetate, sorted by species, and counted. Representative specimens of each species were pinned for subsequent identification.

We analyzed the count data in three ways. First, we determined the total abundance of adult hemipterans collected from each plot. Second, we determined the total number of species (i.e. species richness) of adult hemipterans collected from each plot. We analyzed both total abundance and species richness with a two-way ANOVA using function `aov()` in R (R Core Team 2013). Third, we determined the relative abundance of each insect species collected from each plot. These relative abundance counts were used to determine whether the insect community differed among treatments. The distinction between the insect community and species richness is that two treatments could have the same richness but with different insect species, hence the insect community would be different. The relative abundances were used to calculate a dissimilarity metric called “percent dissimilarity” or “Bray-Curtis dissimilarity” between all possible pairs of plots (Legendre and Legendre 2012). This metric can be interpreted as the percentage of individuals not shared between two plots; i.e. a value of 0 indicates exactly the same community whereas a value of 1 indicates no species in common. The percent dissimilarity matrix was used to create an ordination plot using principal coordinates analysis with function `capscale()` and to test for treatment effects using permutational multivariate analysis of variance (PERMANOVA) with function



adonis() (Oksanen et al. 2013). Principal coordinates analysis is an ordination technique that is a more generalized form of principal components analysis. It is used to visualize high-dimensional data in a 2-dimensional space. PERMANOVA tests for treatment effects by random permutation of the rows of the dissimilarity matrix, which are exchangeable under true null hypotheses. After each permutation, the F statistic is recalculated. After several thousand iterations, a pseudo-F distribution is generated that can be used to calculate an approximate p-value for the observed F statistic (Anderson 2001).

## Results

The results of a two-way ANOVA indicated a significant interaction between Plant Species and Origin for both total abundance and species richness ( $F_{1,16}=31.871$ ,  $p<.001$  and  $F_{1,16}=16.401$ ,  $p<.001$ , respectively). The typical follow-up procedure after finding a significant interaction is to break up the analysis into several one-way ANOVAs at each level of the other factor. However, our main interest was the comparison of wild-type plants with cultivars, so we chose to follow up with only a one-way ANOVA of Plant Origin at each level of Plant Species (i.e. we omitted the analysis of Plant Species at each level of Plant Origin). For total abundance, there was significantly higher insect abundance on wild-type *Coreopsis* vs. the cultivar ( $F_{1,8}=22.16$ ,  $p=.0015$ ), but there was significantly higher abundance on the *Oenothera* cultivar vs. the wild-type ( $F_{1,8}=11.48$ ,  $p=.0095$ ). For species richness, there were significantly more insect species on wild-type *Coreopsis* vs. the cultivar ( $F_{1,8}=15.36$ ,  $p=.0044$ ), but there was no significant difference in the number of insect species for wild-type *Oenothera* vs. the cultivar ( $F_{1,8}=2.53$ ,  $p=.1501$ ). A total of 68 insect species were collected across all plots.

The mean abundance for each treatment is shown (Fig. 2.1), as is the species richness for each treatment (Fig. 2.2). A species accumulation curve is used in lieu of a bar plot because it depicts more information. For example, when Replicates=1, the line is the mean species richness of each treatment and the error bars are  $\pm 1$  standard deviation (SD). Beyond Replicates=1, the line is the total number of insect species found in a random subsample of  $i$  plots (where  $i = 2, 3, 4, \text{ or } 5$ ). The error bars then represent the SD after repeating the subsampling many times. At Replicates=5, all the plots are sampled, so the line is the total number of insect species on all the plots within a treatment, and the SD is zero because there is

only one possible combination of 5 replicates. The shape of the curve is useful for determining whether most of the insect species have been found or whether it is likely more will be found after further sampling. For example, after sampling 5 plots, the number of insect species found begins to level off for the *Oenothera* cultivar, but the slope is still increasing for the wild-type *Oenothera*, suggesting there are still more insect species to find.

An ordination of the treatments is shown below in Figure 2.3. The first axis explained 40.5% of the variation in the data and the second axis explained 27% of the variation in the data. The insect species that contributed most to the ordination are overlain as vectors. One notable feature of the ordination is that replicates from the same treatment tend to group together, and replicates from different treatments tend to separate. Another important feature to note is that only 6 of the 68 total insect species contributed most to the ordination; i.e. the next longest insect vector was substantially shorter than the shortest of these 6. The direction of a vector representing a particular insect species corresponds to the treatment that insect was most associated with, and the length of a vector indicates its contribution to the ordination, which in this case corresponds to the abundance of the insect. For example, the vector representing *Empoasca bifurcata* points between the replicates in the *Oenothera* cultivar treatment and the wild-type *Coreopsis* treatment, indicating that *Empoasca* is most associated with these plants. It is also the longest vector in the ordination, indicating that it was the most abundant insect collected. Also, the angle between two vectors can be interpreted as the correlation between one insect species and another in terms of their abundances.

Principal coordinates analysis is only a visualization technique for high-dimensional data, and therefore provides no information for hypothesis testing. We used PERMANOVA to test whether the insect community differed among treatments. Consistent with the univariate analyses, there was a significant interaction between Plant Species and Origin ( $F_{1,16}=19.45$ ,  $p\text{-value}<.001$ ). Again, we broke up the data and used a one-way PERMANOVA at each level of Plant Species to test for differences in the insect community between wild-type and cultivar. There was a significant difference in the insect community between cultivars and wild-type plants for both *Oenothera* and *Coreopsis* ( $F_{1,8}=16.042$ ,  $p\text{-value}\approx.007$  and  $F_{1,8}=10.085$ ,  $p\text{-value}\approx.009$ , respectively). Although PERMANOVA assumes nothing

about the distribution of the data, it does assume that the dispersion of the data is the same among groups, which is analogous to homogeneity of variances in univariate ANOVA. A test analogous to Levene's test did not indicate any violations of this assumption.

## **Discussion**

The most striking result of this research was the interaction between plant species and plant origin. In the case of *Coreopsis*, the wild-type plants supported more individuals and more species of hemipterans than did the cultivar. In contrast, the cultivar of *Oenothera* supported more individuals of hemipterans than did the wild-type plants, though there was not a significant difference in the number of insect species supported. These results suggest that the ecological value of a plant species does not depend on whether the plant material is a selection (i.e. a cultivar) or wild-propagated, but rather on the particular cultivar that is chosen. In fact, these results suggest that some cultivars may provide a greater benefit to wildlife than their wild counterparts.

If some cultivars have more of a benefit to wildlife than others, the next obvious question is: Which characteristics of a cultivar might be used to predict how well it fills an ecological role in the landscape? The results of this research may provide insight into possible answers. *Coreopsis* 'Tequila Sunrise' is quite distinct from the wild-type plants. Wild-type plants are tall, structurally complex, and produce viable seeds. 'Tequila Sunrise' plants are variegated, clump-forming, apparently sterile (at least no viable seeds were observed during this research), and produce few branching stems. For gardeners who prefer a tidy garden with plants that do not grow tall and flop over, 'Tequila Sunrise' is far superior to the wild form. However, these traits that make it a superior garden plant appear to come at the cost of reduced ecological function. Determining whether the variegated leaves, lack of structural complexity, or some other characteristic is primarily responsible for its reduced ability to support herbivorous insects would require additional research.

It is more difficult to explain why *Oenothera* 'Cold Crick' supported a higher abundance of herbivorous insects than the wild-type plants. Unlike *Coreopsis*, the *Oenothera* cultivar and wild-type plants differ very little. Both are about the same height and have similar structural complexity. Nurseries

promote ‘Cold Crick’ as being more compact than the wild form of *Oenothera*, but this did not appear to be true for this wild population of *Oenothera*. The main difference between the wild-type plants and ‘Cold Crick’ is that ‘Cold Crick’ is sterile. This would explain why *Neopamera bilobata*, an insect that contributed significantly to the ordination and only feeds on seeds, was found in far higher abundances on the wild-type plants than the cultivar. A quantitative measure of structural complexity and knowledge of the phytochemicals present in the leaves could help explain differences in abundances observed for other insect species. An important caveat to note is that these data represent a snapshot of a single day during the first growing season. The patterns observed for both plant species could change depending on the season and the amount of time insects have had to colonize the plots. For example, the species accumulation curve in Figure 2.2 indicated that the number of insect species feeding on the wild-type *Oenothera* is probably much higher than the number suggested by the mean species richness for a single day. Although there were no significant differences in species richness between the wild-type *Oenothera* and the cultivar for the preliminary data, this pattern may not hold after repeated sampling.

We will collect data from all the plant species in the experiment multiple times in 2014. This should provide better insight into whether the patterns observed in the preliminary data extend to other plant species and other seasons of the year. The cultivars used for this experiment were chosen to represent a range of deviations from the wild forms, so data from the full suite of plant species should also provide more information about which characteristics of cultivars best predict their ability (or inability) to function ecologically in the landscape.

### **Acknowledgements**

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### **Literature Cited**

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.

- Burghardt, K. T., D. W. Tallamy, C. Philips, and K. J. Shropshire. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1(5):art11. doi:10.1890/ES10-00032.1
- Ehrlich P.R., and P.H. Raven. 1964 . Butterflies and plants: a study in coevolution. *Evolution* 18:586-608.
- Harborne J.B., and C.A. Williams. 2000. Advances in flavonoid research since 1992. *Phytochemistry* 55:481-504.
- Johnson M.T.J., M.J. Lajeunesse and A.A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24-34.
- Legendre P., and L. Legendre. 2012. *Numerical Ecology Third Edition*. Elsevier, Amsterdam.
- R Core Team. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Simmonds, M.S.J. 2003. Flavonoid-insect interactions: recent advances in our knowledge. *Phytochemistry* 64:21-30.
- Tallamy, D.W. 2004. Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692.
- Tallamy D.W., and K.J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941-947.
- Wimp G.M., W.P. Young, S.A. Woolbright, G.D. Martinsen, P. Keim, T.G. Whitham and T. Meagher. 2004. Conserving plant genetic diversity for dependent animal communities. *Ecology Letters*: 7:776-780.

Figure 2.1. Total Abundance for Plant Species X Origin. Error bars represent  $\pm 1$  SD.

Figure 2.2. Species Accumulation Curve for Plant Species X Origin. See text for an explanation of the error bars.

Figure 2.3. Principal Coordinates Analysis Biplot of Treatments and Insect Species. Percent dissimilarity was used as the distance metric. Only six insect species are shown because the others contributed very little to the ordination. Replicates are identified by treatment and their location in the design (e.g. OC1.4 means *Oenothera* cultivar at row 1, column 4).

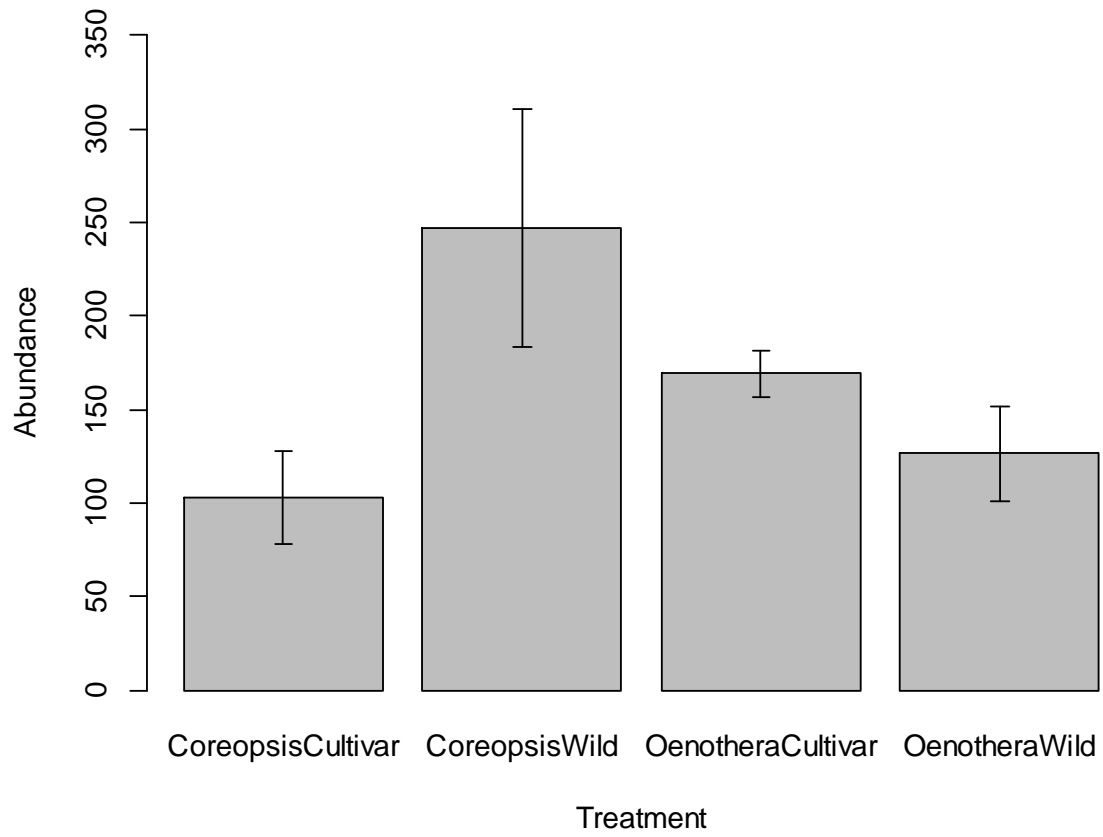


Figure 2.1.

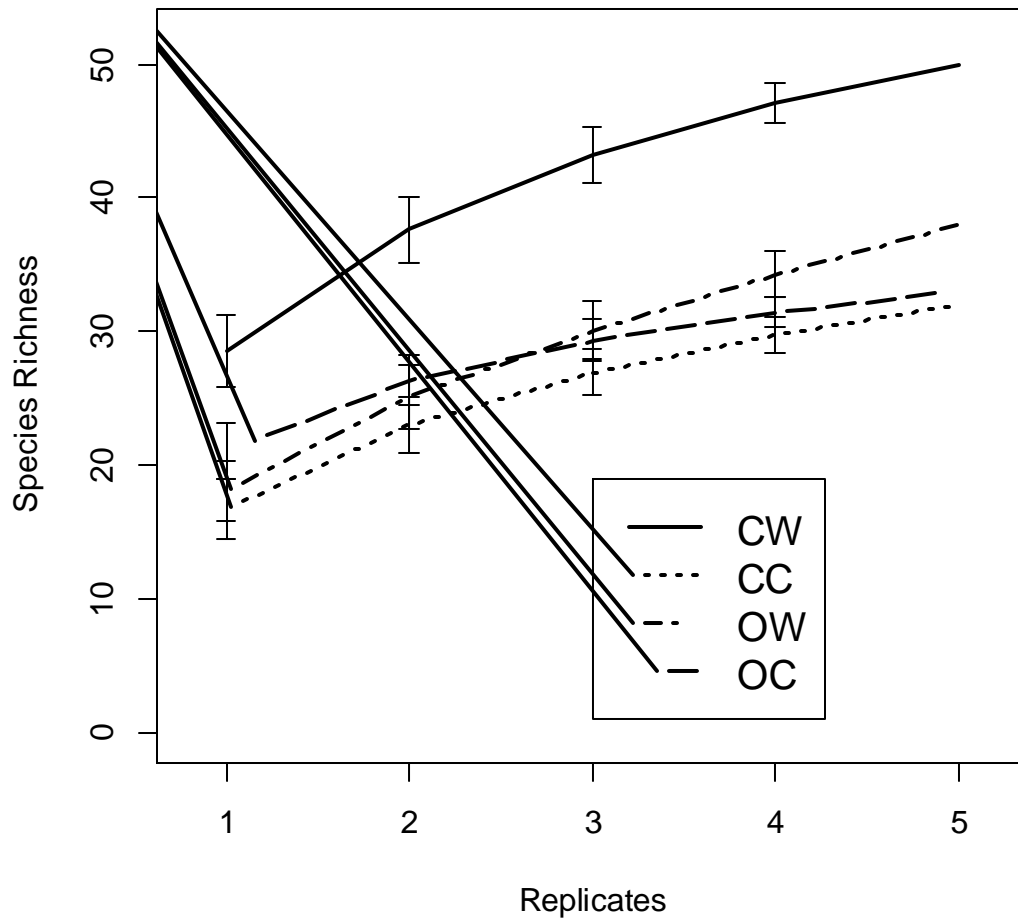


Figure 2.2.



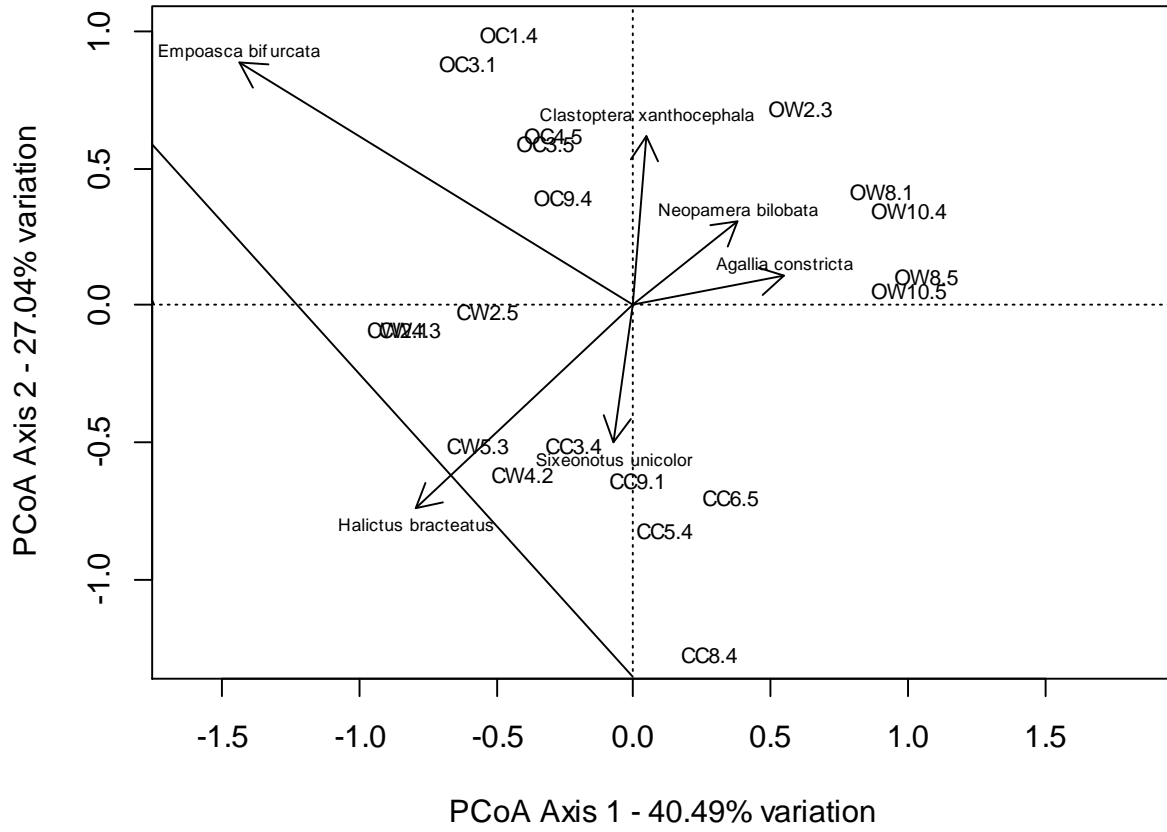


Figure 2.3.

## CHAPTER 3

# ECOLOGICAL VALUE OF NATIVE PLANT CULTIVARS VERSUS WILD-PROPAGATED NATIVE PLANTS FOR PROMOTING INSECT DIVERSITY IN RESIDENTIAL LANDSCAPES<sup>1</sup>

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<sup>1</sup> Poythress, J.C., and J.M. Affolter. To be submitted to *Ecological Applications*.

## Abstract

Research suggests that the exotic plants used ornamentally in landscapes are inferior to natives in providing food for native herbivorous insects. Because of concerns over recent declines in overall biodiversity in suburban areas, gardeners are attempting to improve the ecological functioning of residential landscapes by incorporating native plants. However, it is unknown whether the native plants that are commercially available, typically cultivated varieties (cultivars) of a single genotype, are equally effective as food sources for native herbivorous insects as the local, wild-type plants. We compared the hemipteran communities feeding on cultivars and wild-propagated plants for four species of native perennials commonly used in ornamental horticulture. Of 65 hemipteran species collected, 35 exhibited a strong preference for some plant species over others, indicating a high degree of host-plant specialization. Moreover, there was strong evidence that a distinct insect community was associated with each treatment group, though only 3-4 insect species appeared to discriminate between cultivars and wild-type plants for any given plant species. For phloem- and mesophyll-feeding insects, some species preferred the cultivars, and other species preferred the wild-type plants. However, for seed-feeding insects, differences between cultivars and wild-type plants were only observed when the cultivar was sterile, and insects were always found in higher abundances on the fertile, wild-type plants. In addition, total insect abundance and insect biomass differed significantly between cultivars and wild-propagated plants, but the direction of the difference changed over time and was not consistent among plant species. Species richness and a diversity index did not differ between cultivars and wild-type plants, but one plant species appeared to support more insect species than the others. These data suggest that abundance and diversity of hemipteran insects does not depend on the source of the plant material *per se*, but rather on the particular characteristics of cultivars that distinguish them from the wild type. Identifying which characteristics might predict a loss of ecological function will not only help gardeners make the best choices of plants for their landscapes, but also will enable horticulturalists to select varieties that potentially outperform the wild-type plants in terms of the ecological services they provide.

## **Introduction**

As the population of the United States expands, more land is converted for residential use. As of 2007, approximately 61 million acres were classified as urban use, and 103 million acres were classified as rural residential use in the United States (Nickerson et al. 2011). Landscaping in residential areas typically does not reflect the natural plant community that existed in that area before development; in fact, urban areas are associated with a replacement of native flora by exotic species (McKinney 2006), many of which also invade surrounding areas (Gavier-Pizarro et al. 2010). Most of the exotics that replace natives in landscapes are purchased through the plant trade industry for their aesthetic value (Mack and Lonsdale 2001). There has been some speculation that this prevalence of non-native vegetation in residential landscapes could contribute to a loss of biodiversity in suburban areas (Tallamy 2004).

The purported mechanism by which landscaping with exotic plants would lead to a loss of biodiversity has roots in plant-insect interaction theory. Most insect herbivores specialize on a narrow group of plants, usually plants in three or fewer families (Bernays and Graham 1988). One theory predicts this specialization is a result of coevolution between plants and insects. Plants produce a diverse array of secondary metabolites that act as feeding deterrents, and herbivorous insects develop specialized physiological adaptations for detoxifying those metabolites (Fraenkel 1959; Ehrlich and Raven 1964). When large areas of native vegetation are replaced with exotic vegetation, as is often the case in suburban landscapes, the exotic vegetation may contain secondary metabolites that are not present in the native vegetation, and hence native insects are not equipped to deal with these novel feeding deterrents. Because arthropods often make up the largest proportion of animal biomass in a given ecosystem, removing one of their primary food sources – native plants – could catastrophically disrupt food webs, with effects cascading up to higher trophic levels (Wilson 1987).

Recent research has provided strong empirical evidence that exotic plants support less insect biomass and less diverse insect communities than native plants (Zuefle et al. 2008; Burghardt et al. 2010; Tallamy et al. 2010; Burghardt and Tallamy 2013). There is also evidence that the diversity of organisms in higher trophic levels, especially birds, is highly correlated with the abundance and diversity of insects

in suburban habitats (Kim et al. 2007; Burghardt et al. 2009). The concern that a decline in insect biomass could cause a concomitant decline in overall biodiversity in suburban areas, together with a desire to improve the ecological functioning of landscapes, has spurred an interest in “gardening for wildlife” by replacing exotics with native ornamental plants in landscapes. But are the native plants available commercially, typically cultivated varieties (cultivars) of a single genotype, equally effective as the local, wild-type plants in providing food for native herbivorous insects?

There are several lines of evidence that suggest cultivars and wild-type plants could differ in their abilities to support herbivorous insects. Cultivars are often asexually-propagated, and insect diversity is known to correlate with the genetic diversity of the host plants (Wimp et al. 2004; Johnson et al. 2006). Cultivars are also selected for some characteristic that distinguishes them from the wild form. Pest resistance, altered growth habit, changes in flower or leaf color, and sterility are common goals of plant breeders, and any of these could influence an insect’s ability to feed on the plant (e.g., Tenczar and Krischik 2007; Mphosi and Foster 2010). While many of these traits imply negative consequences for insect communities, it is important to note that some characteristics may actually improve a cultivar’s ecological value relative to the wild form. In the simplest case, selecting for hybrid vigor would make more plant biomass available to support more insects.

We investigated whether these theoretical consequences of cultivar selection actually affect herbivorous insects in a garden setting. We chose several native herbaceous perennials that occur locally in natural areas near the study site and have cultivars available commercially. We determined whether the cultivars differed from plants grown from wild-collected seed in their ability to serve as a food source for native hemipterans (Auchenorrhyncha and Heteroptera), a highly abundant and speciose group associated with grasslands and plants growing in open, disturbed areas (Wallner et al. 2013). We measured hemipteran biomass, abundance, diversity, and community composition over the course of one growing season.

## Materials and Methods

### *Study Site and Plant Material*

Plots were established in an open field at the Mimsie Lanier Center for Native Plant Studies at the State Botanical Garden of Georgia in Athens, Clarke County, Georgia. The Botanical Garden was an ideal study site for this research because it reflects a typical residential setting. It is a mixture of woodlands, lawns, and gardens located just on the outskirts of a medium-sized city. The field in which plots were established is located within the floodplain of the Oconee River and is characterized by periodic flooding and loamy, alluvial soils. There are open and forested areas, both upland and bottomland, immediately surrounding the site.

All wild-type plants were grown from seed locally-collected from populations occurring in natural areas. Here, we define natural areas to mean open sites comprised of mostly native, early-successional vegetation; this includes relatively undisturbed sites, such as granitic outcrops, and sites with man-made disturbance, such as utility rights-of-way maintained by mowing. Seeds of *Amsonia tabernaemontana* were collected from a population at Currahee Mountain in Stephens County, Georgia. Seeds of *Monarda fistulosa* were collected from a natural area within the State Botanical Garden. Seeds of *Coreopsis grandiflora*, *Oenothera fruticosa*, and *Schizachyrium scoparium* were collected from the Rock and Shoals Natural Area, a granitic outcrop at the end of Rock and Shoals Dr. in Clarke County, Georgia. For all plant species, a few seeds were collected from many individuals (usually >50) in order to capture as much of the genetic variation within the population as possible.

Four of the cultivars were purchased as liners from North Creek Nurseries in Landenberg, Pennsylvania. These were *Amsonia* ‘Blue Ice,’ *Coreopsis* ‘Tequila Sunrise,’ *Monarda fistulosa* ‘Claire Grace,’ and *Oenothera* ‘Cold Crick.’ All four cultivars were propagated vegetatively; i.e. they were clones from a single source. The fifth cultivar, *Schizachyrium scoparium* ‘Prairie Blues,’ was donated by Hoffman Nursery in Bahama, NC. This cultivar was propagated by seed. The cultivars were chosen to represent both variety in their genetic origins and their traits of interest. For example, the cultivars of *Coreopsis*, *Oenothera*, and *Amsonia* are all interspecific hybrids or likely hybrids, whereas the cultivars

of *Monarda* and *Schizachyrium* are selections of the straight species. Likewise, *Schizachyrium* and *Coreopsis* were selected for traits that involve a change in leaf chemistry, while *Oenothera*, *Amsonia*, and *Monarda* were selected for traits such as form, sterility, and disease resistance. We provide a full summary of the purported differences between the wild-type plants and cultivars (Appendix A).

Both cultivars and wild-type plants were planted in the field in April 2013. At that point, both wild-type plants and cultivars had root balls that filled square nursery pots approximately 3.5 inches wide and 3 inches deep. By the late summer of 2013, many plants were fully-grown and flowering. By the summer of 2014, just before data were collected, all the plants had reached flowering size and most plots had achieved 100% cover.

#### *Experimental Design*

The experiment followed a fully-randomized two-way analysis of variance (ANOVA) design (schematic diagram in Appendix B). The first factor was plant species and included five levels: *Amsonia*, *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium*. The second factor was plant source and included two levels: cultivar and wild-type. There were five replicates for each treatment, giving a total of 50 experimental units. Each experimental unit was a 2 m x 2 m plot containing 16 plants evenly spaced, and plots were placed 1.5 m apart. The planting density per plot was chosen to be 16 individuals so that percent cover would be close to 100% by the time insects were collected. Plots were kept weed-free throughout the growing season and wood mulch was used in-between plots.

#### *Data Collection*

We collected insects from all the plant species on three dates in 2014: 8 July, 15 August, and 20 September. The collection was broken up into two consecutive days for each sample period because all 50 plots could not be sampled in one day. We only sampled on days that were sunny with low wind speed. Insects were vacuumed for one minute from plots with a modified leaf vacuum (Stihl BG 55) following the design in Wilson et al. (1993). The period of one minute was based on previous trials and chosen to maximize the number of insects vacuumed while minimizing the number of vacuumed insects escaping. The order in which the plots were sampled was randomized to reduce any systematic bias caused by

insects that escaped the vacuum and moved to other plots. Sampling began at 11 a.m. and ended by 2 p.m. to coincide with peak xylem flow. The insects were killed with ethyl acetate, sorted into hemipterans and non-hemipterans, and stored dry in boxes. Representative specimens of each species were pinned for subsequent identification.

We measured two response variables for each experimental unit (plot) at each sampling date: total dry biomass of hemipterans and abundance of each adult hemipteran species. Total dry biomass included both adult hemipterans and nymphs and was measured to the nearest 0.0001 g. For the count data, nymphs were not included because most could not be identified to species. From the abundances of each species, we constructed several other response variables for our statistical analyses. These were total overall abundance of hemipterans, species richness, and the Q-statistic. The Q-statistic is a diversity index that measures the interquartile slope of the species accumulation curve, excluding both low- and high-abundance species from the measure of diversity (Kempton and Taylor 1978). We chose the Q-statistic over more common indices such as Simpson's Index or Fisher's Alpha because many of these indices are highly influenced either by low-abundance species or by dominant species. In the context of this experiment, infrequently-collected insects more likely represent "tourists" (Gaston 1996) rather than rare species that are actually associated with a given plant, and hence should carry less weight instead of more. The Q-statistic provides a good compromise for measuring diversity when it is desirable to reduce the influence of both low- and high-abundance species.

#### *Standardization by Plant Biomass*

Because plant species, and sometimes cultivars and wild-type plants, differed in size, we standardized total insect biomass and total abundance by the dry weight of the plants they were collected from. We could only measure plant dry weight in September, however, because it involved destructively sampling the plants. Within two weeks following the September sampling, we harvested all of the above-ground plant material from each plot and stored it in large paper bags. We dried all of the plant material in a forced-air drying oven at 60°C for 7 days. After drying, we recorded the total dry weight of each plot to



the nearest 0.1 kg. The dry weights were used to transform the September insect data as total abundance or total insect biomass per kilogram plant biomass.

### *Statistical Analyses*

We used repeated measures two-way ANOVA to analyze total abundance and total dry biomass of insects. Several variants of repeated measures ANOVA exist. We used the variant that performs multivariate analysis of variance (MANOVA) on the differences between adjacent time periods (a.k.a. profile analysis) to test for the effects of plant species, plant source, time, and their interactions. We used the function `manova()` in R (R Core Team 2013). The standardized abundance and insect biomass data from September were analyzed with univariate two-way ANOVA using function `aov()`.

Rather than analyze species richness and the Q-statistic by sampling date (i.e. with repeated measures ANOVA), we pooled data over all three sampling periods to compare diversity among treatments for the entire growing season. We analyzed richness and the Q-statistic with two-way ANOVA using function `aov()` in R (R Core Team 2013). The normality assumption of ANOVA was tested with function `shapiro.test()` and the homogeneity of variances assumption was tested with function `bartlett.test()`. To visually compare species richness among treatments, we constructed a sample-based rarefaction curve using function `specaccum()` in package ‘vegan’ in R (Oksanen et al. 2013). Although all the experimental units were the same size and sampling effort was equal among treatments, we rescaled the x-axis by number of individuals to account for differences in insect density among treatments (Gotelli and Colwell 2001).

We also used the pooled count data to test whether the insect communities differed among treatments. We used two fundamentally different multivariate analyses to test for differences in the insect communities. The first was a distance-based approach, and was used both to visualize the data and to test hypotheses. We used the semi-metric dissimilarity measure called “percent dissimilarity” (a.k.a. Bray-Curtis dissimilarity) in all of our distance-based analyses (Legendre and Legendre 2012). We created a Non-metric Multidimensional Scaling (NMDS) ordination of the plots with function `metaMDS()` in package ‘vegan’ in R to visualize the data and tested hypotheses with permutational multivariate analysis

of variance (PERMANOVA) using function `adonis()` (Oksanen et al. 2013). We used 1000 permutations to obtain  $p$  values for PERMANOVA.

Differences in location are usually the main interest of hypothesis tests, but distance-based analyses are also sensitive to differences in dispersion (Anderson 2001). They also frequently fail to detect differences among communities unless the effects are present in taxa with relatively high abundances (Warton et al. 2012). To ensure that these issues were not affecting our results, we also used multivariate analyses based on generalized linear models (GLMs) to model the counts of each insect species directly. In particular, we fit the abundance data for each insect species to separate negative binomial models using function `manyglm()` in package ‘`mvabund`’ in R (Wang et al. 2014). We specified the identity matrix as the correlation structure for our multivariate tests and used the likelihood ratio test for Analysis of Deviance. The function provides a multivariate test for the entire community and univariate tests for each insect species, with  $p$  values for the univariate tests corrected for multiple comparisons using a resampling-based procedure. We used 1000 permutations to obtain  $p$  values.

## **Results**

Overall, we collected almost 12,000 adult hemipterans representing 130 different species. Exactly half of the species had abundances less than or equal to five in the entire dataset, so we excluded these species from all analyses. These species were likely “transients” or “tourists,” and not actually feeding on the plants they were collected from. Because arthropods are highly mobile, it is not surprising that such a large proportion of the species collected would be transients (see Pimentel and Wheeler (1973) for a similar result). Although including these species in the analyses would make little difference for response variables such as total abundance, they would be highly influential for diversity measures such as species richness. Even the Q-statistic, which is meant to exclude both infrequent and highly abundant species, can be biased when the majority of the species are singletons (Magurran 2004). We provide a list of all the insect species excluded from the analyses and their abundances (Appendix C).

Only one species of hemipteran was found feeding on the *Amsonia* wild-type plants and cultivars, and only 9 individuals of this species were collected over the entire growing season, so the *Amsonia* wild-

type and cultivar treatments were excluded from all analyses. The species found feeding on *Amsonia* was the broad-headed sharpshooter, *Oncometopia orbona*.

#### *Total Abundance and Insect Biomass*

Repeated measures ANOVA indicated a three-way interaction among plant species, plant source, and time for both total abundance of insects and total insect biomass. We broke up both analyses at each level of plant species and plotted these results as a function of time (Fig. 3.1a and Fig. 3.1b). For most plant species, there were significant interactions between plant source and time. Hence, we compared abundance or biomass of cultivars and wild-type plants for each plant species at each date. *P* values were corrected for multiple comparisons using the Bonferroni method. The Bonferroni method is the most conservative multiple comparison adjustment so we displayed significant differences both at an experiment-wise  $\alpha=.05$  ( $p$  value $<0.00417$ ) and at  $\alpha=.10$  ( $p$  value $<0.00833$ ), denoted by three asterisks and one asterisk, respectively.

Generally, there was close correspondence between insect abundance and insect biomass. The most notable exception was *Monarda*. The *Monarda* wild-type plants consistently had 2-5 times higher insect abundance than the cultivars, but insect biomass was not significantly different between cultivars and wild-type plants at any sampling date. Another notable pattern was that some treatments increased in abundance and biomass over the growing season, whereas others decreased (and some changed little). In particular, insect abundance and biomass increased on the *Coreopsis* and *Schizachyrium* cultivars over the growing season, but decreased on the *Coreopsis* and *Oenothera* wild-type plants. For the *Oenothera* cultivar and wild-type comparison, abundance and biomass were 3 times higher on wild-type plants early in the season, but there were no differences by the end of the season. For *Schizachyrium*, there were no differences in abundance or biomass early in the season, but insect abundance and biomass were approximately 2 and 3.5 times higher, respectively, on the cultivar by the last sampling date. The *Coreopsis* had perhaps the most striking pattern. Abundance and biomass were approximately 1.5 times higher on the wild-type plants on the first sampling date, but were 3-4 times higher on the cultivar by the

end of the season. However, this difference in pattern is most likely due to the fact that many of the *Coreopsis* wild-type plants had died by the last sampling date.

### *Species Diversity*

Two-way ANOVA of species richness indicated no significant interactions between plant species and plant source, but a significant overall effect of plant species (plant source:  $F_{1,32}=2.012$ ,  $p=0.166$ ; plant species:  $F_{3,32}=7.256$ ,  $p<0.001$ ; interaction:  $F_{3,32}=2.407$ ,  $p=0.085$ ). The results of two-way ANOVA of the Q-statistic were similar (plant source:  $F_{1,32}=0.010$ ,  $p=0.920$ ; plant species:  $F_{3,32}=9.898$ ,  $p<0.001$ ; interaction:  $F_{3,32}=1.444$ ,  $p=0.248$ ). That is, there was no indication of differences in richness or the Q-statistic between wild-type plants and cultivars for any plant species. Mean richness and mean Q-statistic were significantly higher for *Oenothera* than all other plant species after correcting for multiple comparisons with Tukey's HSD test (Fig. 3.2a and Fig. 3.2b, respectively). *Oenothera* had on average 5-6 more insect species than the other plants. There were no differences in richness or the Q-statistic among the other plant species.

The rarefaction curve of species richness generally agreed with the results of ANOVA with the exception of the *Monarda* cultivar and wild-type plants (Appendix D). For example, the curves for the *Oenothera* cultivar and wild-type are above all the other treatments, indicating that species richness is higher on *Oenothera* than the other plant species. Also, the wild-type and cultivar curves overlap for *Coreopsis*, *Oenothera*, and *Schizachyrium*, indicating that there was no effect of plant source. However, for *Monarda*, the curve for the cultivar lies above the curve for the wild-type. This discrepancy is due to differences in the density of insects on the *Monarda* wild-type plants versus the cultivars. The pooled abundance for the *Monarda* wild-type treatment was approximately 4 times higher than the cultivar treatment, despite that the area sampled for each treatment was the same. The *Monarda* wild-type treatment actually had higher absolute richness, and hence would explain why ANOVA indicated no difference in average richness between the cultivar and wild-type.

### *Insect Community*

The NMDS ordination of the plots indicated that very different insect communities are associated with grasses and herbaceous plants (Fig. 3.3a). This difference was so great that the relationship among the herbaceous plant species was obscured in the ordination. However, a separate NMDS ordination with grasses excluded revealed that insect communities differed among the herbaceous plant species (Fig. 3.3b). The ordinations also revealed that different insect communities were associated with cultivars and wild-type plants for a given plant species. We used PERMANOVA to determine whether the differences in insect communities among treatments were statistically significant. The full two-way model indicated a significant interaction between plant species and plant source ( $F_{3,32}=14.071$ ,  $p\approx 0.001$ ). Because our main interest was differences in the insect community between wild-types and cultivars, we only tested the effect of plant source at each level of plant species in our follow-up analyses. For every plant species, PERMANOVA indicated a significant effect of plant source (*Coreopsis*:  $F_{1,8}=14.228$ ,  $p\approx 0.001$ ; *Monarda*:  $F_{1,8}=17.694$ ,  $p\approx 0.008$ ; *Oenothera*:  $F_{1,8}=19.803$ ,  $p\approx 0.005$ ; *Schizachyrium*:  $F_{1,8}=8.131$ ,  $p\approx 0.01$ ). These results provide strong evidence that cultivars and wild-type plants differ in terms of their associated hemipteran communities.

The multivariate GLM test for the entire insect community also indicated a significant interaction between plant species and plant source in the full model ( $p\approx 0.001$ ). Although the interaction was significant for the multivariate test, this does not imply that the interaction would be significant for each univariate test. We also provide the results of univariate tests under the full model and plots of the abundances of each species (Appendices E and F, respectively). There was a significant effect of plant species (and no interaction) for over half of the insect species; i.e. most of the insect species prefer to feed on some plant species over others. These results fit well with plant-insect interaction theory, but are not the main interest of this experiment. So, as in the PERMANOVA, we only tested the effect of plant source at each level of plant species in our follow-up analyses. The multivariate GLMs gave similar results as PERMANOVA. There was a significant effect of plant source for every plant species (*Coreopsis*:  $p\approx 0.003$ ; *Monarda*:  $p\approx 0.01$ ; *Oenothera*:  $p\approx 0.006$ ; *Schizachyrium*:  $p\approx 0.024$ ). That is, there

was strong evidence that the hemipteran community differed between cultivars and wild-type plants for every plant species. After correcting  $p$  values for multiple comparisons, univariate tests indicated that 3-4 insect species were responsible for the differences in insect communities between cultivars and wild-type plants (Table 3.1). Note that, for *Coreopsis* and *Oenothera*, many more insect species had significantly different abundances between cultivars and wild-type plants before adjusting  $p$  values.

We assigned each insect we collected to a feeding guild based on information about its life history (Appendix G, which also contains food plant records for each insect). Insects were classified as feeding on xylem, phloem, leaf/stem mesophyll, or fruits/seeds, and an insect species could belong to multiple guilds. Of the many xylem-feeding insect species collected, few showed a preference between cultivars and wild-type plants, and there were none with significantly different abundances after adjusting  $p$  values (Table 3.1). However, there were examples of insect species that preferred either the cultivar or the wild-type plant for each of the other three feeding guilds. For phloem-feeding and mesophyll-feeding insects, some insect species appeared to prefer the wild-type plants, while others appeared to prefer the cultivars (Fig. 3.4 and Fig. 3.5). In most cases, the differences in abundance were quite large. For example, the abundance of *Empoasca* sp. was over 8 times higher on the *Monarda* wild-type than the cultivar, and *Sixeonotus unicolor* was almost 6 times higher on the *Coreopsis* cultivar than the wild-type. Differences for the other insect species ranged from approximately four-fold to almost eight-fold. Although the abundances of many of these insects were relatively high, a few showed statistically significant differences between wild-types and cultivars despite having low abundances. For example, the average abundances for *Blissus leucopterosus* on the *Schizachyrium* wild-type and *Ceratocapsus punctulatus* on the *Oenothera* wild-type were 6.2 and 3.6, respectively, yet both were significantly higher than their corresponding cultivars.

For seed-feeding insects, in every instance where there was a significant difference in insect abundance between cultivar and wild-type, it was the wild-type plants that were preferred (Fig. 3.6). Again, the observed differences were very large. *Neopamera bilobata* was over 17 times more abundant on the *Oenothera* wild-type than on the cultivar. *Lygus lineolaris* was 4 times more abundant on the

*Coreopsis* wild-type than the cultivar and over 10 times more abundant on the *Oenothera* wild-type than the cultivar. The abundances of the other two seed-feeding insects were relatively low. *Xyonysius californicus* and *Homaemus proteus* had average abundances of 3.0 and 1.8, respectively, on the *Coreopsis* wild-type, but no individuals of either species were found on the *Coreopsis* cultivar.

#### *Standardized Data*

We observed significant differences in total insect abundance and total insect biomass between cultivars and wild-type plants for several plant species in September. Because this was our last sampling date, we were able to harvest all of the plant material and standardize our insect counts by the amount of plant biomass in plots to determine whether the observed differences were due to an inherent effect of plant source or simply the amount of plant biomass available. Most of the *Coreopsis* individuals in the wild-type treatment were dead by this point, so we excluded both the *Coreopsis* wild-type and cultivar treatments from the analyses. The results of two-way ANOVAs of standardized abundance and standardized insect biomass revealed that standardization actually accentuated the observed differences between cultivars and wild-type plants (Fig. 3.7a and Fig. 3.7b). For example, for *Monarda* the raw abundance was approximately 4 times higher on wild-type plants than cultivars in September, but the standardized abundance was almost 6 times higher on wild-type plants than the cultivars. For *Schizachyrium*, the raw abundance was approximately 2 times higher on the cultivars than the wild-type plants in September, but the standardized abundance was almost 4 times higher on cultivars. The same general result was true for raw insect biomass versus standardized insect biomass. These results indicate plant source, and not differences in the amount of plant biomass available to insects, better explain the number of insects (and insect biomass) collected from plants.

#### **Discussion**

Given that 90% of insect species are host-plant specialists (Bernays and Graham 1988), we expected to find different insect communities associated with each plant species; here, we refer to host-plant specialists as insect species that feed on plants in three or fewer families, and generalists as species that feed on plants in more than three families. Our results agreed with this expectation, providing strong

evidence that different hemipteran species are associated with different plant species. Overall, the largest difference in insect communities was between herbaceous plants and grasses, though there was also strong evidence that a distinct insect community was associated with each herbaceous plant species. The actual number of insect species observed to prefer some plants over others was 35 of 65 – well below the expected 90%. One possible reason for this discrepancy is that our sample size was small, so power may not have been sufficient to detect differences for some of the other insect species, especially those species with low overall abundances. In fact, there were 42 insect species with significantly different abundances among plant species before adjusting  $p$  values, and many that were not significant after adjustment had low overall abundances. Another possibility is that insect species were included in the analyses that were not actually feeding on the plants; these species would more likely show a random pattern of host-plant association rather than being found on one particular plant species. We attempted to reduce the number of these “tourist” species by excluding all species with an overall abundance of 5 or less. We chose a conservative threshold to reduce the possibility of excluding from the analyses any rare species that were actually feeding on the plants, but there is the tradeoff of increasing the probability of including more tourist species. Another explanation is that the proportion of specialists among hemipterans is not as high as the proportion of specialists among herbivorous insects in general. Many of the hemipteran species we collected feed on xylem. There may be less host-plant specialization among these species because xylem generally contains fewer secondary metabolites that might act as feeding deterrents (Peck and Thompson 2008). Note also that we measured the abundances of insects on different species of plants, which implies, but does not directly measure, which plants the insects were feeding on. Therefore, our data give an indication of host plant preferences for individual insect species, but these preferences do not preclude the possibility of the insects having much broader host ranges. In order to actually classify insects as specialists or generalists empirically from the data, direct measures of feeding behavior (and a larger suite of plants to test) would be necessary. Unfortunately, we were also unable to use host plants records from the literature to classify insects as specialists or generalists because records for most species were



ambiguous, insufficient, or nonexistent (e.g. in Appendix G, the best available food plant records for several species was “herbaceous plants”).

Our main interest in this study was not whether different insect species are associated with different species of ornamental plants, but rather does plant source affect the insect community associated with a particular plant. For each of the plant species we tested, we found strong evidence that the hemipteran community differed between cultivars and wild-propagated plants. Our individual tests revealed that insect species belonging to all four of the major feeding guilds were contributing to the overall differences in the insect communities. Xylem-feeding insects showed the weakest pattern, as none had large enough differences in abundance to meet the adjusted level of significance. Again, xylem-feeding insects likely experience fewer secondary metabolites, and this may explain why they were less discriminating between cultivars and wild-types.

For phloem- and mesophyll-feeders, there were examples of insect species that preferred either the cultivar or wild-type plant. The phloem-feeding species included two leafhoppers (Cicadellidae: Megophthalminae and Deltocephalinae), one fulgoroid (Derbidae), and one seed bug (Lygaeidae). The seed bug, *Blissus leucopterosus*, feeds on the phloem of grasses rather than the seeds, as do all other members of the genus (Slater and Baranowski 1990). For three of the species, the wild-type plants were preferred. However, *Balclutha neglecta* exhibited a strong preference for the *Schizachyrium* cultivar. When attempting to explain why certain insect species preferred either the cultivar or wild-type, it is important to note that the individual tests for each species were performed on the pooled dataset, and therefore do not incorporate any information about the seasonal abundances of species. *B. neglecta* did not become abundant until the last sampling date. By this time, most of the wild-type *Schizachyrium* were starting to enter dormancy, whereas the cultivars had a slightly delayed phenology. This difference in phenology of the host-plants in combination with late-season peak abundance of *B. neglecta* could explain the observed preference for the cultivar. For the other phloem-feeding species, it is not clear what differences between cultivars and wild-types might be driving the observed preference for wild-types. Phloem-feeding insects are known to respond strongly to the overall nitrogen content of the phloem as

well as to particular amino acids that act as feeding stimulants (Cook and Denno 1994). However, we did not measure the chemical composition of the phloem (or any other parameters influencing host-plant quality), so any causal mechanisms are entirely speculative.

Among the mesophyll-feeding insects exhibiting the largest differences in abundance between cultivars and wild-types, three were plant bugs (Miridae) and one was a leafhopper (Cicadellidae:Typhlocybinae). Both of these groups use the “lacerate and flush” feeding strategy, in which they use their stylets to pierce the leaf tissue, lacerate the cells, and imbibe the cell contents (Wheeler 2001). Although mesophyll contains more nutrients than xylem or phloem, lacerating the cells also exposes the insect to whatever secondary metabolites that plant may produce as feeding deterrents, suggesting that insects with this feeding strategy would be particularly sensitive to differences in leaf chemistry. Because neither plant bugs nor typhlocybinae leafhoppers were overly represented among the species showing preferences between cultivars and wild-type plants, this suggests either that the cultivars and wild-type plants have similar leaf chemistry or that other characteristics of the plants are playing an equally important role in influencing the host-plant preferences of insects. As with the phloem-feeding species, three species preferred the wild-type plants and only one preferred the cultivar (though there was weak evidence that *Ceratocapsus punctulatus* preferred the *Coreopsis* cultivar to the wild-type). The species preferring the cultivar, *Sixeonotus unicolor*, has been recorded to feed on “garden coreopsis” (Wheeler 2001). It is not clear from the host plant record whether this refers to a cultivated variety of *C. grandiflora* or simply a *Coreopsis* species commonly used for ornamental purposes. One interesting point to note is that none of the four mesophyll-feeding species were collected from *Schizachyrium* (except for 2 individuals of *C. punctulatus*, which were likely tourists). A probable explanation is that the lacerate and flush feeding strategy is not compatible with the particular defenses used by grasses. Grasses typically contain lignin and high levels of silica targeted at mechanically abrading the mouthparts of chewing insects (Cook and Denno 1994). Although hemipterans are not chewing insects, lignin and silica likely defend against the lacerate component of the feeding strategy with similar efficacy.

The seed- and fruit-feeding insects included two lygaeoids (Lygaeidae and Rhyparochromidae), one shield-backed bug (Scutelleridae), and one plant bug (Miridae). The plant bug, *Lygus lineolaris*, can also feed on leaf and stem mesophyll, but appears to prefer the nectar, pollen, and immature fruits from flowers of herbaceous plants (Wheeler 2001). It is considered a serious pest for some agricultural crops and has an unusually broad host range, having been recorded from more than 300 plant species in many different families (Young 1986). In contrast to phloem- and mesophyll-feeders, the seed-feeding insects observed to have the largest differences in abundance between cultivars and wild-types consistently preferred the wild-type plants to the cultivars. Moreover, the only plant species in which a difference was observed were species where the cultivar was sterile. That is, the seed-feeding insects we collected appeared to prefer the *Coreopsis* and *Oenothera* wild-types over the cultivars because the cultivars were sterile, whereas we observed no differences between *Monarda* and *Schizachyrium* cultivars and wild-types, presumably because the cultivars produced viable seeds. The lygaeoids we collected were species that climb plants to feed on seeds, which is a less common strategy among lygaeoids than feeding on seeds that fall to the ground (Slater and Baranowski 1990). Our sampling method would not have collected ground-dwelling insects very effectively, so we may be underestimating the actual number of species of seed-feeding insects that sterile cultivars fail to support. In addition to finding no difference in the numbers of *Xyonysius californicus* and *L. lineolaris* on *Monarda* cultivars and wild-types (Fig. 3.6), we collected several specialist seed-feeding species on both *Monarda* and *Schizachyrium* that did not discriminate between the cultivars and wild-types. For example, the scentless plant bug *Arhyssus nigristernum* (Rhopalidae), a specialist on *Monarda* and other mints (Schaefer and Chopra 1982), and the seed bug *Paromius longulus* (Rhyparochromidae), a specialist on grasses (Slater and Baranowski 1990), were found in similar numbers on cultivars and wild-types (Appendix F). It is clear why seed-feeding insects would be less abundant on sterile plants, but an additional point to note is that both of the sterile cultivars were hybrids, whereas both fertile cultivars were selections of the straight species. A common mechanism by which hybrid plants become sterile is crossing two species with an even, but different ploidy level to produce offspring with an odd ploidy level. Although we did not measure the chromosome

number of our plants, this or another genetic mechanism is likely causing the sterility observed in the *Coreopsis* and *Oenothera* cultivars. We originally speculated that the genetic diversity of the host plants may influence the insects that feed on those plants, and while these results do not necessarily imply this is the case, they do support the idea that the genetic origin of cultivars is important.

In addition to determining whether there were differences in the insect community, we wanted to know whether cultivars and wild-type plants differed for more general parameters, such as total insect abundance, biomass, and diversity. There was close correspondence between total abundance and total insect biomass overall, with the exception of *Monarda* cultivars and wild-types. Insect abundance was significantly higher on *Monarda* wild-type plants for every sampling date, but there were no differences in insect biomass. The analyses of the insect community give some insight into the reason behind this discrepancy. The most abundant insect collected from *Monarda* was a species of *Empoasca*, and its average pooled abundance was over 8 times higher on the wild-type plants than the cultivars. *Empoasca* belongs to a subfamily of leafhoppers that are especially small, usually between 3 and 4 mm (DeLong 1931). Because of their small size relative to the other species of hemipterans we collected, they represented only a small proportion of the total biomass, despite being numerically dominant. Another trend to note in the abundance and biomass data is that, for the most part, differences between cultivars and wild-types were not consistent across sampling date, and in one case the pattern actually reversed. More insects and more insect biomass were collected from the *Coreopsis* wild-type on the first sampling date, but insect abundance and biomass were much higher on the cultivar by the last sampling date. This pattern can be explained by the fact that very few individuals of the *Coreopsis* wild-type were alive by the end of the growing season. Some individuals of the *Coreopsis* cultivar also died during the experiment, but more were alive on the last sampling date than had died. An obvious question is: did the higher feeding pressure on the *Coreopsis* wild-type plants early in the year cause their decline? While it is certainly possible, *Coreopsis grandiflora* is a short-lived perennial and most likely had reached the end of its life cycle. Other trends to note include a sharp decline in insect abundance and biomass on the *Oenothera* wild-type plants and an increase in insect abundance and biomass on the *Schizachyrium*

cultivar. Again, the analyses of the insect communities give insights into these patterns. *Neopamera bilobata*, a seed-feeding insect, was more abundant on the *Oenothera* wild-type than the cultivar and made up a large proportion of the total insect biomass collected from *Oenothera* wild-types. *Oenothera* blooms in early May and sets seed shortly after, with most seeds being dispersed by late summer. Although it is not apparent in the pooled data, *N. bilobata* was especially abundant on the first sampling date and declined substantially on each subsequent sampling, suggesting its population size was responding to the phenology of the *Oenothera* wild-types. For *Schizachyrium*, the most abundant insect species collected was *B. neglecta*, and, as noted earlier, the combination of its late season peak abundance and early onset of dormancy in the wild-type plants likely explains its preference for the cultivars.

There was no evidence for a difference in hemipteran diversity between cultivars and wild-types for any of the plant species we tested. Given the other variables we measured, this is not surprising. The differences we observed in total abundance and total biomass were largely due to single, numerically dominant species. Because species richness does not measure the dominance or evenness of the community, single species that have a large effect on parameters such as total abundance and biomass would not have an undue influence on diversity. Also, when we investigated which insect species were contributing to the differences we observed in the overall community, we found that some species preferred cultivars and others preferred wild-type plants. Together, the overall differences in the insect community and the lack of difference in diversity suggest that cultivars and wild-types support a similar number of insect species, but the particular species are different. Species richness is often criticized as a poor measure of diversity (Magurran 2004). To confirm that other methods would give similar results, we also used individual-based rarefaction [Hurlbert's (1971) formulation] and a diversity index called the Q-statistic to assess diversity (Kempton et al. 1978). Like species richness, the Q-statistic is robust to the presence of over-dominant species because it excludes both the most and least abundant species from the measure. Unlike species richness, however, it incorporates information about the relative abundances of insects. The Q-statistic gave exactly the same overall conclusion as species richness, and rarefaction gave a similar conclusion. The primary difference evident in the rarefaction curve is that the *Monarda* cultivar

appeared to support more species of insects than the wild-type plants. Again, this effect is largely due to the higher abundance of *Empoasca* sp. on the wild-type plants relative to the cultivar. Although a higher absolute richness was observed for the wild-type plants, the high density of *Empoasca* sp. on the wild-types extends the wild-type curve to such a degree that it lies below the cultivar curve. Given this caveat, it is difficult to discern whether a difference in diversity actually exists.

Previous research investigating the ecological value of ornamental plants has either focused entirely on exotics vs. natives or compared cultivars with wild-type plants only in terms of the pollinators they support. Moreover, the work with exotics and natives primarily focused on chewing insects and woody plants, with very little mention of sucking/piercing insects. With woody plants, it makes more sense to focus on a group of chewing insects, such as lepidopteran larvae, because woody plants support many more species than herbaceous plants (Tallamy and Shropshire 2009). However, for this same reason, we chose to focus on hemipterans rather than chewing insects because they are often the dominant group associated with herbaceous plants. Although most work has been focused on chewing insects, one study did include piercing/sucking insects. Burghardt and Tallamy (2013) found that phloem-feeding insects, but not xylem- or mesophyll-feeding insects, were more abundant on native plants than exotics. This difference was present whether the exotics had close native relatives or not, but was only statistically significant on one of their three sampling dates. Our results were similar in the sense that differences between cultivars and wild-type plants were inconsistent over multiple sample dates. However, it is difficult to make more comparisons because we compared the insects feeding on cultivars and wild-types of the same plant species, whereas they compared groups of native and exotic plants; i.e. their data are insect abundances that were combined across multiple plant species.

Studies that compared cultivars of native ornamental plants with wild-types in terms of their abilities to support native insects primarily focused on pollinators. Corbet et al. (2001) compared single-flowered varieties of several native perennials and one exotic perennial with double-flowered varieties of the same species. In all species but one, they found that the double-flowered forms secreted less nectar and were visited by fewer pollinators than the single-flowered forms. For the species in which no

differences were observed, the double flower resulted from a morphological change that did not alter nectar secretion, and presumably did not affect insect visitors for this reason. Other research compared wild-types with cultivars that differed in flower morphology (specifically, presence vs. absence of a nectar spur, large vs. normal size flowers, radial vs. bilateral symmetry, and double vs. single), but not in nectar levels, and found that the abundances of particular species of pollinators, and sometimes overall pollinator abundance, were lower on cultivars (Comba et al. 1999). They speculated that differences in flower accessibility were affecting certain pollinator species. Although the feeding strategy of pollinators is quite different from that of hemipterans, the results we observed with regard to seed-feeding insects are directly analogous to the results of these pollinator experiments. In both Comba et al. (1999) and Corbet et al. (2001), fewer insects were supported because the cultivars did not produce the food resource that the insects needed, or the food resource was unavailable. Similarly, we found fewer seed-feeding insect on sterile cultivars because their food resource was absent. The codependency between insects and flowers for plant reproduction has long been recognized (Sprengel 1793). These mutualistic relationships are a result of a long history of coevolution. Our results provide additional evidence that selecting for traits that alter the reproduction biology of the plants, and hence perturb the result of millions of years of increasing specialization, has a strong negative impact on the insects that utilize those plants.

Other studies have evaluated ornamental cultivars with respect to the insects that feed on them, but all were from the perspective of deterring insects rather than supporting them; i.e. the authors were looking for insect resistant varieties or attempting to determine which plant characteristics promote insect resistance. Several studies tested cultivar susceptibility to a single or a handful of insect species that were considered pests of particular importance (Bentz and Townsend 1999; Bentz and Townsend 2001; Bentz and Townsend 2003; Seagraves et al. 2013). In some cases, susceptibility was measured in terms of plant parameters (e.g. defoliation, number of flagging shoots, etc.), and in other cases susceptibility was measured in terms of insect parameters (e.g. number of eggs laid, percentage of nymphs reaching adulthood, etc.). In all cases, susceptibility varied widely among cultivars, regardless of the host plant, insect species, or response variable of interest. Additional studies have considered the insect community

as a whole rather than a single species. For example, Bentz and Townsend (2005) compared the leafhopper communities of 17 different cultivars of red maple. Both abundance and diversity of leafhoppers differed among the cultivars, though the differences were largely due to one or two cultivars with much higher or much lower abundance/diversity than the others. The percentage similarity of the leafhopper communities (measured as Renkonen index) ranged from 56% to 90% similar. Although these studies illustrate that cultivars can differ in terms of the number of insects and number of insect species they support, none compared cultivars with wild-type plants. One study compared cultivars of ninebark with the “native” type, though it is not clear whether native refers to seed-propagated plants or simply clones collected from a wild population (Tenczar and Krischik 2007). They found that a leaf-feeding beetle fed more and laid more eggs on the native type and a cultivar with light green leaves than a cultivar with dark purple leaves. Although the authors approached the question of insect feeding on cultivars from a different perspective, taken together, their results provide the same overall conclusion as our study: plants of the same species can support different herbivorous insects when their genetic origins differ.

Future research should not only address the differences in the insect communities associated with cultivars and wild-type plants, but also what characteristics of the plants are driving these differences. One possible explanation for the differences we observed is variation in the composition or concentration of secondary metabolites that act as feeding deterrents. Diverse assemblages of flavonoid glycosides have been found in both *Oenothera fruticosa* and *Coreopsis grandiflora* (Crawford and Smith 1980; Johnson et al. 2014), and these are known to act as feeding deterrents for hemipterans (Cook and Denno 1994). *Amsonia tabernaemontana* produces latex containing indole alkaloids, a potent group of secondary metabolites that deter many types of herbivores (Treimer and Zenk 1979), and the presence of these alkaloids may explain why only one species of leafhopper was found feeding on *Amsonia*. Another possibility is that insects were responding to variation in physical feeding deterrents, such as the density or types of leaf trichomes. Trichomes are especially effective against leafhoppers, either by entangling nymphs of small species or by acting as a physical barrier that prevents stylet access. Pubescent varieties of several crop species, including cotton (e.g. Butler et al. 1991; Atakan et al. 2004), okra (e.g. Hooda et



al. 1997), and potato (e.g. Kaplan et al. 2009), tend to be more resistant to leafhopper pests than glabrous varieties. Glandular trichomes are doubly effective because they not only provide a physical defense, but also deter insects by entrapping them in sticky residues or releasing chemicals that are unpalatable or toxic. For example, glandular-haired varieties of alfalfa deter the leafhopper *Empoasca fabae*, a major pest of that crop (Elden and McCaslin 1997; Sulc et al. 2001; Casteel et al. 2006), and some evidence indicates that unpalatable or toxic chemicals contained in the hairs are at least partially responsible for conferring resistance (Ranger et al. 2004). Like other mints, the pubescence of *Monarda fistulosa* typically includes both glandular hairs and punctate glands, and these glands contain essential oils. The glands usually contain a mixture of different oils, with thymol often being found in the highest concentration (Pfab et al. 1980; Zamurenko et al. 1989; Contaldo et al. 2011), though some populations are known to contain mostly geraniol (Simon et al. 1986). It is possible that either the density or chemical composition of these hairs was responsible for the differences in insect abundance we observed between *Monarda* cultivars and wild-types.

Rather than feeding deterrents, insects could have instead been responding to differences in feeding stimulants. Hemipterans are known to prefer host plants with higher concentrations of amino acids in the phloem, and specific amino acids sometimes act as feeding stimulants (Cook and Denno 1994). *Empoasca fabae* laid more eggs and survived to adulthood in higher percentages on elm and maple cultivars with higher leaf nitrogen (Bentz and Townsend 2001) and oviposited more often on maple cultivars that were fertilized with higher concentrations of nitrogen (Bentz and Townsend 2003). Similarly, a species of leaf beetle preferred a cultivar and native form of ninebark with higher nitrogen content to a cultivar with lower nitrogen content; however, the less preferred cultivar also had higher concentrations of anthocyanins, a type of flavonoid known to act as a feeding deterrent, confounding the possible effect of lower leaf nitrogen on feeding (Tenczar and Krischik 2007). Because hemipterans in particular are known to respond strongly to nitrogen content, this aspect of host plant quality may be equally important as more frequently cited drivers of host plant specialization, such as secondary

metabolite chemistry , and should be investigated in any future research that aims to determine why herbivorous insects discriminate between cultivars and wild-type plants.

Although we mentioned that the amount of genetic diversity contained in cultivars versus wild-type plants propagated from seed could be driving differences in insect abundance on the plants, this research did not investigate that question directly. All of the plants we used in this experiment were outbreeding species (Carman and Hatch 1982; Crawford and Smith 1984; Cruden et al. 1984; Godfrey and Johnson 2014), and so should contain much higher genetic diversity than the cultivars propagated asexually. However, the *Schizachyrium* cultivar is propagated by seed, so it may, but does not necessarily, contain lower genetic diversity than the wild-type plants. In *Oenothera*, genetic variation among individual host plants was correlated with variation in the associated arthropod communities (Johnson and Agrawal 2005; Johnson and Agrawal 2007; Johnson 2008), and more diverse plant assemblages supported more diverse arthropod assemblages (Johnson et al. 2006). It is possible that genetic variation results in variation in secondary metabolites, nitrogen utilization, leaf pubescence, or other traits that are known to affect insect herbivores. Future research should investigate how genetics might interact with host plant quality to affect the insect community on cultivars and wild-type plants.

This research was conducted in the field, and hence tested whether insects discriminate among food plants when given a choice. Although we found that many insect species preferred certain plant species over others and some insect species preferred the wild-type plants over cultivars (or vice versa), the results do not necessarily imply that the insects were unable to feed on the non-preferred plants in either case. That is, under a different scenario, such as no-choice feeding experiment, we may not have observed such a high degree of specialization or discrimination between cultivars and wild types. In light of this, future research should not only investigate which characteristics of the plants are most associated with the patterns in host use, but also should address whether these characteristics actually prevent insect species from feeding on the non-preferred plants (i.e. reflect true host plant specialization) or simply deter insects when higher quality food plants are available. If the latter case is true, an observed difference in abundance for a species of insect may overestimate the differences in host plant quality among plant

groups (e.g. plant species, source, etc.). This is particularly important to consider when comparing the ecological value of cultivars and wild-type plants. For example, consider an insect species that was found in much lower abundance on the cultivar of a plant than it was on the wild type. The low abundance of the insect on the cultivar may not indicate that the cultivar is an inferior host; it may only indicate that the wild-type plants are preferred under a choice setting. If only the cultivar had been planted (no-choice setting), the cultivar may prove to support an equal number of individuals of the insect as the wild-type plants. Note that an intermediate response is also possible. When planted alone, a cultivar may support a higher abundance of a particular insect species than when the insects are provided a choice, but the productivity of the insect may be lower on the cultivar than the wild-type plant.

## **Conclusions**

Although cultivars and wild-type plants of every plant species we tested differed in terms of their associated hemipteran communities, they did not differ in hemipteran species diversity. In addition, the differences in total hemipteran biomass and abundance we observed appeared to be related to single species of insect that preferred the wild-type over the cultivar (or vice versa), and these differences were not consistent over the growing season. These results suggest hemipteran abundance and diversity does not depend on the source of the plant material *per se*, but rather on the particular characteristics of the cultivar that distinguish it from the wild type. Certain characteristics are likely detrimental for wildlife, such as altering the reproductive biology of the plants by changing flower morphology or selecting for sterility. Other characteristics, perhaps nitrogen utilization or plant architecture, may actually benefit wildlife, and identifying these characteristics should be a priority for future research. This knowledge could enable plant breeders to select varieties that potentially outperform the wild-type plants in terms of their abilities to support wildlife.

Possibly the best way to improve landscapes for wildlife is to include more plant species, regardless of whether they are cultivars or wild-type plants propagated from seed. We observed differences in abundance for more insect species when we compared different plant species than we did when we compared cultivars and wild-types within a plant species. These results fit both with the

expectations of plant-insect interaction theory and with empirical evidence that host plant diversity drives arthropod diversity. Our results also suggest that planting unrelated species will do more to enhance insect diversity than will planting species within one family or within a few genera. Although there is a growing interest in this sort of enhancement of residential landscapes, the greater challenge remains encouraging more people to convert monoculture lawns into gardens containing diverse assemblages of ornamental plants. When the amount of land in residential development is on the scale of hundreds of millions of acres, it will take more than a niche interest in native plant gardening among homeowners to make a measurable impact on reversing the large-scale ecosystem trend of declining biodiversity.

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### **Literature Cited**

- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32-46.
- Atakan, E., K. Boyaci, and O. Gencer. 2004. Population development of leafhoppers *Asymmetrasca decedens* (Paoli) and *Empoasca decipiens* Paoli (Homoptera: Cicadellidae) on some cotton varieties. *Turkiye Entomoloji Dergisi* 28:267-273.
- Bentz, J. A., and A. M. Townsend. 1999. Feeding injury, oviposition, and nymphal survivorship of the potato leafhopper on red maple and Freeman maple clones. *Environmental Entomology* 28:456-460.
- Bentz, J. A., and A. M. Townsend. 2001. Leaf element content and utilization of maple and elm as hosts by the potato leafhopper (Homoptera : Cicadellidae). *Environmental Entomology* 30:533-539.

- Bentz, J. A., and A. M. Townsend. 2003. Nitrogen fertilization and use of container-grown maple selections as hosts by the potato leafhopper. *Journal of the American Society for Horticultural Science* 128:821-826.
- Bentz, J. A., and A. M. Townsend. 2005. Diversity and abundance of leafhopper species (Homoptera: Cicadellidae) among red maple clones. *Journal of Insect Conservation* 9:29-39.
- Bernays, E., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886-892.
- Burghardt, K. T., and D. W. Tallamy. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. *Diversity and Distributions* 19:1553-1565.
- Burghardt, K. T., D. W. Tallamy, C. Philips, and K. J. Shropshire. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1(5):art11. doi:10.1890/ES10-00032.1
- Burghardt, K. T., D. W. Tallamy, and W. G. Shriver. 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology* 23:219-224.
- Butler, G. D., F. D. Wilson, and G. Fishler. 1991. Cotton leaf trichomes and populations of *Empoasca lybica* and *Bemisia tabaci*. *Crop Protection* 10:461-464.
- Carman, J. G., and S. L. Hatch. 1982. Aposporous apomixis in *Schizachyrium* (Poaceae, Andropogoneae). *Crop Science* 22:1252-1255.
- Casteel, C. L., C. M. Ranger, E. A. Backus, M. R. Ellersieck, and D. W. Johnson. 2006. Influence of plant ontogeny and abiotic factors on resistance of glandular-haired alfalfa to potato leafhopper (Hemiptera : Cicadellidae). *Journal of Economic Entomology* 99:537-543.
- Comba, L., S. A. Corbet, A. Barron, A. Bird, S. Collinge, N. Miyazaki, and M. Powell. 1999. Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* 83:73-86.

- Contaldo, N., M. G. Bellardi, L. Cavicchi, F. Epifano, S. Genovese, M. Curini, and A. Bertaccini. 2011. Phytochemical effects of phytoplasma infections on essential oil of *Monarda fistulosa* L. Bulletin of Insectology 64(Supplement):S177-S178.
- Cook, A.G., and R.F. Denno. 1994. Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense, and host plant specialization. Pages 114-139 in R.F. Denno and T.J. Perfect, editors. Planthoppers: their ecology and management. Chapman and Hall, New York.
- Corbet, S. A., J. Bee, K. Dasmahapatra, S. Gale, E. Gorringer, B. La Ferla, T. Moorhouse, A. Trevail, Y. Van Bergen, and M. Vorontsova. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. Annals of Botany 87:219-232.
- Crawford, D. J., and E. B. Smith. 1980. Flavonoid chemistry of *Coreopsis grandiflora* (Compositae). Brittonia 32:154-159.
- Crawford, D. J., and E. B. Smith. 1984. Allozyme divergence and intraspecific variation in *Coreopsis grandiflora* (Compositae). Systematic Botany 9:219-225.
- Cruden, R. W., L. Hermanutz, and J. Shuttleworth. 1984. The pollination biology and breeding system of *Monarda fistulosa* (Labiatae). Oecologia 64:104-110.
- DeLong, D.M. 1931. A revision of the American species of *Empoasca* known to occur north of Mexico. Technical bulletin N-231. United States Department of Agriculture, Washington, D.C.
- Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608.
- Elden, T. C., and M. McCaslin. 1997. Potato leafhopper (Homoptera: Cicadellidae) resistance in perennial glandular-haired alfalfa clones. Journal of Economic Entomology 90:842-847.
- Fraenkel, G. S. 1959. The raison d' être of secondary plant substances. Science 129:1466-1470.
- Gaston, K.J. 1996. Species richness: measure and measurement. Pages 77-113 in K.J. Gaston, editor. Biodiversity: a biology of numbers and difference. Blackwell Science, Oxford, UK.

- Gavier-Pizarro, G. I., V. C. Radeloff, S. I. Stewart, C. D. Huebner, and N. S. Keuler. 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20:1913-1925.
- Godfrey, R. M., and M. T. J. Johnson. 2014. Effects of functionally asexual reproduction on quantitative genetic variation in the evening primroses (*Oenothera*, Onagraceae). *American Journal of Botany* 101:1906-1914.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379-391.
- Hooda, V. S., B. S. Dhankhar, and R. Singh. 1997. Evaluation of okra cultivars for field resistance to the leafhopper *Amrasca biguttula biguttula* (Ishida). *Insect Science and its Application* 17:323-327.
- Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577-586.
- Johnson, M. T. J. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89:145-154.
- Johnson, M. T. J., and A. A. Agrawal. 2005. Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology* 86:874-885.
- Johnson, M. T. J., and A. A. Agrawal. 2007. Covariation and composition of arthropod species across plant genotypes of evening primrose (*Oenothera biennis*). *Oikos* 116:941-956.
- Johnson, M. T. J., A. R. Ives, J. Ahern, and J.P. Salminen. 2014. Macroevolution of plant defenses against herbivores in the evening primroses. *New Phytologist* 203:267-279.
- Johnson, M. T. J., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9:24-34.
- Kaplan, I., G. P. Dively, and R. F. Denno. 2009. The costs of anti-herbivore defense traits in agricultural crop plants: a case study involving leafhoppers and trichomes. *Ecological Applications* 19:864-872.
- Kempton, R. A., and L. R. Taylor. 1978. The Q statistic and the diversity of floras. *Nature* 275: 252 -253.

- Kim, J., J. Chae, and T.H. Koo. 2007. Variation in bird diversity in relation to habitat size in the urban landscape of Seoul, South Korea. *Acta Ornithologica* 42:39-44.
- Legendre, P., and L. Legendre. 2012. *Numerical Ecology*. 3<sup>rd</sup> edition. Elsevier, Amsterdam.
- Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. *Bioscience* 51:95-102.
- Magurran, A. E. 2004. *Measuring biological diversity*. Blackwell Pub., Maldan, MA.
- McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127:247-260.
- Mphosi, M. S., and S. P. Foster. 2010. Female preference and larval performance of sunflower moth, *Homoeosoma electellum*, on sunflower pre-breeding lines. *Entomologia Experimentalis Et Applicata* 134:182-190.
- Nickerson C., R. Ebel, A. Borchers, and F. Carriazo. 2011. *Major uses of land in the United States, 2007*. EIB-89. U.S. Department of Agriculture, Economic Research Service.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2013. *vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>.
- Peck, D.C., and V. Thompson. 2008. Spittlebugs (Hemiptera:Cercopoidea). Pages 3512-3516 in J.L. Capinera, editor. *Encyclopedia of entomology*. 2<sup>nd</sup> edition. Springer, Netherlands.
- Pfab, I., G. Heinrich, and W. Francke. 1980. Glucoside bound components in the volatile oil of *Monarda fistulosa*. *Biochemie Und Physiologie Der Pflanzen* 175:194-207.
- Pimentel, D., and A.G.J. Wheeler. 1973. Species and diversity of arthropods in the alfalfa community. *Environmental Entomology* 2:659-668.
- R Core Team. 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.



- Ranger, C. M., E. A. Backus, R. E. K. Winter, G. E. Rottinghaus, M. R. Ellersieck, and D. W. Johnson. 2004. Glandular trichome extracts from *Medicago sativa* deter settling by the potato leafhopper *Empoasca fabae*. *Journal of Chemical Ecology* 30:927-943.
- Schaefer, C.W., and N.P. Chopra. 1982. Cladistic analysis of the Rhopalidae (Hemiptera, Coreoidea) with a list of food plants. *Annals of the Entomological Society of America* 75:224-233.
- Seagraves, B. L., C. T. Redmond, and D. A. Potter. 2013. Relative resistance or susceptibility of maple (*Acer*) species, hybrids and cultivars to six arthropod pests of production nurseries. *Pest Management Science* 69:112-119.
- Simon, D. Z., J. Beliveau, and C. Aube. 1986. Extraction by hydrodiffusion of the essential oil of *Monarda fistulosa* grown in the province of Quebec, Canada: assay of geraniol in the hydrodiffused oil. *International Journal of Crude Drug Research* 24:120-122.
- Slater, J.A., and R.M. Baranowski. 1990. Lygaeidae of Florida (Hemiptera: Heteroptera). *Arthropods of Florida and Neighboring Land Areas* 14:1-211.
- Spengel, C.K. 1793. *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen*. Berlin.
- Sulc, R. M., E. van Santen, K. D. Johnson, C. C. Sheaffer, D. J. Undersander, L. W. Bledsoe, D. B. Hogg, and H. R. Willson. 2001. Glandular-haired cultivars reduce potato leafhopper damage in alfalfa. *Agronomy Journal* 93:1287-1296.
- Tallamy, D. W. 2004. Do alien plants reduce insect biomass? *Conservation Biology* 18:1689-1692.
- Tallamy, D.W., and K.J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. *Conservation Biology* 23:941-947.
- Tallamy, D. W., M. Ballard, and V. D'Amico. 2010. Can alien plants support generalist insect herbivores? *Biological Invasions* 12:2285-2292.
- Tenczar, E. G., and V. A. Krischik. 2007. Effects of new cultivars of ninebark on feeding and ovipositional behavior of the specialist ninebark beetle, *Calligrapha spiraeae* (Coleoptera : Chrysomelidae). *Hortscience* 42:1396-1399.

- Treimer, J. F., and M. H. Zenk. 1979. Purification and properties of strictosidine synthase, the key enzyme in indole alkaloid formation. *European Journal of Biochemistry* 101:225-233.
- Wallner, A. M., B. Molano-Flores, and C. H. Dietrich. 2013. Using Auchenorrhyncha (Insecta: Hemiptera) to develop a new insect index in measuring North American tallgrass prairie quality. *Ecological Indicators* 25:58-64.
- Waloff, N. 1980. Studies on grassland leafhoppers (Auchenorrhyncha, Homoptera) and their natural enemies. *Advances in Ecological Research* 11:81-215.
- Wang, Y., U. Naumann, S. Wright, and D. Warton. 2014. mvabund: Statistical Methods for Analysing Multivariate Abundance Data. R package version 3.9.3. <http://CRAN.R-project.org/package=mvabund>
- Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3:89-101.
- Wheeler, A.G. 2001. *Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists.* Cornell University Press, Ithaca, New York.
- Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1:344-346.
- Wilson, S. W., J. L. Smith, and A. H. Purcell. 1993. An inexpensive vacuum collector for insect sampling. *Entomological News* 104:203-208.
- Wimp, G. M., W. P. Young, S. A. Woolbright, G. D. Martinsen, P. Keim, T. G. Whitham, and T. Meagher. 2004. Conserving plant genetic diversity for dependent animal communities. *Ecology Letters* 7:776-780.
- Young, O. P. 1986. Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera, Miridae). *Annals of the Entomological Society of America* 79:747-762.
- Zamureenko, V. A., N. A. Klyuev, B. V. Bocharov, V. S. Kabanov, and A. M. Zakharov. 1989. Investigation of the component composition of *Monarda fistulosa* essential oil. *Chemistry of Natural Compounds* 5:549-551.

Zuefle, M. E., W. P. Brown, and D. W. Tallamy. 2008. Effects of non-native plants on the native insect community of Delaware. *Biological Invasions* 10:1159-1169.

Table 3.1. Individual insect species contributing to differences in the insect communities of cultivars and wild-type plants of *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium* according to univariate GLMs of insect abundance.

Comparison	Insect Species	Family	Feeding Guild <sup>1</sup>	Unadjusted <i>p</i> value (approx.)	Adjusted <i>p</i> value <sup>2</sup> (approx.)
<i>Coreopsis</i> Cultivar vs. Wild-type	<i>Sixeonotus unicolor</i>	Miridae	M	0.002	0.005*
	<i>Lygus lineolaris</i>	Miridae	M, F	0.002	0.003*
	<i>Halticus bracteatus</i>	Miridae	M	0.020	0.126
	<i>Ceratocapsus punctulatus</i>	Miridae	M	0.017	0.117
	<i>Homaemus proteus</i>	Scutelleridae	F	0.002	0.014*
	<i>Xyonysius californicus</i>	Lygaeidae	F	0.002	0.005*
	<i>Paraulacizes irrorata</i>	Cicadellidae	X	0.048	0.373
	<i>Graminella nigrifrons</i>	Cicadellidae	P	0.037	0.286
	<i>Liburniella ornata</i>	Delphacidae	P	0.039	0.372
<i>Monarda</i> Cultivar vs. Wild-type	<i>Scaphytopius acutus</i>	Cicadellidae	P	0.022	0.252
	<i>Agallia constricta</i>	Cicadellidae	P	0.004	0.031*
	<i>Empoasca sp.</i>	Cicadellidae	M	0.003	0.001*
	<i>Halticus bracteatus</i>	Miridae	M	0.004	0.022*
<i>Oenothera</i> Cultivar vs. Wild-type	<i>Coelidia olitoria</i>	Cicadellidae	P	0.032	0.231
	<i>Osbornellus clarus</i>	Cicadellidae	P	0.035	0.819
	<i>Scaphytopius acutus</i>	Cicadellidae	P	0.027	0.480
	<i>Agallia constricta</i>	Cicadellidae	P	0.001	0.004*
	<i>Typhlocybinæ spp.</i>	Cicadellidae	M	0.012	0.547
	<i>Draeculacephala robinsoni</i>	Cicadellidae	X	0.035	0.358
	<i>Clastoptera xanthocephala</i>	Clastoperidae	X	0.001	0.152
	<i>Spissistilus festinus</i>	Membracidae	P	0.008	0.111
	<i>Neopamera bilobata</i>	Rhyparochromidae	F	0.001	0.004*
	<i>Heraeus plebejus</i>	Rhyparochromidae	F	0.005	0.185
	<i>Lygus lineolaris</i>	Miridae	M, F	0.001	0.011*
	<i>Ceratocapsus punctulatus</i>	Miridae	M	0.001	0.031*
<i>Schizachyrium</i> Cultivar vs. Wild-type	<i>Tylozygus bifida</i>	Cicadellidae	X	0.007	0.072
	<i>Balclutha neglecta</i>	Cicadellidae	P	0.004	0.005*
	<i>Blissus leucopterus</i>	Blissidae	P	0.003	0.006*
	<i>Anotia burnetii</i>	Derbidae	P	0.007	0.042*
	<i>Paramysidia mississippiensis</i>	Derbidae	P	0.011	0.051

<sup>1</sup> Abbreviations are M, Mesophyll (leaf and stem); P, Phloem; X, Xylem; and F, Fruit/seed.

<sup>2</sup> After correcting for multiple comparisons, only 3-4 insect species for any given plants species had significantly different abundances at  $\alpha=.05$  (denoted by an asterisk).

Figure 3.1. Plots of (a) total abundance of adult hemipterans and (b) total hemipteran biomass for cultivars and wild-type plants of each plant species at three sampling dates. Asterisks indicate significant differences in means between cultivars and wild-type plants for a given plant species on a given date. Three asterisks represent differences that were significant after a Bonferroni correction for multiple comparisons with an experiment-wise  $\alpha=.05$  (p-value<0.00417). One asterisk represents differences that were significant after a Bonferroni correction with an experiment-wise  $\alpha=.10$  (p-value<0.00833). Error bars are SD.

Figure 3.2. Plots of (a) species richness and (b) Q-statistic for cultivars and wild-type plants of each plant species pooled over three sampling dates. Species richness and the Q-statistic were used as measures of species diversity of adult hemipterans for each treatment. Different letters denote means of plants species that were significantly different at  $\alpha=.05$  after correcting for multiple comparisons with Tukey's HSD test. *Oenothera* had higher average species richness and values of the Q-statistic than the other three plant species. There was no evidence for a difference in richness or the Q-statistic between wild-type plants and cultivars for any plant species. Error bars are SD.

Figure 3.3. Non-metric Multidimensional Scaling ordinations for (a) cultivars (CV) and wild-type (WT) plants of *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium* and (b) cultivars and wild-type plants of *Coreopsis*, *Monarda*, and *Oenothera* only. The ordinations use the semi-metric "percent dissimilarity" (i.e. Bray-Curtis dissimilarity). In (a), the three herbaceous plants form a group distinct from the grasses, but groupings by treatment are not clear. In (b), plots within a treatment are closer than plots between treatments, suggesting that each treatment has a distinct insect community associated with it.

Figure 3.4. Abundances of phloem-feeding insects that showed the strongest differences between cultivars and wild-type plants for *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium*. Asterisks indicate plant species where there was a significant difference between the cultivar and wild-type at  $\alpha=0.05$  after correcting for multiple comparisons. Error bars are SD.

Figure 3.5. Abundances of mesophyll-feeding insects that showed the strongest differences between cultivars and wild-type plants for *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium*. Asterisks indicate plant species where there was a significant difference between the cultivar and wild-type at  $\alpha=0.05$  after correcting for multiple comparisons. Error bars are SD.

Figure 3.6. Abundances of seed- and fruit-feeding insects that showed the strongest differences between cultivars and wild-type plants for *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium*. Note that *Lygus* feeds on both fruits and mesophyll. Asterisks indicate plant species where there was a significant difference between the cultivar and wild-type at  $\alpha=0.05$  after correcting for multiple comparisons. Error bars are SD.

Figure 3.7. Plots of (a) standardized abundance of adult hemipterans and (b) standardized insect biomass on cultivars and wild-type plants of *Monarda*, *Oenothera* and *Schizachyrium* in September. *Coreopsis* cultivars and wild-type plants were not included because most of the plants were dead by September. Asterisks represent significant differences in mean abundance or biomass between cultivars and wild-type plants for a given plant species after a Bonferroni correction with an experiment-wise  $\alpha=.05$  ( $p\text{-value}<0.0167$ ). The differences in standardized abundance and biomass were actually greater (and in the same direction) than the differences observed for the raw abundance and biomass; i.e. standardization accentuated the differences observed using the raw data. Error bars are SD.

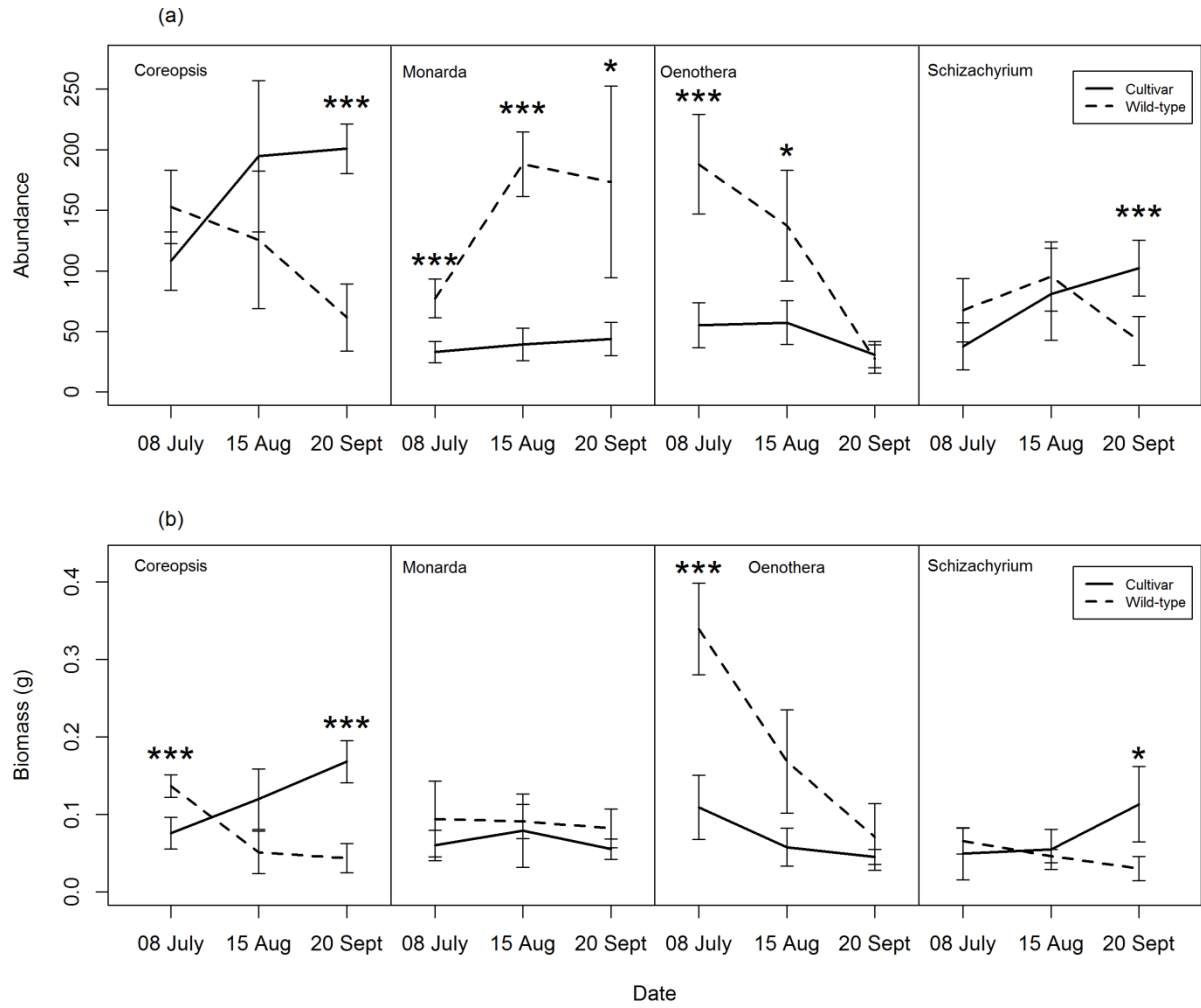


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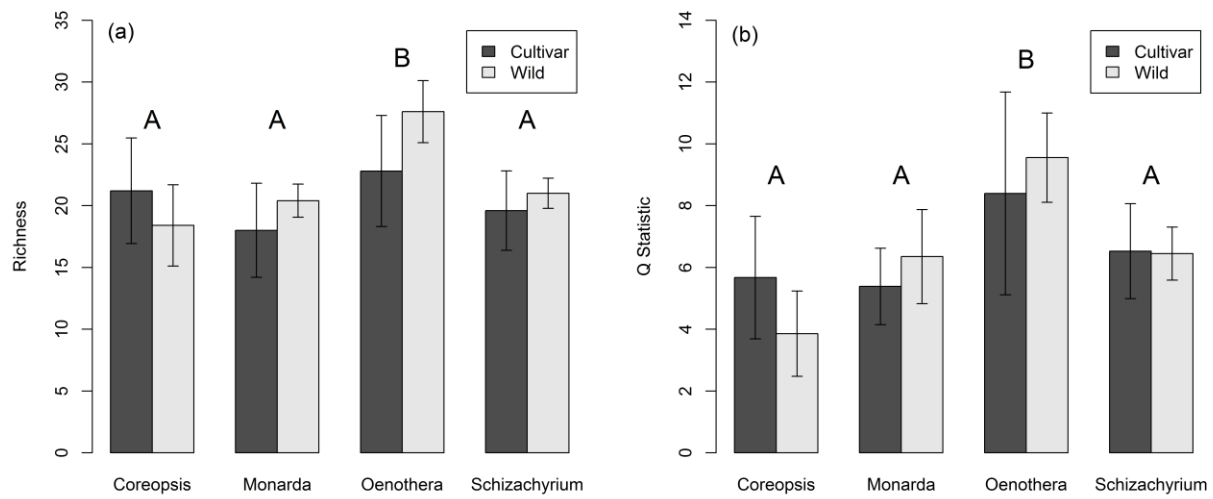


Figure 3.2.



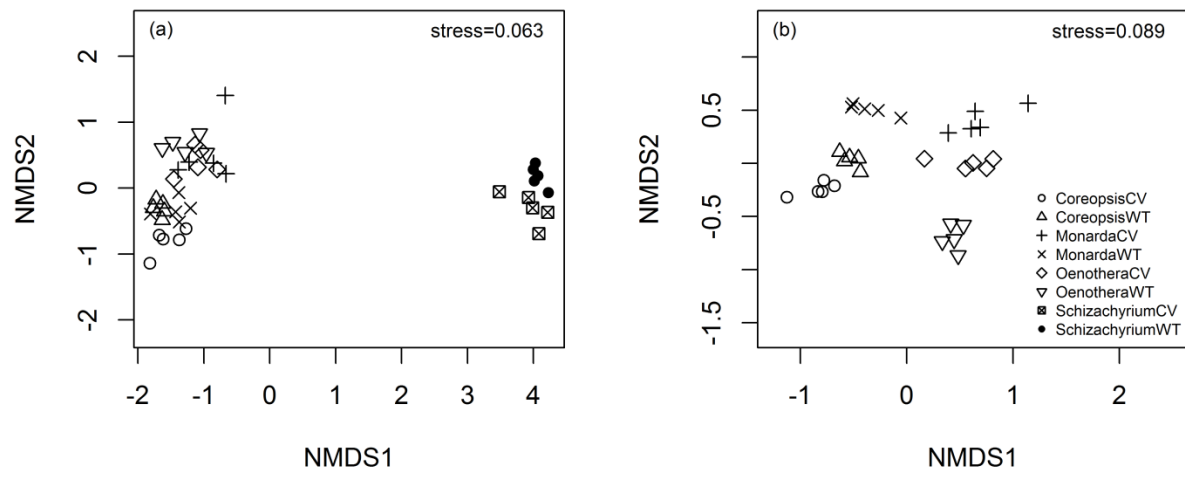


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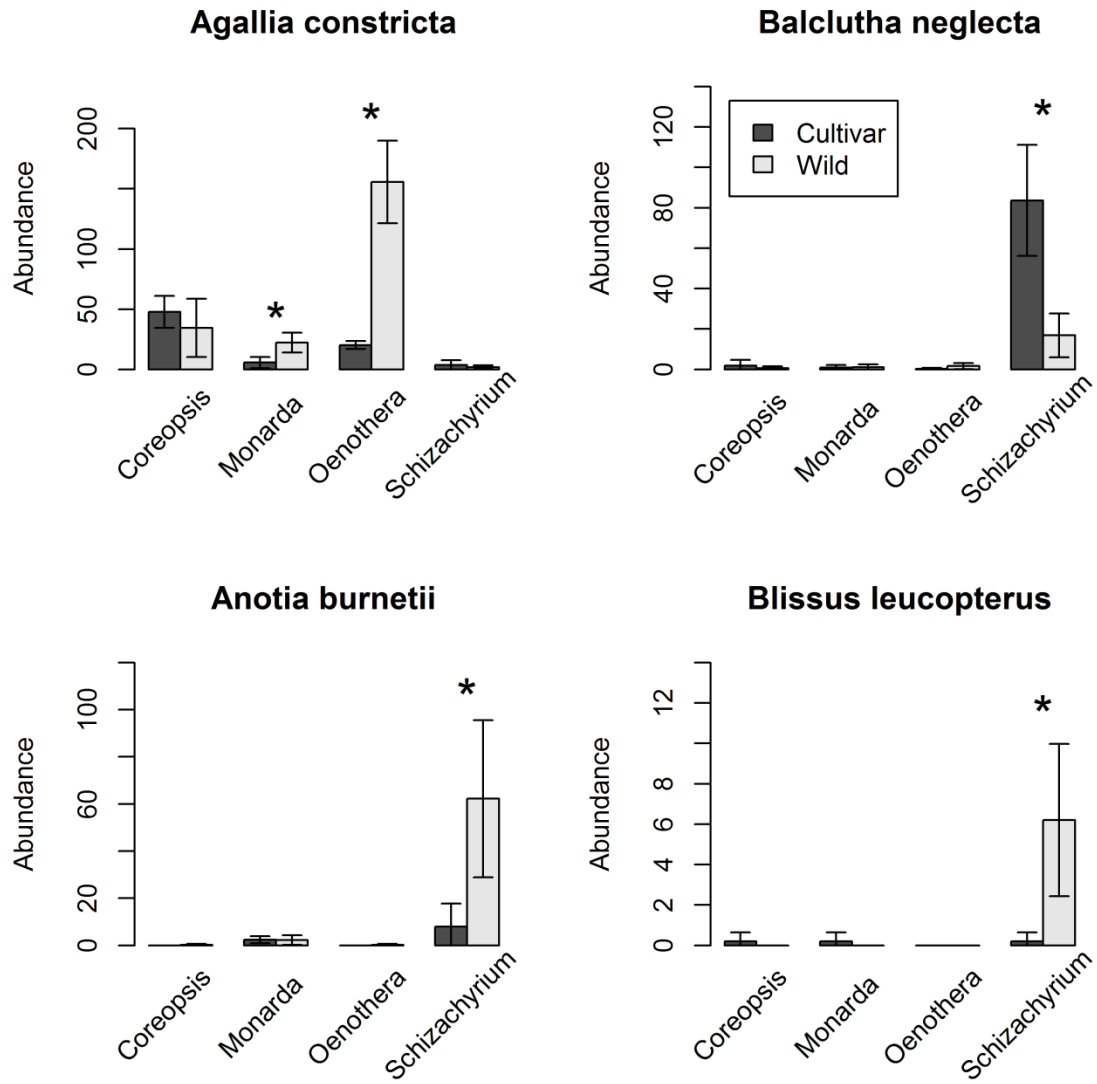


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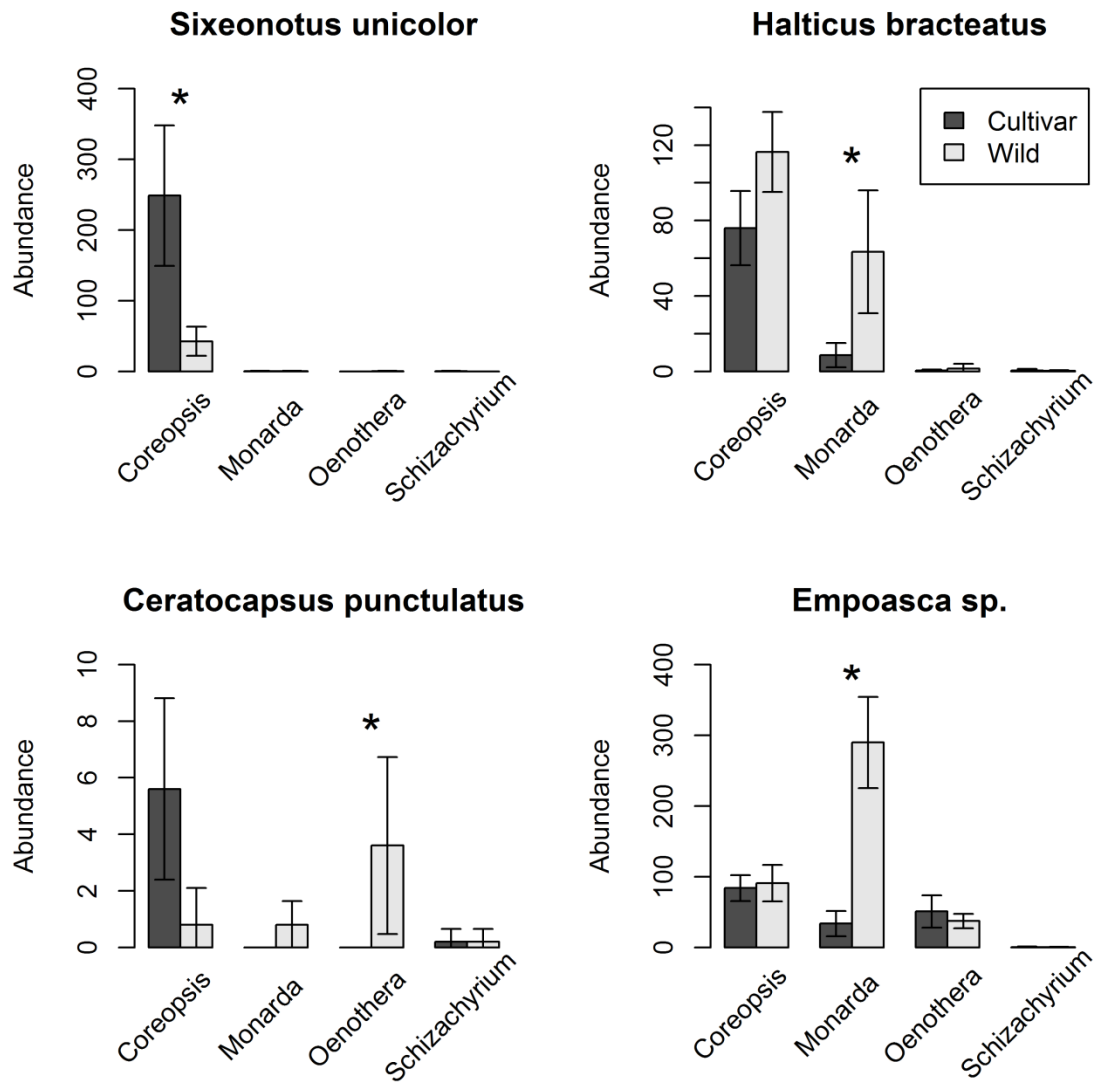


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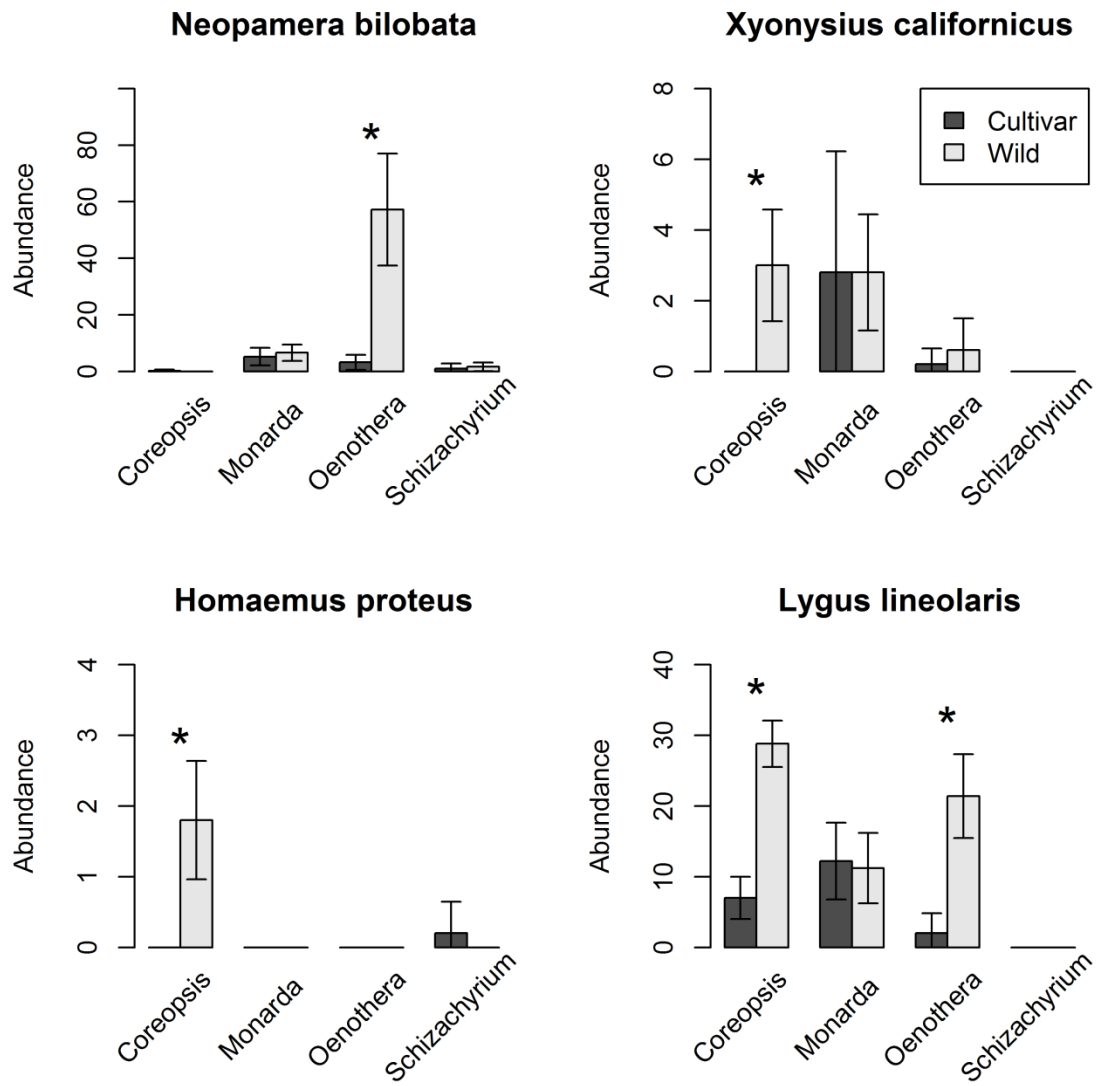


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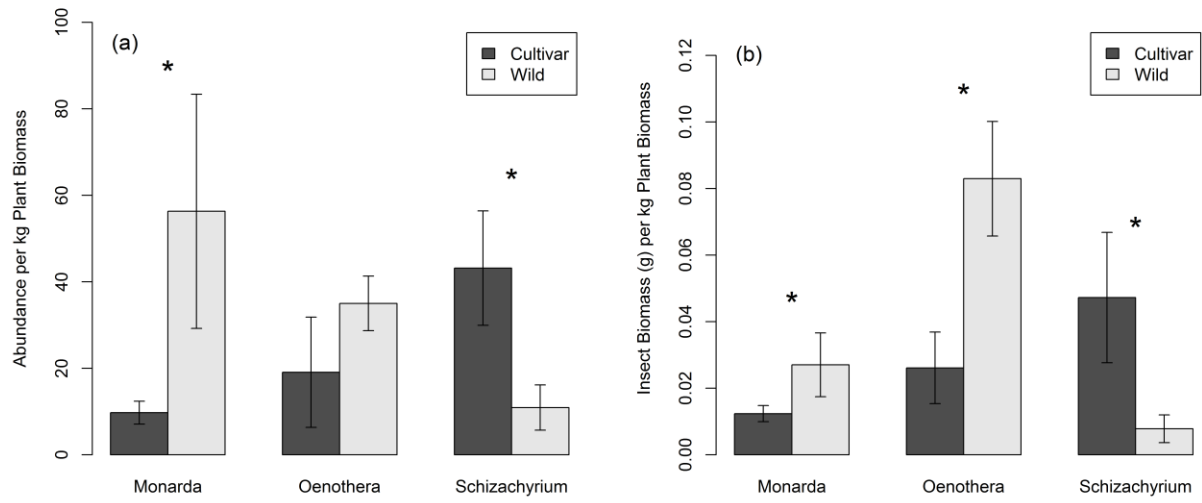


Figure 3.7.

## CHAPTER 4

### CONCLUSIONS

Although the full-scale experiment was conducted during the 2014 growing season, it is worthwhile to compare the preliminary results from 2013 with the results obtained in 2014. In both 2013 and 2014, distinct hemipteran communities were associated with cultivars and wild-type plants for every plant species tested. Similarly, the insect species that contributed most to the differences in the overall communities in 2013 were also important in 2014 (many additional species were identified as important in 2014, but this was because the analyses used for the 2014 data were also sensitive to species with relatively low abundances). Despite that the overall conclusion was the same, it is apparent from the two datasets that the composition of the insect communities changes over time. For example, *Empoasca bifurcata* was the most abundant species collected in 2013, and was found mainly on the *Coreopsis* wild-type plants. Yet in 2014, no individuals of *E. bifurcata* were collected at all (the species of *Empoasca* collected on *Monarda* in 2014 was different). If *E. bifurcata* is a species that does not appear until late in the growing season, this would explain its absence in 2014, as most of the *Coreopsis* wild-type plants were dead by August. However, it is also possible that populations of individual insect species vary widely from year to year. The abundances of other species support the latter possibility. *Clastoptera xanthocephala* was more abundant in 2013 than 2014, and was found in similar numbers on cultivars and wild-type *Oenothera* in 2013 (it showed a weak preference for the wild-type plants in 2014). Because there were no obvious differences in the *Oenothera* plants from one year to the next, there are no obvious explanations for the observed differences in abundance besides natural variation.

These results lead to two conclusions that are important when considering the question of whether cultivars and wild-type plants support similar insect communities. First, insects are highly sensitive to their host plant material. How and why they respond to changes in plant source are difficult to predict. Second, complex ecological systems involve many variables – both abiotic (e.g. drought, excessive

rainfall, extreme temperatures, etc.) and biotic (e.g. predator-prey dynamics, intra- and interspecific competition, parasite burden, etc.) – that can create significant variation in insect populations over time. The large number of variables involved makes it difficult to separate the effect of one variable from the others. In addition, variation over time results in effects that may be prominent at one time point and completely absent at another. Consequently, the results observed during this experiment should be interpreted with care. The data were collected from a small number of plant species at one location over a relatively short timeframe. A similar experiment at a different site using different plants may yield a different interpretation.

The more general parameters of insect productivity that we measured, namely total abundance and species richness of hemipterans, were also inconsistent between years. This was at least partially due to that fact that some plants were not completely established by the end of the first year and other plants were already dying by the end of the second year. Total abundance and species richness were higher on the *Coreopsis* wild-type plants than the cultivars in the first year, but showed a different pattern in 2014. Insect abundance started off higher on the *Coreopsis* wild-type plants in 2014, but declined throughout the growing season as more plants died, to the point that abundance was much higher on the cultivars in September. Species richness did not differ between cultivars and wild-type plants in 2014. Although it is unfortunate that so many of the *Coreopsis* wild-type plants died during the year that we collected the majority of our data, the 2013 data and the data from the first sampling date in 2014 at least give some insight into the expected difference between cultivars and wild-type plants. That is, given healthy plants, the wild-type *Coreopsis* would most likely support higher hemipteran abundance than the cultivars, and possibly more species of hemipterans than the cultivars. For *Oenothera*, insect abundance was higher on the cultivar in 2013, but was much higher on the wild-type plants early in the season in 2014. Mean species richness did not differ between the cultivars and wild-type plants in either year, though rarefaction curves indicated higher absolute richness on the *Oenothera* wild-type plants in both years. In this case, the discrepancy observed for insect abundance between years is most likely because of plant size. The cultivars established much more quickly than the wild-type plants, and hence were much larger than the

wild-type plants in 2013. Few insects were supported by the *Oenothera* wild-type plants simply because so little biomass was available. In 2014, not only were the cultivars and wild-type plants similar sizes, but we were also able to standardize our data by the amount of plant biomass available (the September data only). This standardization showed that the differences were truly an effect of plant source and not plant size. Had we been able to standardize our data in 2013, it may have shown that the higher abundance of insects on the cultivars was actually an effect of the small size of the wild-type plants.

Because we observed different patterns in hemipteran abundance on cultivars versus wild-type plants between years, at different times during the growing season, and among different plant species, it is difficult to draw overall conclusions about which group of plants is better at supporting native herbivorous hemipterans. If anything, we found little evidence that hemipteran diversity differed between cultivars and wild-type plants, suggesting that there is no inherent difference between cultivars and plants propagated from locally-collected seeds in terms of their abilities to serve as food source for hemipteran insects. However, our analyses of the composition of the insect communities revealed a more complex story and perhaps a slightly different interpretation. Though the number of insect species did not differ between cultivars and wild-type plants, we consistently found that the actual species comprising the community differed. So even though our results suggest that cultivars and wild-type plants fulfill a similar ecological role, the results also suggest that herbivorous insects are highly sensitive to their host plant material and will respond to changes in the source of that material.

Besides determining whether cultivars and wild-type plants differ in terms of the abundance, diversity, or communities of insects they support, an additional objective of this research was to identify any characteristics of cultivars that might inhibit or enhance their abilities to serve as food sources for herbivorous insects. When we examined which insects were associated with particular plants based on the insects' feeding guilds, we found strong evidence that sterile cultivars were not suitable host plants for seed- and fruit-feeding insects. For the other feeding guilds (xylem-, phloem-, and mesophyll-feeders), we also found many insect species that discriminated between cultivars and wild-type plants, but in most cases it was not apparent which characteristics of the plants were causing the insects to prefer some plants



over others. More work is needed in this area, especially for plant parameters such as leaf chemistry and nitrogen content, to determine which features of the plants insects are most sensitive to. As a recommendation to gardeners who wish to improve the ecological functioning of their landscapes by incorporating more native ornamental plants, one thing is clear: cultivars selected for sterility provide no food resource for a large and ecologically important feeding guild and should be avoided.

Although seed/fruit-feeding insects always preferred the wild-type plants to the sterile cultivars, this was not the case for the other feeding guilds. Some insect species preferred the cultivars to the wild-type plants. These results suggest that plant breeders could develop cultivars that are actually superior to the wild-type plants in terms of their abilities to support insect diversity, though additional research is needed to identify which characteristics breeders should be targeting. One character that would be relatively easy to select for and may promote higher insect diversity is architectural complexity. Generally, plants with more structural complexity support higher insect diversity (Strong et al. 1984), possibly because there are more niches available or because there are more areas for insects to feed (e.g. higher surface/area to volume ratio). In agreement with this expectation, the plants in our study with finer vegetation structure (i.e. thinner stems and culms) and higher stem/culm density tended to support higher hemipteran abundance and/or biomass. For example, the *Schizachyrium* cultivars, *Monarda* wild-type plants, and *Coreopsis* wild-type plants (before they started dying), supported higher abundance and/or biomass than their more coarsely textured counterparts. Additionally, the wild-type plants exhibited significant variation in the degree of branching, size of stems, and stem/culm density, suggesting there is ample opportunity to breed for these traits and create improved selections. Although many other traits are likely influencing the insects that feed on the plants, and hence represent potential breeding opportunities, plant architecture is at least a clear place to start.

The main objective of this study was to evaluate the ecological value of cultivars relative to plants propagated from material sourced from local, wild populations. This information is of value to gardeners who wish to enhance the functioning of their landscapes by improving the landscape's ability to support wildlife. The results of this study, in conjunction with the results obtained by others, suggest there are two

things gardeners should keep in mind when choosing plants for their landscapes that will have the greatest impact on promoting wildlife. First, native plants are far superior to exotic plants. A substantial amount of evidence has accumulated supporting this conclusion. Second, plant species diversity is a more important factor than plant source. Given the large number of insect species we observed to exhibit some degree of specialization in the plant species they fed on, and the relatively small number of species observed to discriminate between cultivars and wild source material, incorporating more plant species into a landscape should have a much greater effect on enhancing insect diversity than using plants from one source over another. In theory, enhancing the insect diversity should then translate to higher overall wildlife diversity supported by the landscape.

We also observed that some plant species supported higher hemipteran diversity than others, with *Oenothera* supporting the most insect species and *Amsonia* supporting almost none. Although this would suggest some plants may be superior to others in their abilities to support wildlife, and perhaps should be favored when selecting plants for the landscape, there are drawbacks to this approach. It is important to remember that we examined only a single group of insects, and just because a plant like *Amsonia* is a poor food resource for hemipterans does not mean it is not important for other groups, such as chewing insects and pollinators. In fact, many insects that are host plant specialists depend on plants like *Amsonia*. These plants contain potent feeding deterrents that are very effective against generalist feeders, but at the same time open up niches for insects that have evolved the specialized adaptations to feed on them. Avoiding these plants in landscape would exclude some of the species most vulnerable to extinction, such as the monarch butterfly, an insect that feeds exclusively on milkweeds during its larval stage.

Although it is important to make the right choices about which plants to use ornamentally in landscapes, the larger challenge remains getting more people to replace portions of their lawns with more diverse gardens. There is growing awareness that the lawn aesthetic is contributing to losses of biodiversity in suburban areas, and many people are proactively making changes to reverse that trend. However, “gardening for wildlife” can still be described more as a niche interest, where most homeowners are choosing to stick with the status quo of landscape designs. The highest priorities should

be changing opinions about which landscape designs are aesthetically pleasing and encouraging more people to develop an interest in gardening. Only changes at the ecosystem scale will make an appreciable impact on declines in biodiversity, and for that we need to recruit more people than just those who are already conservation-minded.

### **Literature Cited**

Strong, D.R., J.H. Lawson, and R. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Harvard University Press, Cambridge.

## APPENDIX A

### DESCRIPTIONS OF PLANT SPECIES AND CULTIVARS

The table below summarizes information about the plant species and particular cultivars used in this experiment. Plant species were chosen such that they were not close phylogenetic relatives. Cultivars were chosen for variety in their genetic origins and in the characteristics that distinguish them from the wild form. All wild-type plants were propagated from seed collected in natural populations in Athens, GA. Cultivars were purchased from North Creek Nurseries in Landenberg, PA, except for *Schizachyrium scoparium* ‘Prairie Blues,’ which was donated by Hoffman Nursery in Bahama, NC.

<b>Plant Species</b>	<b>Common Name</b>	<b>Cultivar</b>	<b>Family</b>	<b>Cultivar Origin</b>	<b>Difference from Wild-type</b>
<i>Amsonia tabernaemontana</i>	Eastern bluestar	‘Blue Ice’	Apocynaceae	Interspecific hybrid <sup>1</sup>	Longer bloom, darker flowers, compact form
<i>Coreopsis grandiflora</i>	Large-flowered tickseed	‘Tequila Sunrise’	Asteraceae	Interspecific hybrid	Variegated leaves, compact form
<i>Monarda fistulosa</i>	Wild bergamot	‘Claire Grace’	Lamiaceae	Straight species	Powdery mildew resistant, darker flowers
<i>Oenothera fruticosa</i>	Southern Sundrops	‘Cold Crick’	Onagraceae	Interspecific hybrid <sup>1</sup>	Sterile, compact form
<i>Schizachyrium scoparium</i>	Little bluestem	‘Prairie Blues’ <sup>2</sup>	Poaceae	Straight species	Blue-green foliage turning wine-red in fall

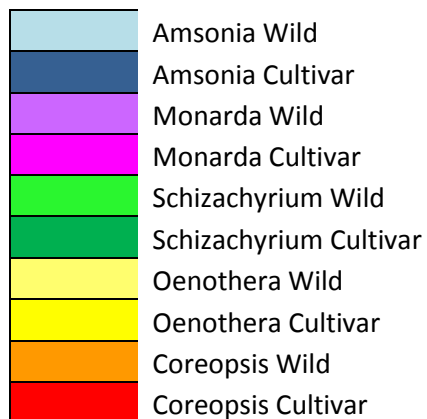
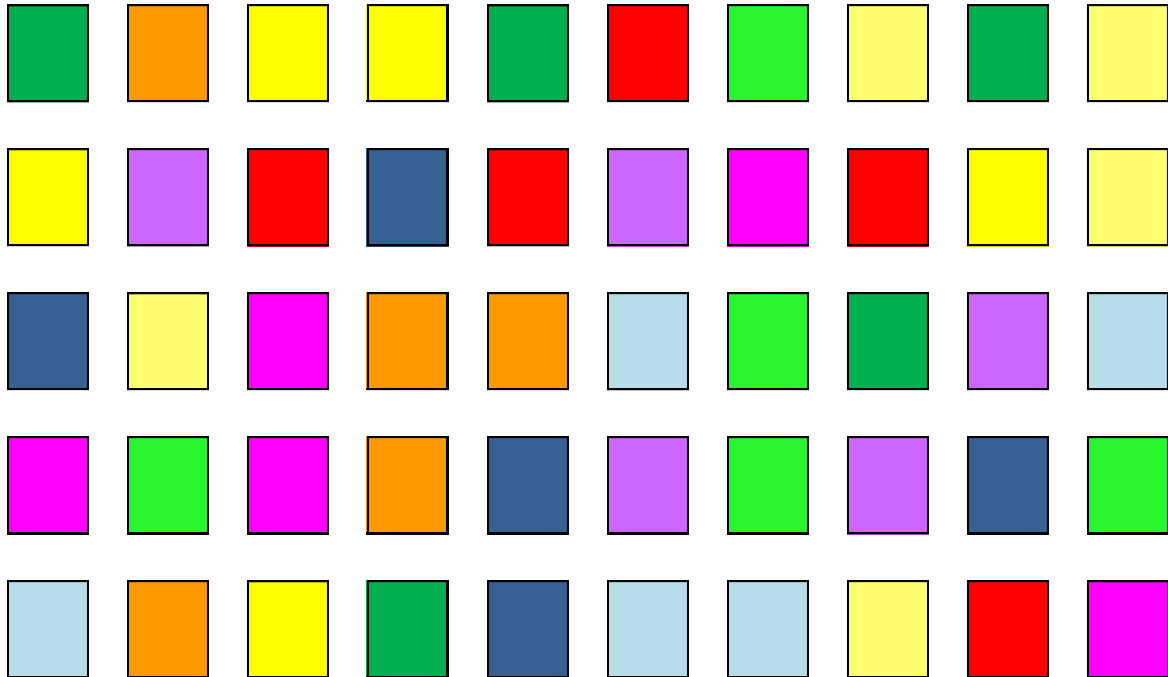
<sup>1</sup> purported hybrid

<sup>2</sup> propagated from seed

## APPENDIX B

### SCHEMATIC OF EXPERIMENTAL DESIGN

Plots were randomly assigned to treatments following a two-way ANOVA design. Each plot was 2 m x 2 m and contained 16 plants, evenly spaced. Plots were separated by 1.5 m, with wood mulch in-between.



## APPENDIX C

### INSECT SPECIES EXCLUDED FROM ANALYSES

Sixty-five insect species that were collected from *Coreopsis*, *Oenothera*, *Monarda*, and *Schizachyrium* were excluded from statistical analyses because of low overall abundance. The table below summarizes these species and their overall abundance across the entire dataset (except individuals collected on *Amsonia*). The identifications of most species were not confirmed by a taxonomist.

<b>Insect Species</b>	<b>Abundance</b>	<b>Insect Species</b>	<b>Abundance</b>
Erythroneura sp. 4*	0	Mirid sp. 4	1
Pentatomid sp. 4*	0	Mirid sp. 5	1
Mirid sp. 3*	0	Xyphon flaviceps	2
Oncometopia orbona	1	Exitianus exitiosus	2
Graphocephala coccinea	1	Paraphlepsius irroratus	2
Colladonus clitellarius	1	Graminella sp. 1	2
Tylozygus geometricus	1	Erythroneura sp. 7	2
Graminella sp. 3	1	Delphacid sp. 3	2
Erythroneura sp. 5	1	Entylia bactriana	2
Erythroneura sp. 9	1	Mormidea lugens	2
Erythroneura sp. 10	1	Corimelaena sp. 1	2
Stirellus bicolor	1	Nysius/Xyonysius sp.	2
Cicadellid sp. 2	1	Neortholomus scolopax	2
Cicadellid sp. 3	1	Sibovia occatoria	3
Cicadellidae sp. 4	1	Spanbergiella quadripunctata	3
Delphacodes campestris	1	Polyamia sp.	3
Delphacid sp. 1	1	Erythroneura sp. 1	3
Delphacid sp. 2	1	Erythroneura sp. 8	3
Delphacid sp. 4	1	Pentatomid sp. 2	3
Delphacid sp. 5	1	Galgupha sp.	3
Delphacid sp. 6	1	Phera insolita	4
Delphacid sp. 7	1	Provancherana tripunctata	4
Brachyapterous Delphacid sp. 1	1	Agallia deleta	4
Brachyapterous Delphacid sp. 2	1	Graminella villica	4
Brachyapterous Delphacid sp. 3	1	Pentatomid sp. 1	4

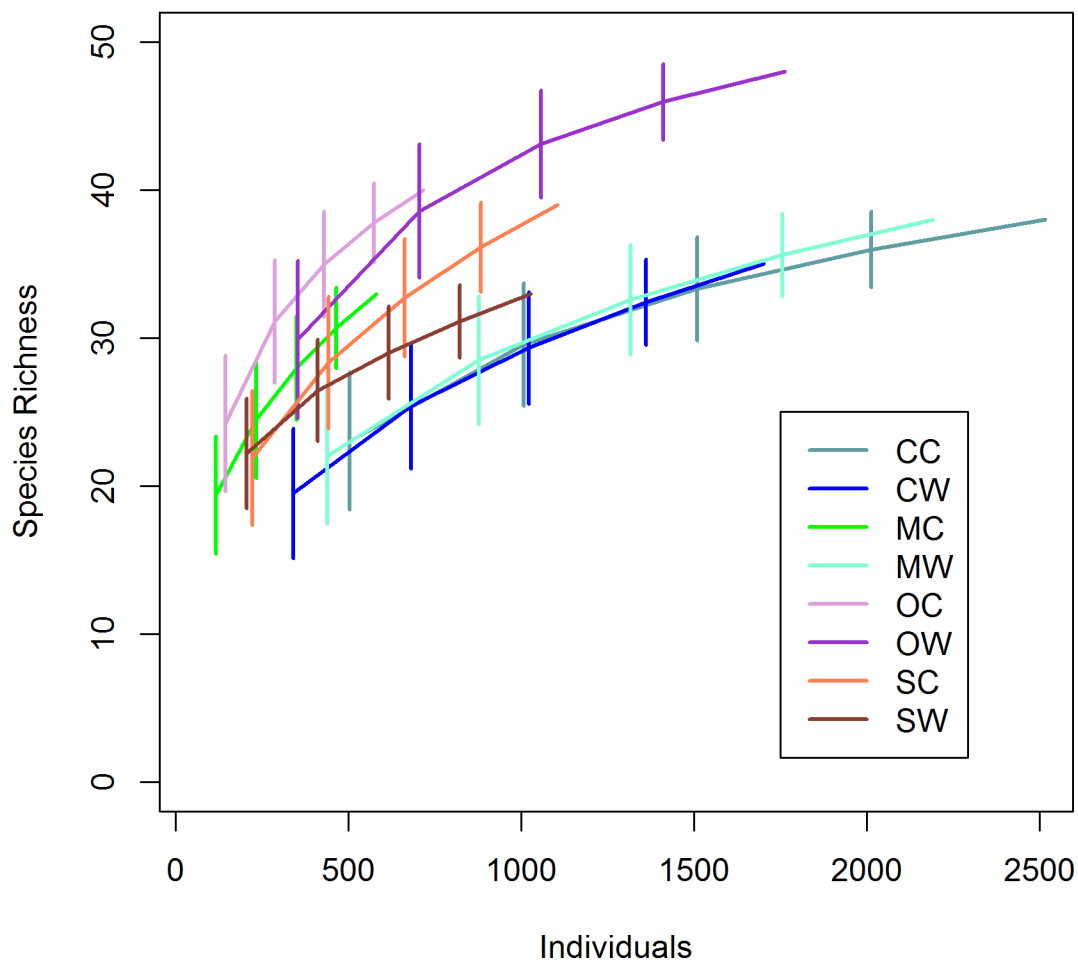
Brachyapterous Delphacid sp. 4	1	Corimelaena pulicaria	4
Brachyapterous Delphacid sp. 5	1	Ligyrocoris barberi	4
Cedusa sp.	1	Spanagonicus albofasciatus	4
Flatid sp.	1	Graminella sp. 2	5
Fulgoroid sp.	1	Muellerianella laminalis	5
Alydid sp.	1	Aculatis tartarea	5
Rhopalid sp.	1	Pycnoderes drakei	5
Mirid sp. 2	1		

\* Singleton species collected on *Amsonia*

## APPENDIX D

### RAREFACTION CURVE OF SPECIES RICHNESS

The figure below is a sample-based rarefaction curve of hemipteran species richness for cultivars and wild-types of each plant species. Data were pooled over all three sampling dates and the x-axis was rescaled to individuals instead of samples. The lines of the rarefaction curve are the expected species richness for a given number of individuals sampled and the bars are 2 SE. Treatments are shown in the legend, where CC denotes *Coreopsis* cultivar, CW *Coreopsis* wild-type, etc.





APPENDIX E

GENERALIZED LINEAR MODEL RESULTS FOR INDIVIDUAL INSECT SPECIES

The multivariate test for the entire insect community indicated a significant interaction between plant species and plant source. However, a significant interaction for the multivariate test does not imply there will be an interaction for each univariate test. The table below summarizes *p* values from univariate GLMs (under the full model) for each of the 65 insect species included in the analyses. Insects with a significant effect of plant species, but without an effect in the interaction term, can be interpreted as preferring to feed on some plant species more than others.

Insect	Unadjusted p-value			Adjusted p-value		
	Plant Source	Plant Species	Interaction	Plant Source	Plant Species	Interaction
<b>Cuerna costalis</b>	0.0625	0.0025	0.2025	0.8575	0.1125	1
<b>Paraulacizes irrorata</b>	0.4325	0.1675	0.05	1	0.5025	0.675
<b>Coelidia olitoria</b>	0.215	0.0325	0.01	1	0.295	0.8425
<b>Graphocephala versuta</b>	0.565	0.0025	0.2525	1	0.0025	0.965
<b>Idiodonus brittoni</b>	0.055	0.13	0.655	0.7925	0.5825	1
<b>Xerophloea minor</b>	0.1025	0.0075	0.155	0.985	0.075	0.985
<b>Texananus excultus</b>	0.4875	0.0025	0.085	1	0.0025	0.985
<b>Paraphlepsius tennesus</b>	0.4525	0.2175	0.145	1	0.5825	0.9675
<b>Scaphoideus spp.</b>	0.87	0.01	0.1725	1	0.13	0.965
<b>Osbornellus clarus</b>	0.71	0.0025	0.1325	1	0.005	0.9675
<b>Scaphytopius frontalis</b>	0.425	0.0025	0.945	1	0.0025	1
<b>Scaphytopius acutus</b>	0.0425	0.0025	0.105	0.8525	0.0025	0.83
<b>Deltocephalus flavicosta</b>	0.92	0.06	0.135	1	0.305	0.895
<b>Tylozygus bifida</b>	0.04	0.0025	0.79	0.8175	0.0025	1
<b>Draeculacephala balli</b>	0.9375	0.015	0.0525	1	0.0675	0.675
<b>Draeculacephala robinsoni</b>	0.13	0.1425	0.1575	0.985	0.545	0.9625
<b>Draeculacephala antica</b>	0.6625	0.0025	0.375	1	0.0025	0.9975
<b>Chlorotettix galbanatus</b>	0.4175	0.015	0.4575	1	0.0725	0.9975
<b>Agallia constricta</b>	0.05	0.0025	0.0025	0.4725	0.0025	0.0025
<b>Agalliopsis novella</b>	0.72	0.0025	0.01	1	0.0025	0.14

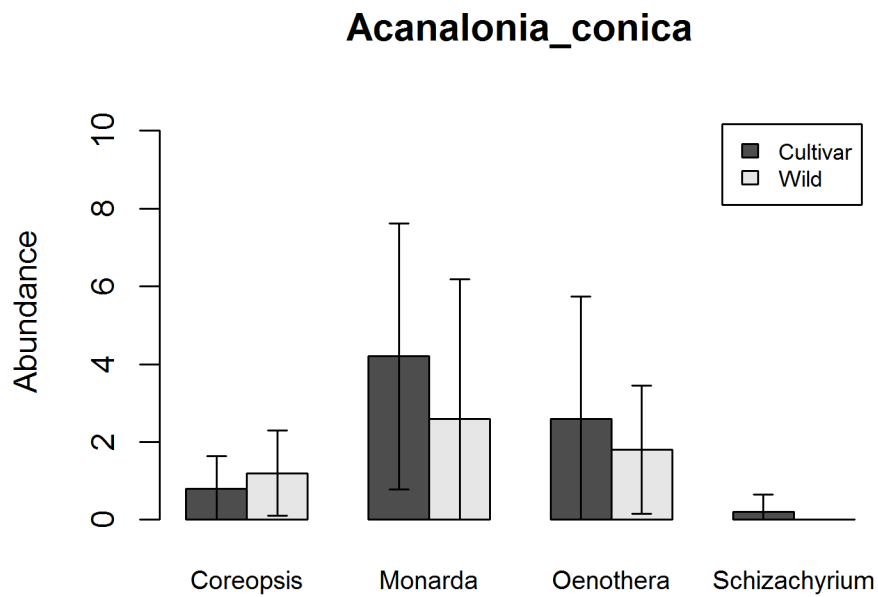
<b>Aceratagallia sanguinolenta</b>	0.1425	0.0075	0.065	0.99	0.1425	0.965
<b>Xestocephalus pulicarius</b>	0.7025	0.005	0.4375	1	0.0425	0.985
<b>Macrosteles lepidus</b>	0.5725	0.005	0.585	1	0.075	1
<b>Graminella nigrifrons</b>	0.6675	0.0025	0.1025	1	0.0025	0.5775
<b>Graminella sonora</b>	0.4825	0.005	0.405	1	0.0575	1
<b>Balclutha abdominalis</b>	0.58	0.005	0.2325	1	0.005	0.985
<b>Balclutha neglecta</b>	0.0825	0.0025	0.01	0.8575	0.0025	0.0425
<b>Dikraneura sp.</b>	0.5775	0.0025	0.485	1	0.0025	1
<b>Empoasca sp.</b>	0.0325	0.0025	0.0025	0.905	0.0025	0.0025
<b>Typhlocybae spp.</b>	0.1975	0.1775	0.15	1	0.5825	0.9675
<b>Erythroneura sp. 2</b>	0.57	0.1425	0.6625	1	0.5825	1
<b>Erythroneura sp. 3</b>	0.4725	0.1925	0.1	1	0.5825	0.9675
<b>Erythroneura sp. 6</b>	0.5	0.0075	0.0075	1	0.13	0.65
<b>Saccharosydne saccharivora</b>	0.495	0.0025	0.4275	1	0.0025	1
<b>Pissonotus piceus</b>	0.285	0.07	0.6475	1	0.3825	1
<b>Delphacodes andromeda</b>	0.4	0.0025	0.1025	1	0.0325	0.985
<b>Isodelphax basivitta</b>	0.11	0.195	0.1075	0.9975	0.5825	0.9725
<b>Delphacodes puella</b>	0.29	0.0025	0.145	1	0.0025	0.7775
<b>Liburniella ornata</b>	0.67	0.0025	0.0375	1	0.0025	0.28
<b>Anotia burnetii</b>	0.08	0.0025	0.0225	0.73	0.0025	0.53
<b>Anotia bonnetii</b>	0.4725	0.0025	0.2675	1	0.0025	0.97
<b>Paramysidia mississippiensis</b>	0.015	0.005	0.9475	0.305	0.025	1
<b>Acanalonia conica</b>	0.47	0.0025	0.6025	1	0.0075	0.9975
<b>Prosapia bicincta</b>	0.6875	0.0025	0.5925	1	0.0025	1
<b>Lepyronia quadrangularis</b>	0.895	0.0175	0.4575	1	0.075	0.9825
<b>Clastoptera xanthocephala</b>	0.465	0.0025	0.345	1	0.0025	0.985
<b>Spissistilus festinus</b>	0.9375	0.015	0.005	1	0.0725	0.145
<b>Euschistus servus servus</b>	0.2525	0.065	0.4975	1	0.3825	1
<b>Homaemus proteus</b>	0.058	0.001	0.017	0.829	0.02	0.745
<b>Neopamera bilobata</b>	0.01	0.0025	0.005	0.1275	0.0025	0.0025
<b>Paromius longulus</b>	0.65	0.0025	0.55	1	0.0025	1
<b>Heraeus plebejus</b>	0.15	0.305	0.0225	0.9925	0.5825	0.485
<b>Xyonysius californicus</b>	0.183	0.001	0.017	0.999	0.002	0.215
<b>Ptochiomera nodosa</b>	0.655	0.0025	0.6525	1	0.0025	1
<b>Blissus leucopterus</b>	0.0625	0.0025	0.0175	0.8025	0.005	0.21
<b>Myodocha serripes</b>	0.855	0.0025	0.5275	1	0.0025	1
<b>Arhyssus nigristernum</b>	0.73	0.0025	0.22	1	0.0025	1
<b>Prepops rubrovittatus</b>	0.62	0.0025	0.235	1	0.0025	0.9975
<b>Sixeonotus unicolor</b>	0.07	0.0025	0.045	1	0.0025	0.885
<b>Phytocoris tibialis</b>	0.2175	0.005	0.25	1	0.025	0.8825
<b>Lygus lineolaris</b>	0.0075	0.0025	0.0025	0.61	0.0025	0.0025
<b>Neurocolpus nubilus</b>	0.3525	0.0025	0.605	1	0.005	1
<b>Ceratocapsus punctulatus</b>	0.905	0.0125	0.0025	1	0.0725	0.0025

<b>Halticus bracteatus</b>	0.09	0.0025	0.0125	1	0.0025	0.095
<b>Plagiognathus guttulosus</b>	0.3975	0.0025	0.0425	1	0.005	0.9275

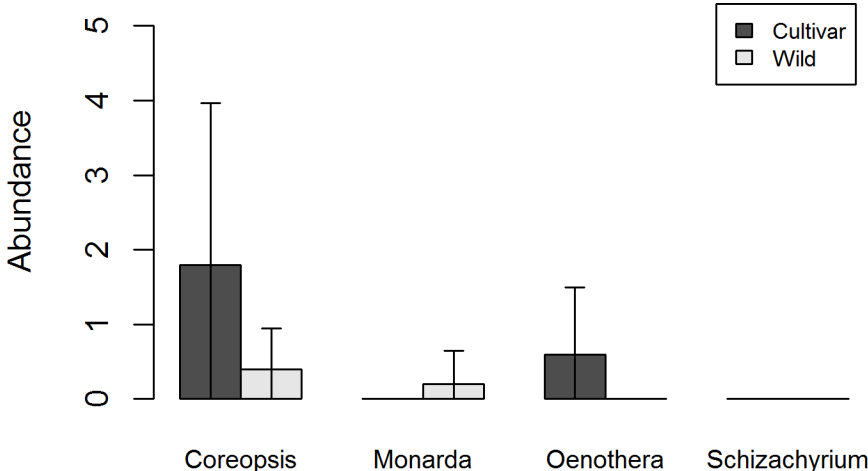
## APPENDIX F

### PLOTS OF ABUNDANCES FOR INDIVIDUAL INSECT SPECIES

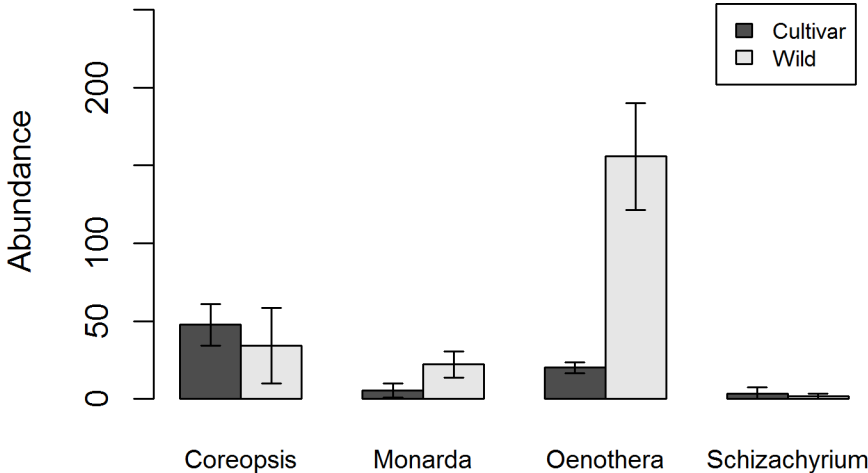
For many insect species, there was a significant effect of plant species, but not plant source or the interaction term, according to the GLM models. Plots of the abundances of the 65 insect species found on cultivars and wild-types of *Coreopsis*, *Monarda*, *Oenothera*, and *Schizachyrium* reveal that these insect species were specializing on some plant species and not others (most often feeding on either the herbaceous plants or the grasses, but not both); i.e. they had high abundances on one or a few plant species, but were not found at all on the other plant species. Error bars are SD.



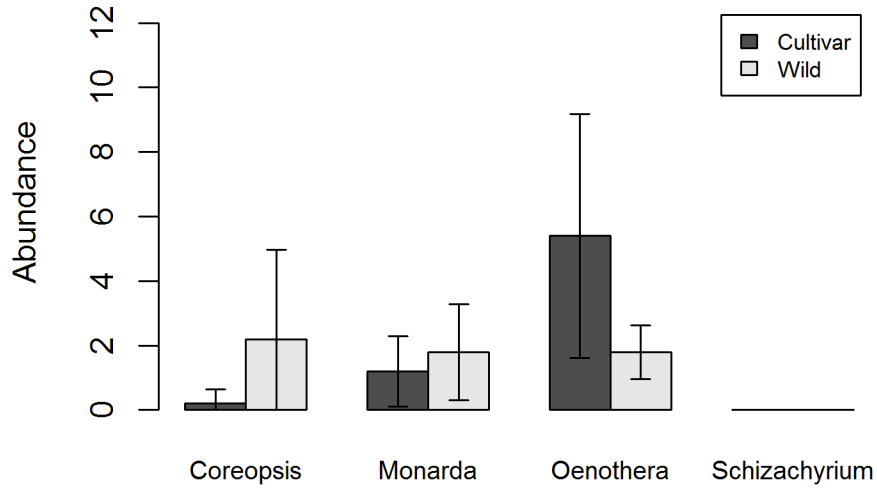
### Aceratagallia\_sanguinolenta



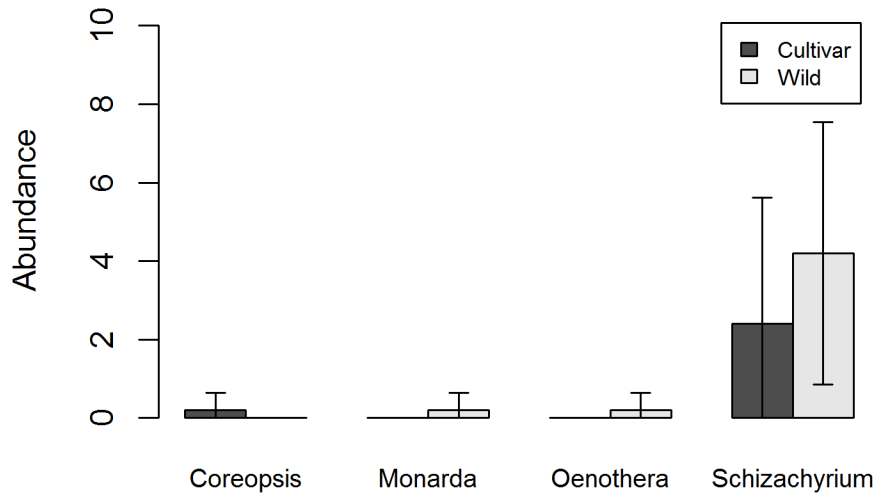
### Agallia\_constricta



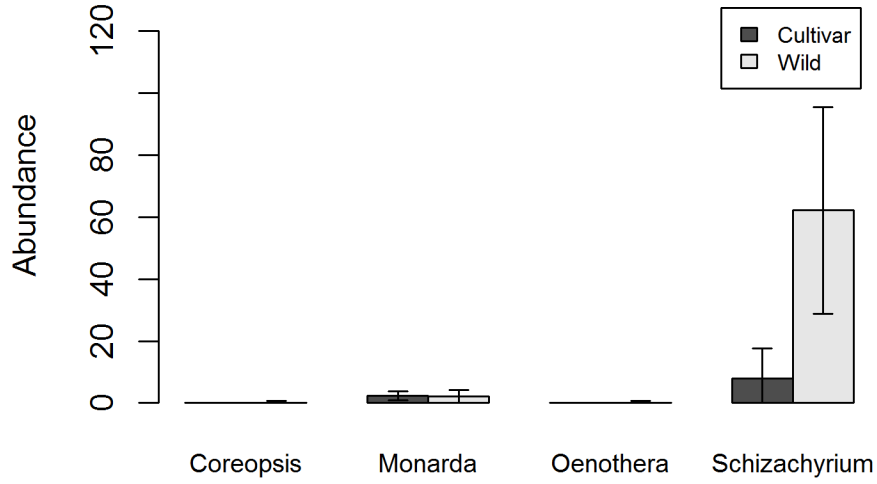
### Agalliopsis\_novella



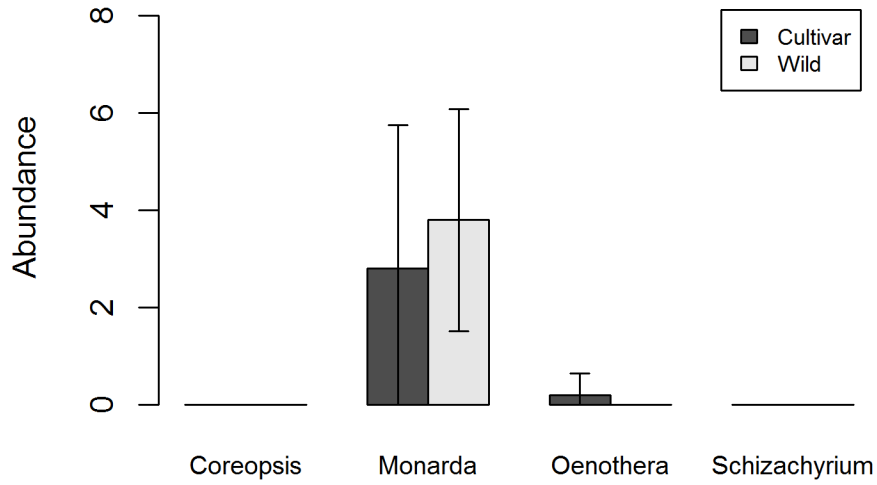
### Anotia\_bonnetii



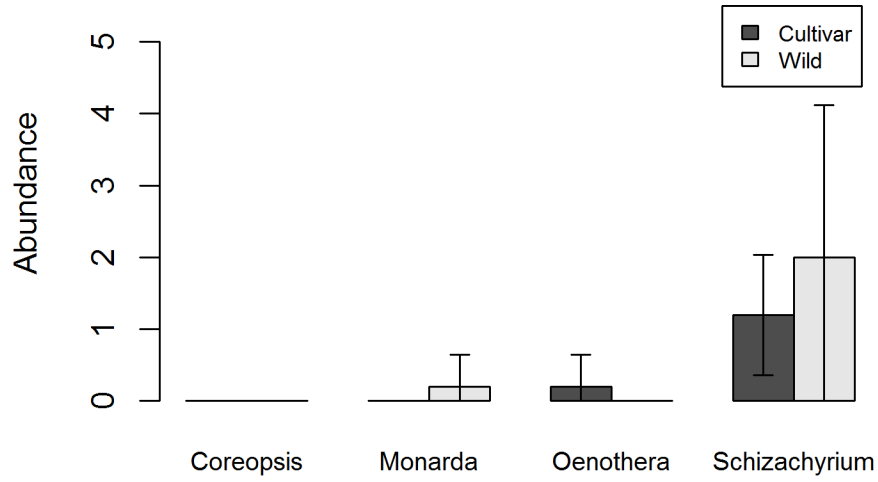
### *Anotia\_burnetii*



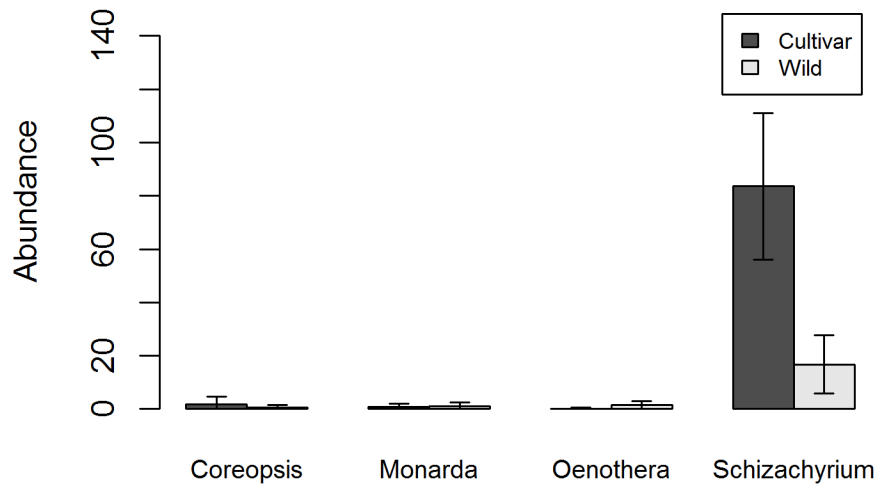
### *Arhyssus\_nigristernum*



### Balclutha\_abdominalis

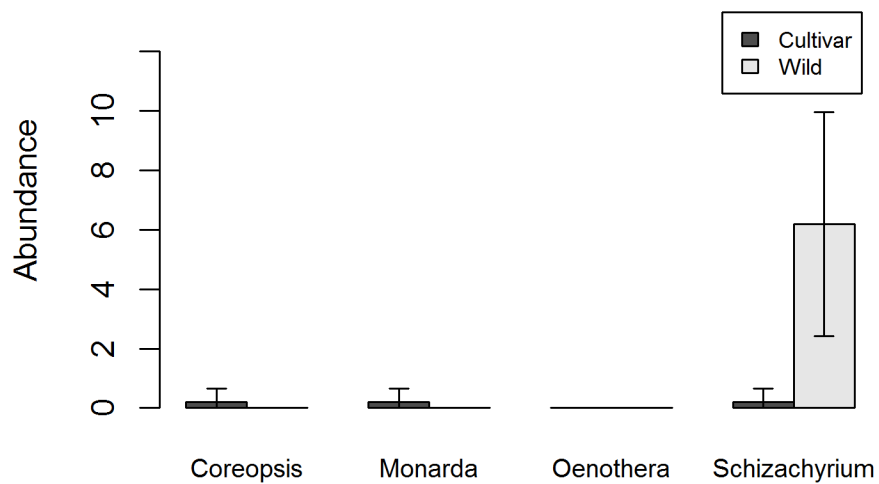


### Balclutha\_neglecta

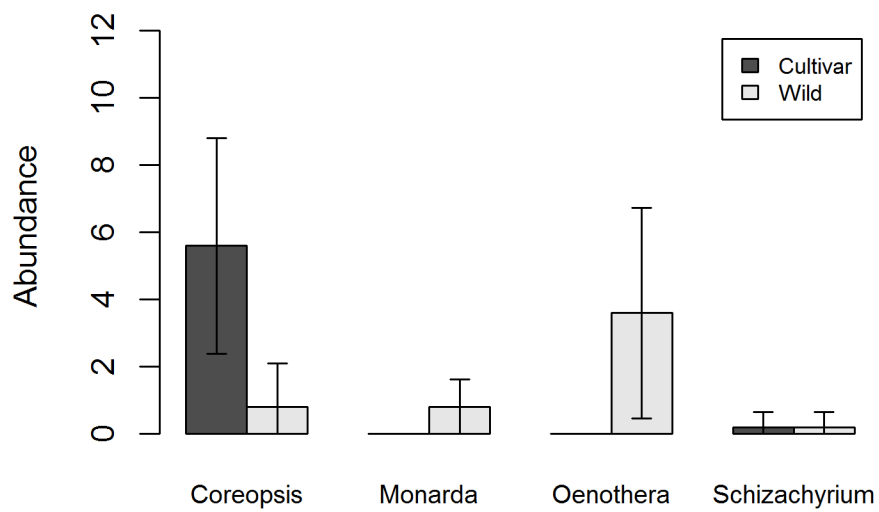




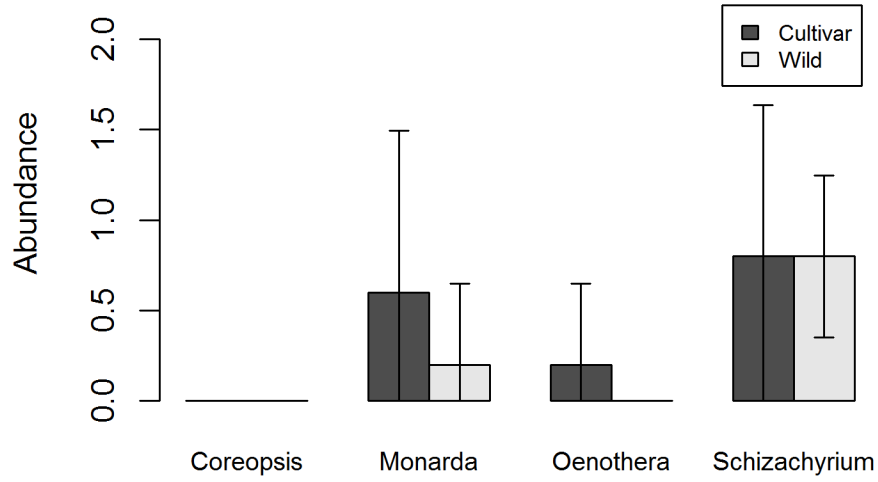
## Blissus leucopterus



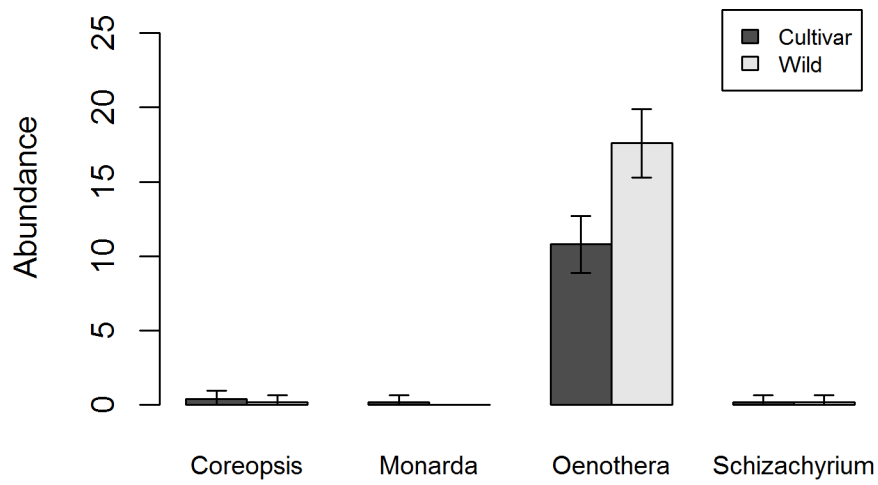
## Ceratocapsus punctulatus



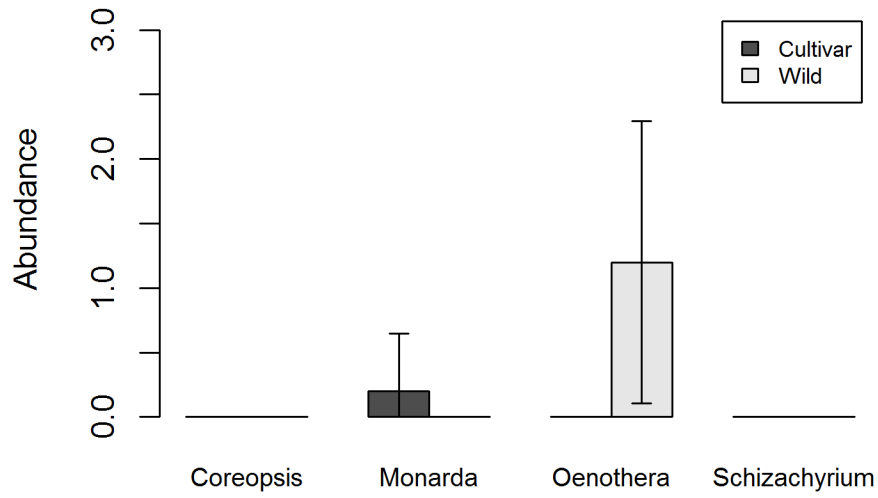
### Chlorotettix\_galbanatus



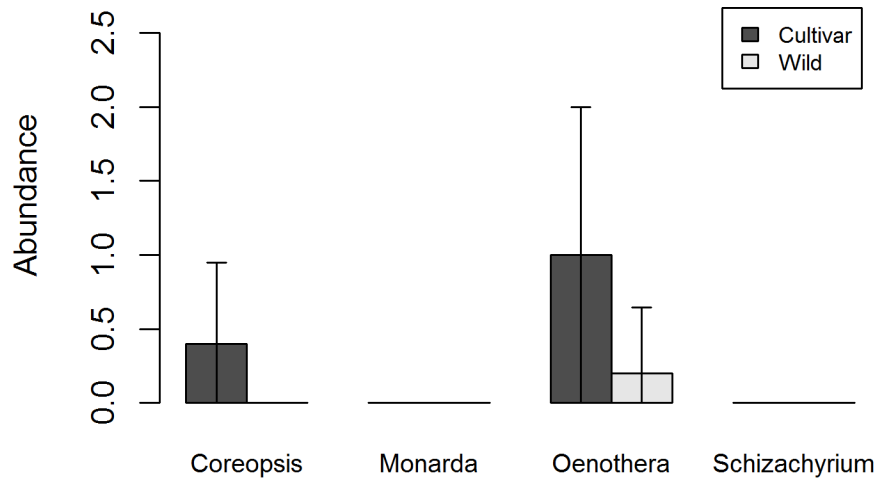
### Clastoptera\_xanthocephala



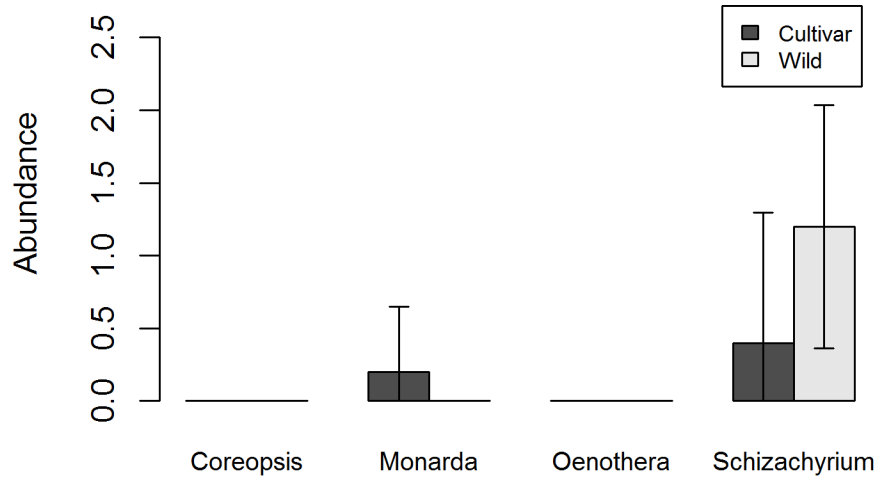
### Coelidia\_olitoria



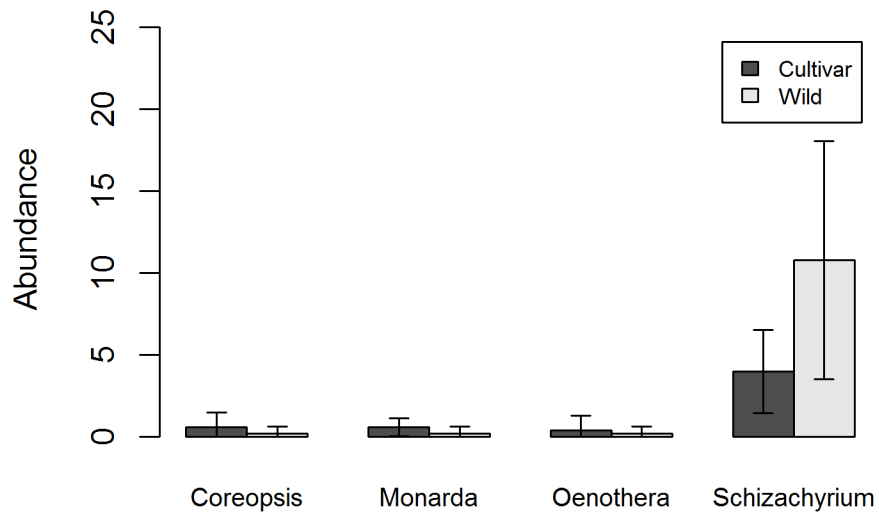
### Cuerna\_costalis



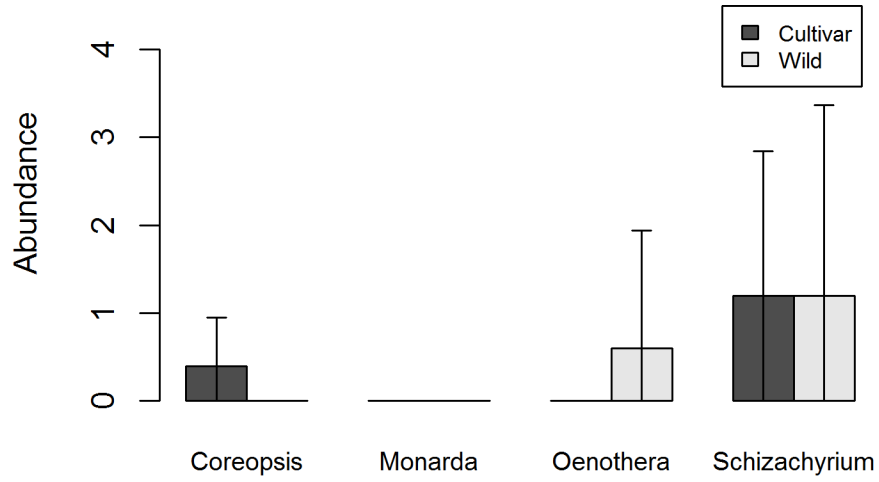
## Delphacodes\_andromeda



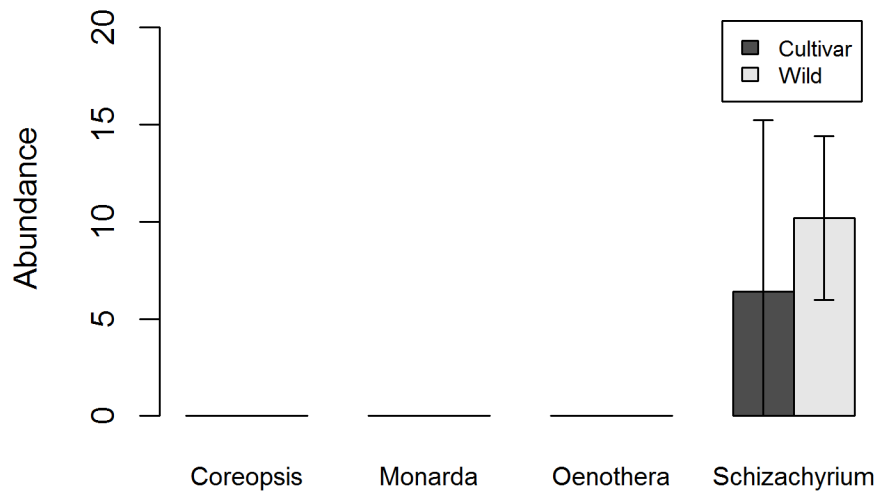
## Delphacodes\_puella



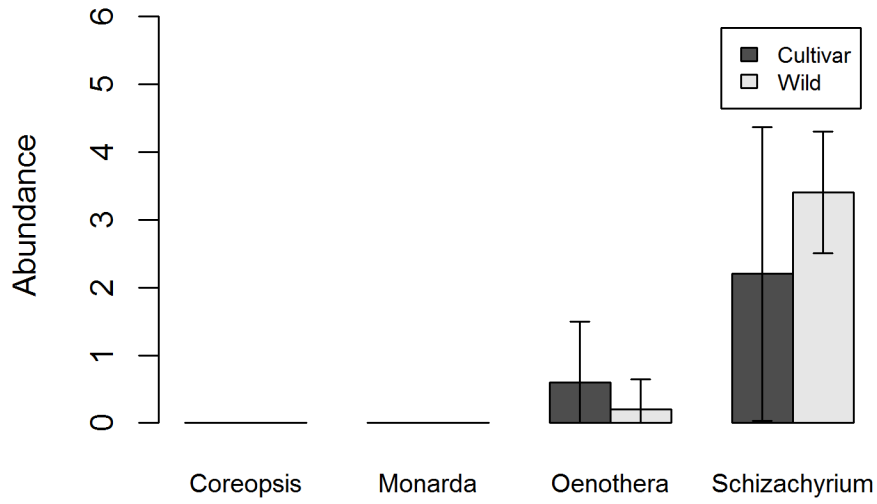
## *Deltocephalus flavicosta*



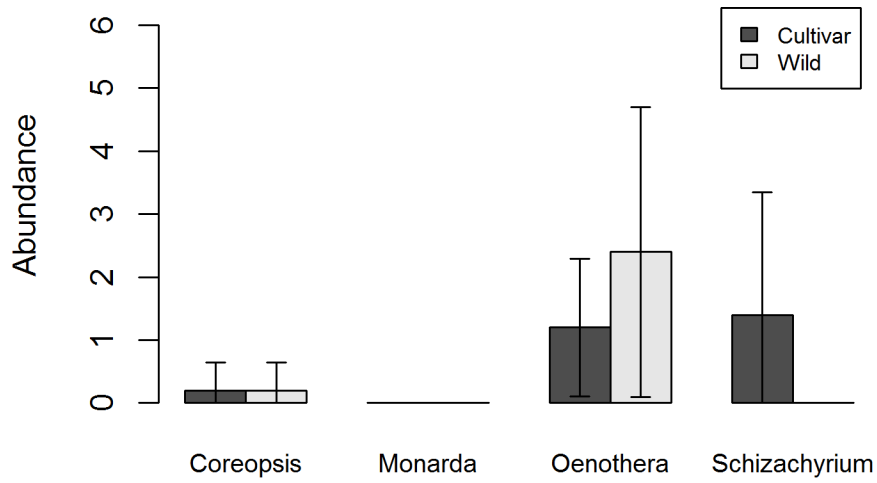
## *Dikraneura sp*



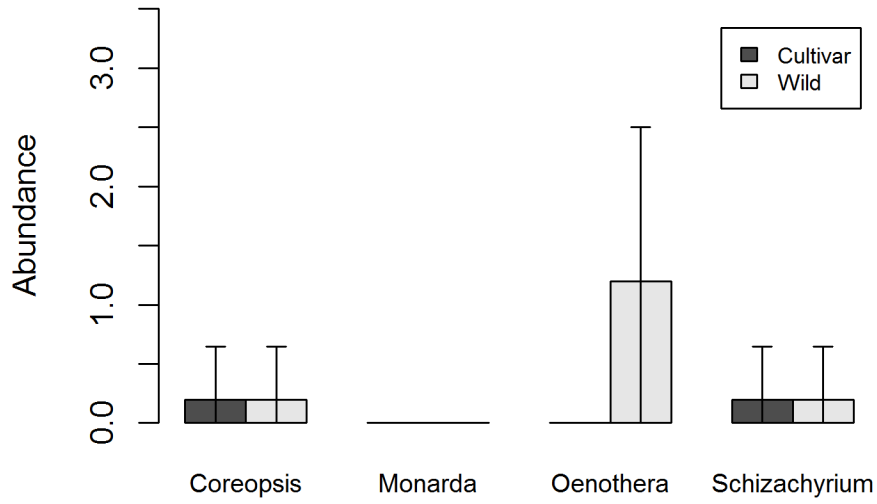
### Draeculacephala\_antica



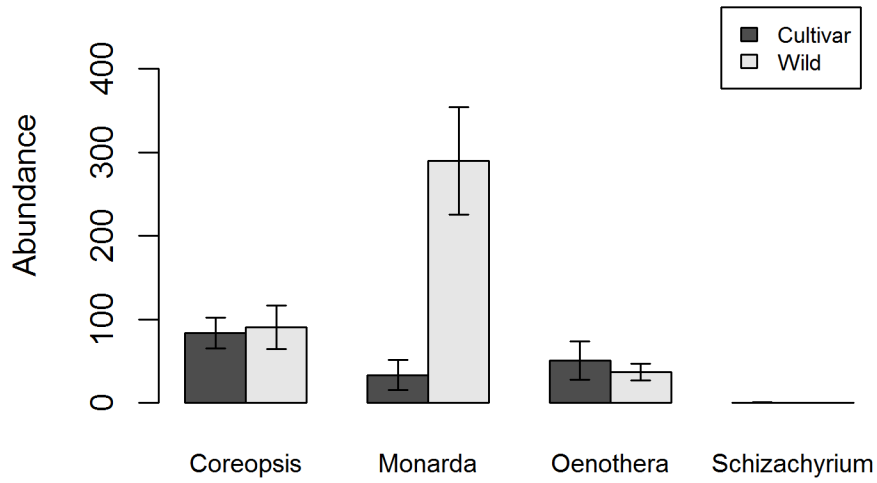
### Draeculacephala\_balli



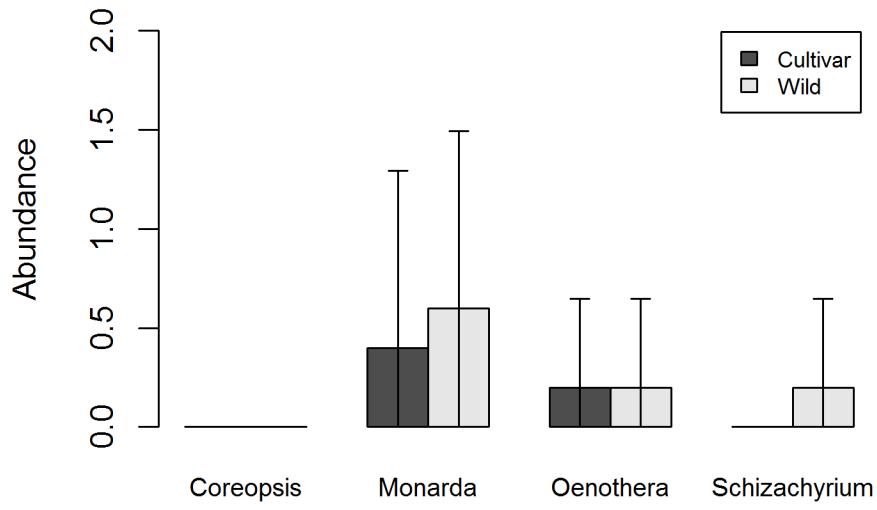
### Draeculacephala\_robinsoni



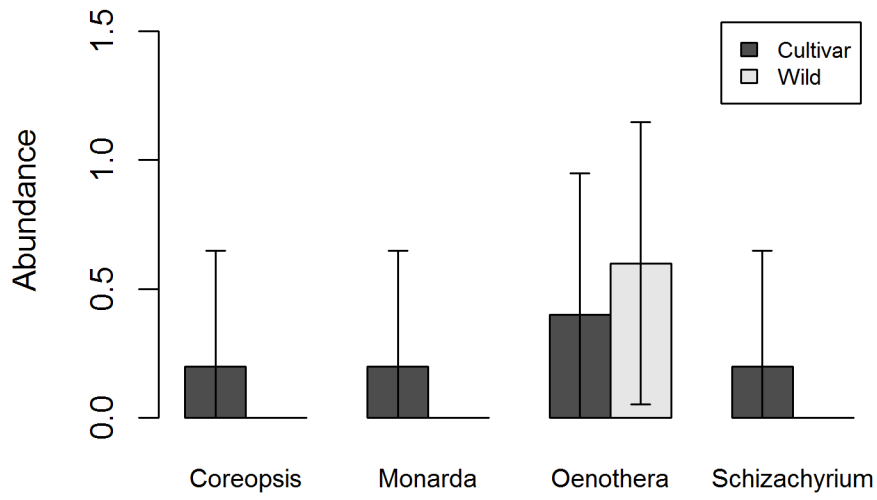
### Empoasca\_sp1



### Erythroneura\_sp2

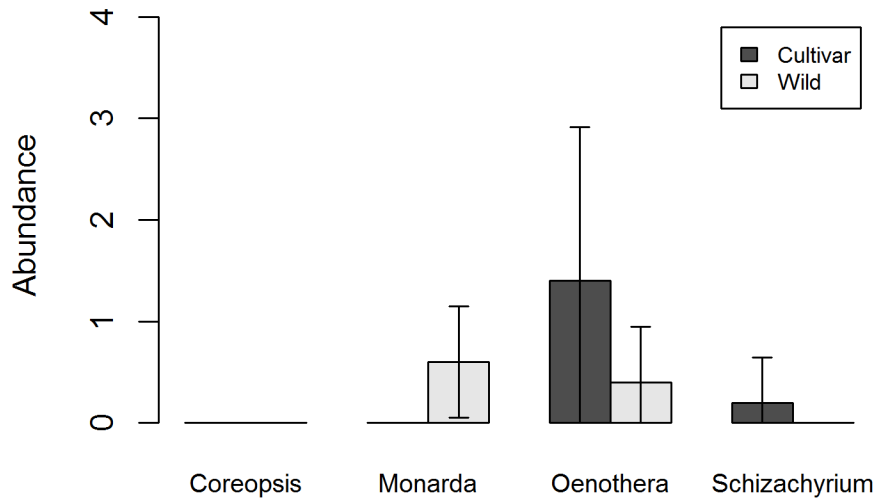


### Erythroneura\_sp3

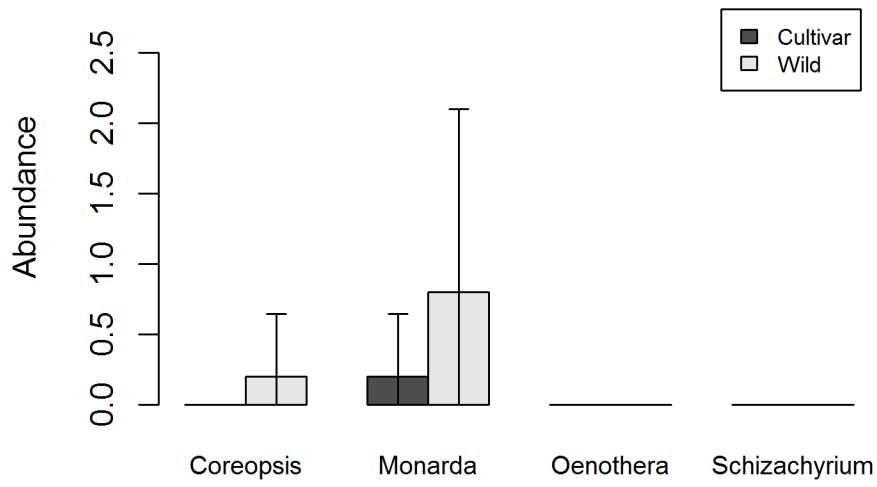




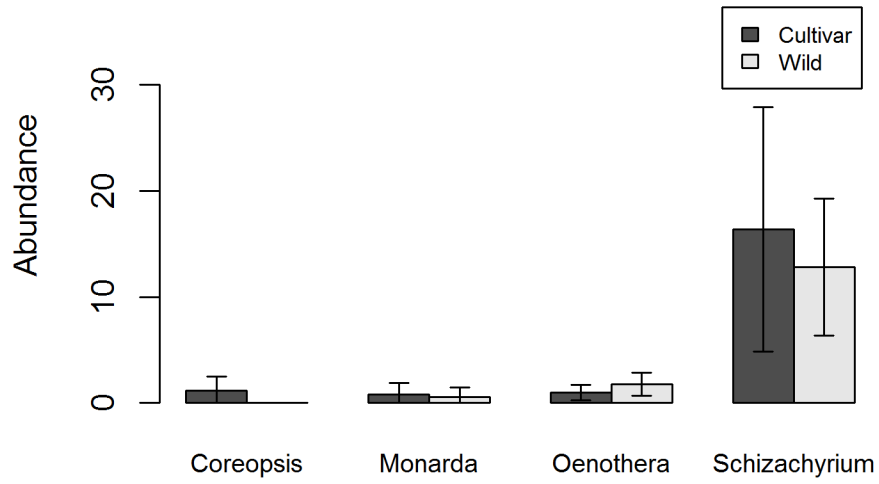
### Erythroneura\_sp6



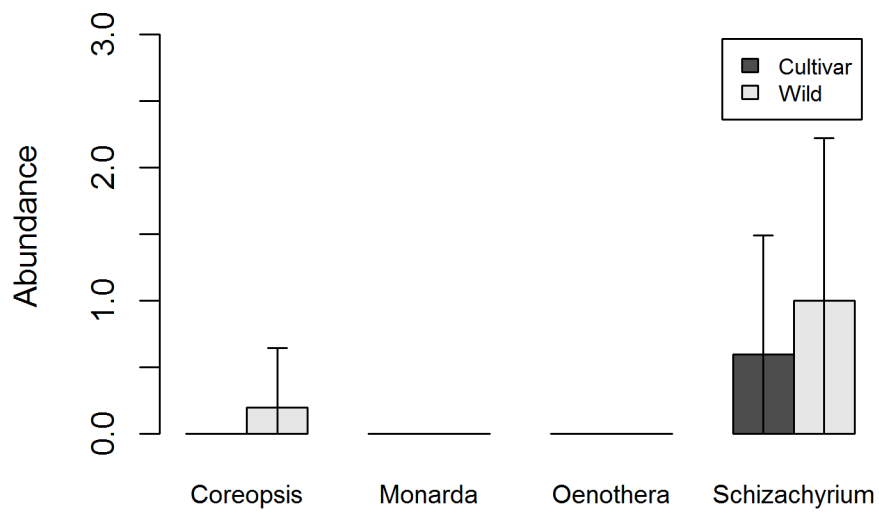
### Euschistus\_servus\_servus



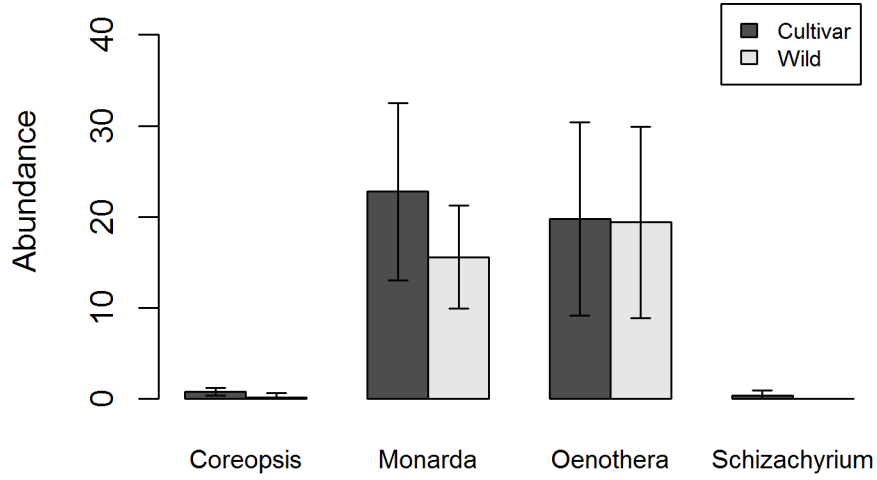
## Graminella\_nigrifrons



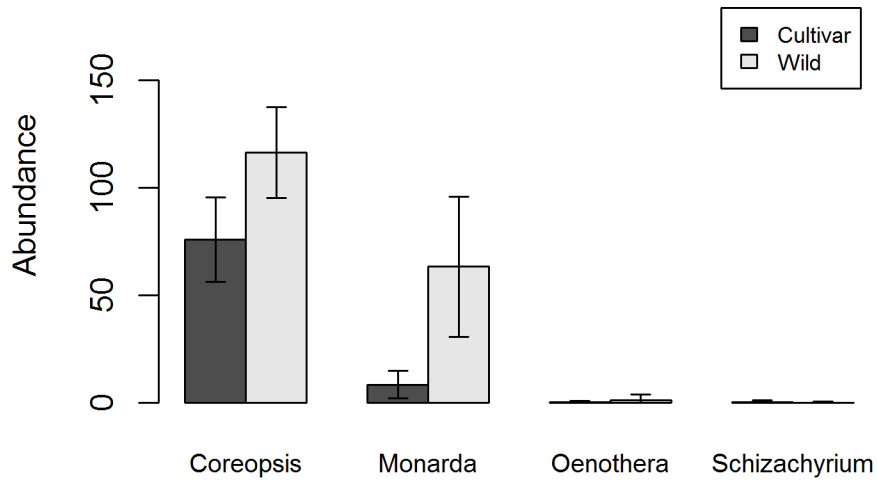
## Graminella\_sonora



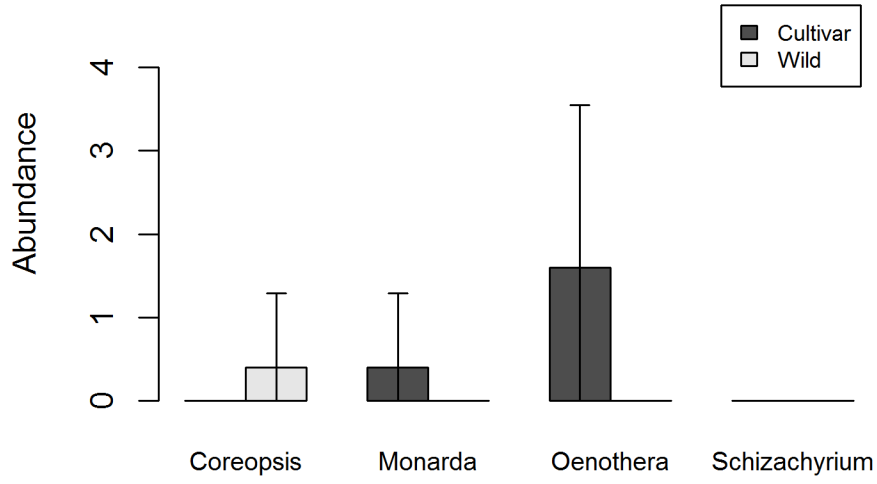
## Graphocephala\_versuta



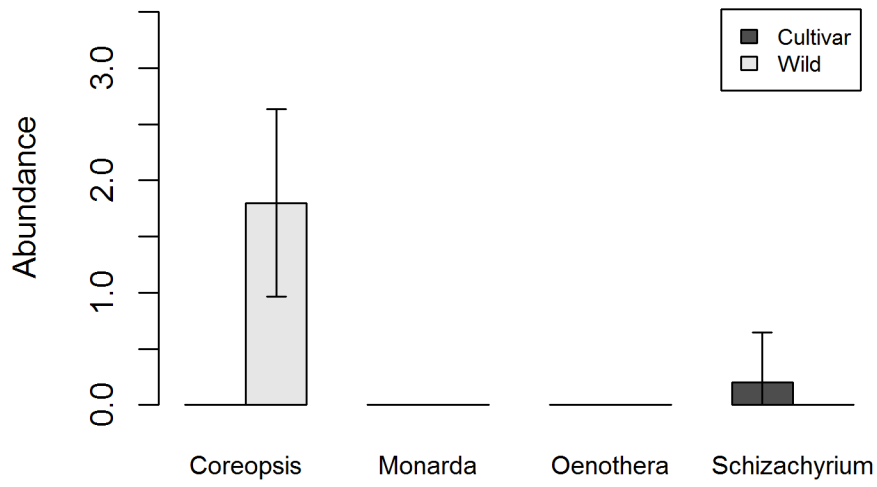
## Halticus\_bracteatus



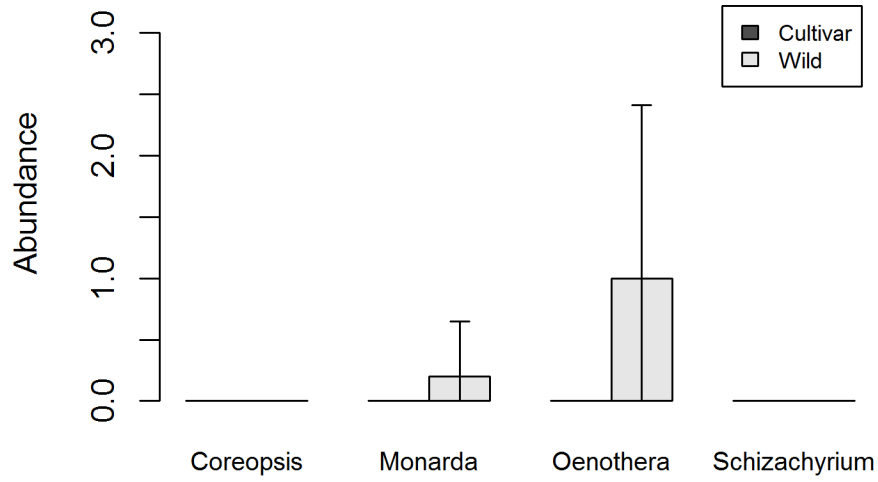
### Heraeus\_plebejus



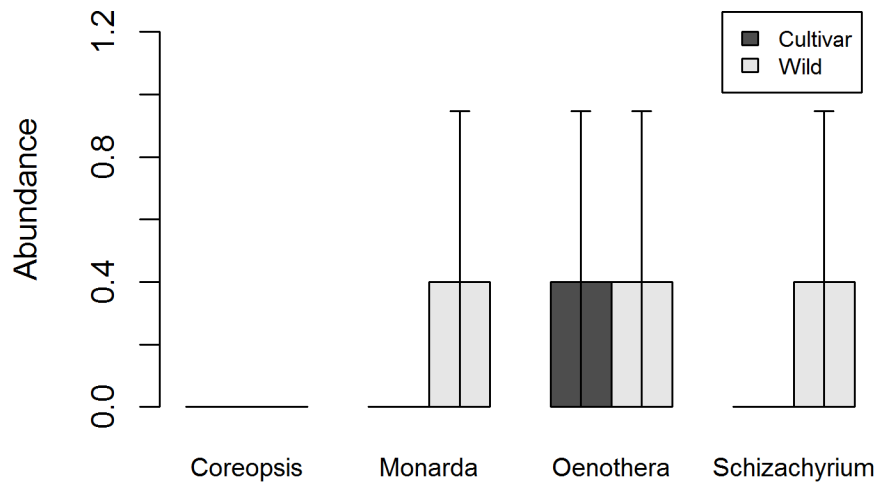
### Homaemus\_proteus



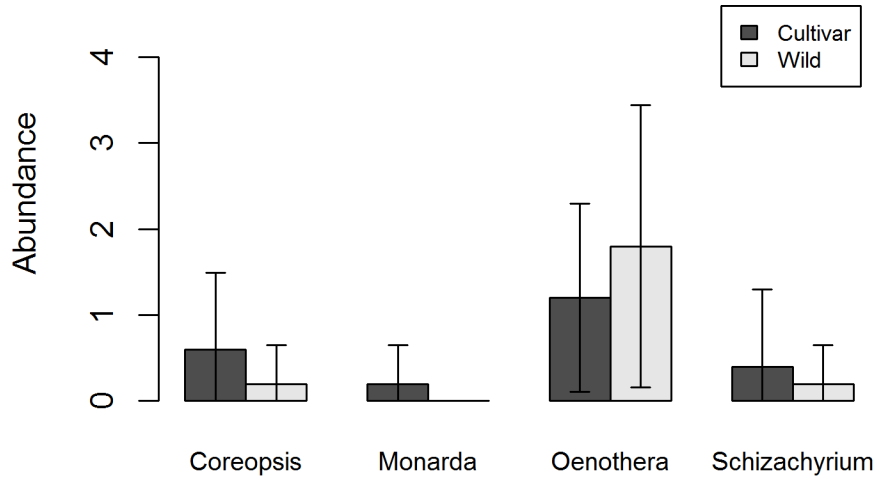
### Idiodonus\_brittoni



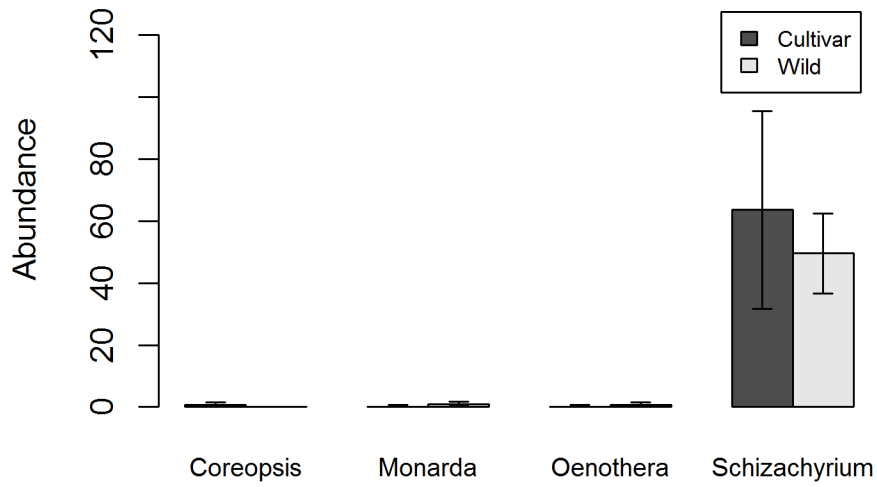
### Isodelphax\_basivitta



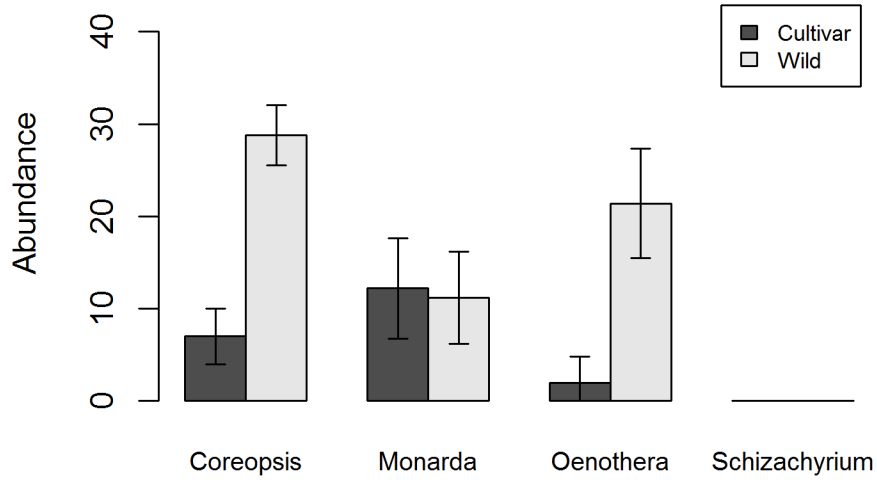
## Lepyronia\_quadrangularis



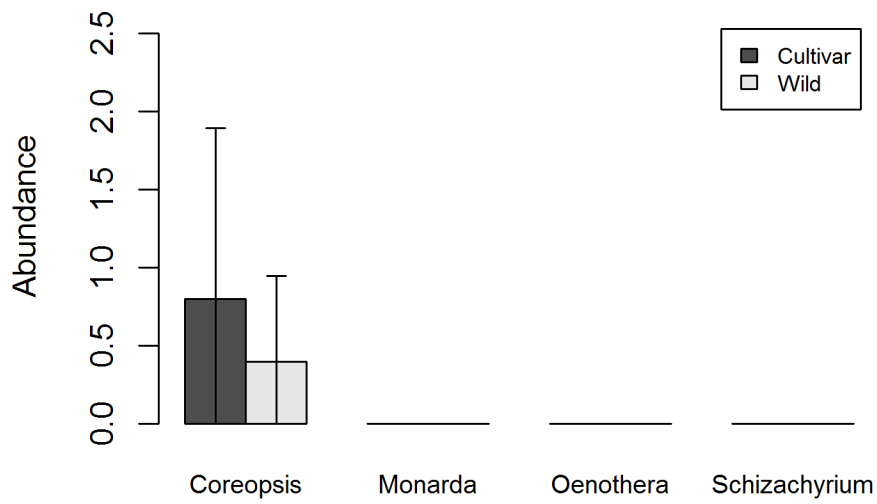
## Liburniella\_ornata



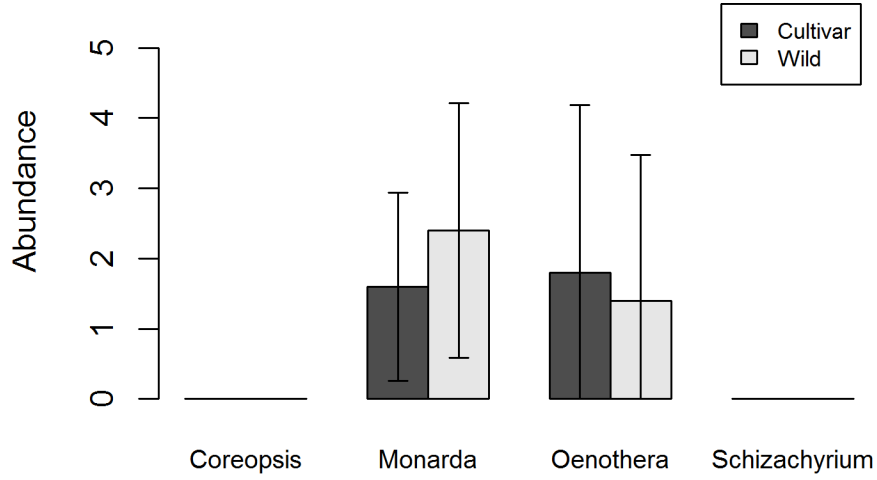
### Lygus\_lineolaris



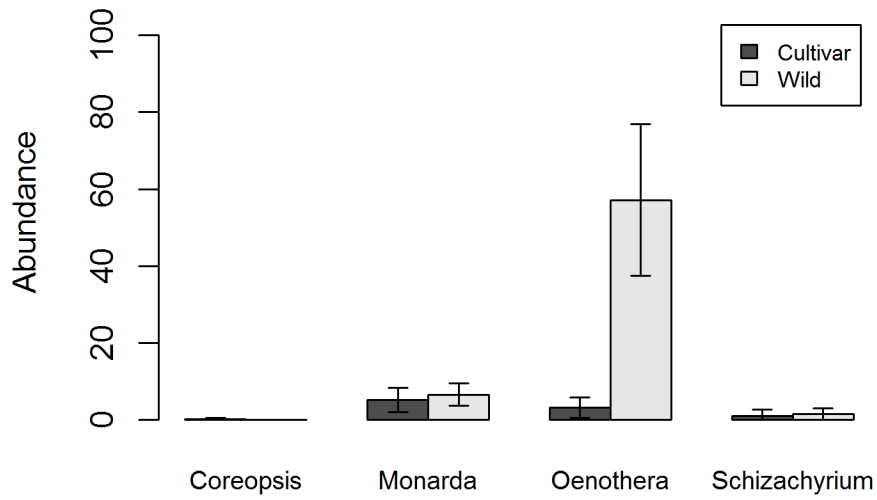
### Macrosteles\_lepidus



### Myodocha\_serripes

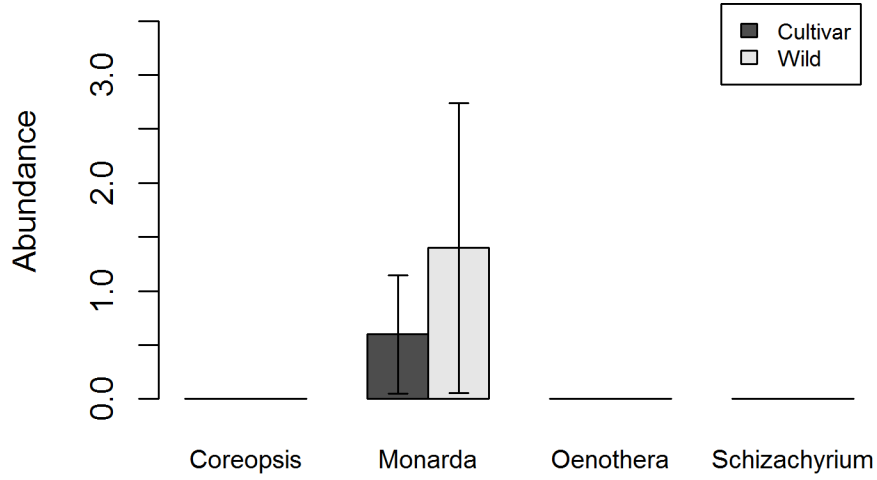


### Neopamera\_bilobata

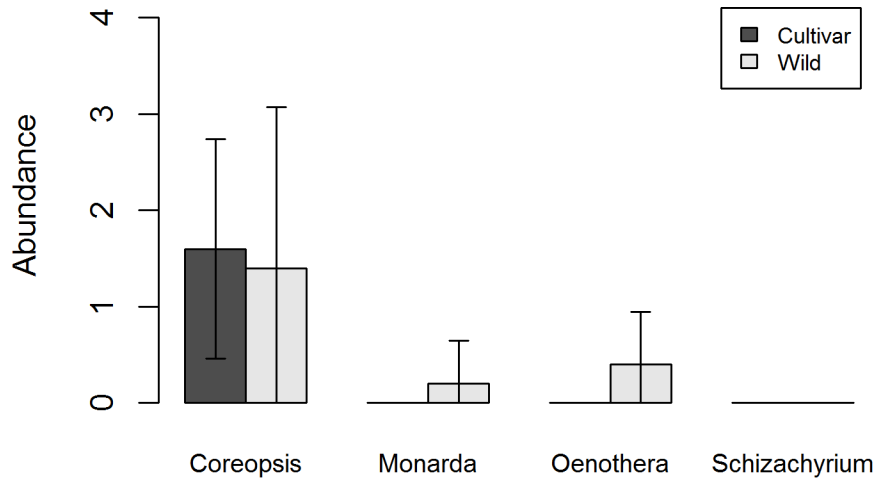




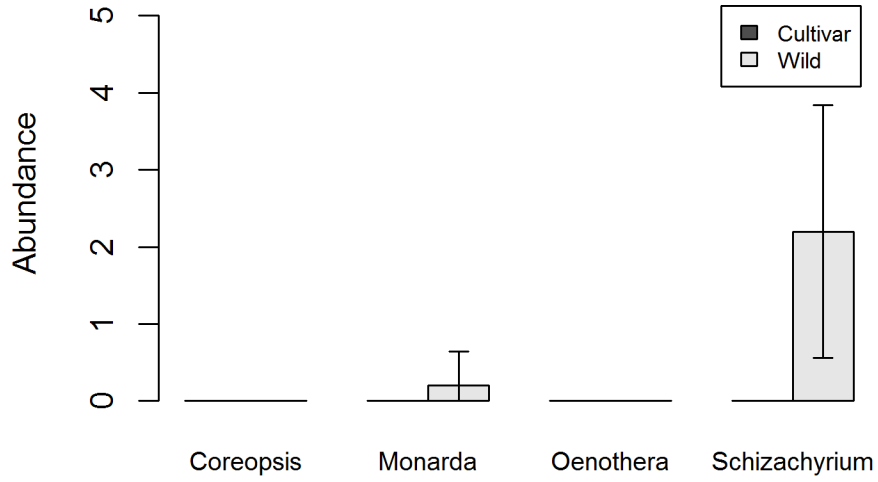
### Neurocolpus\_nubilus



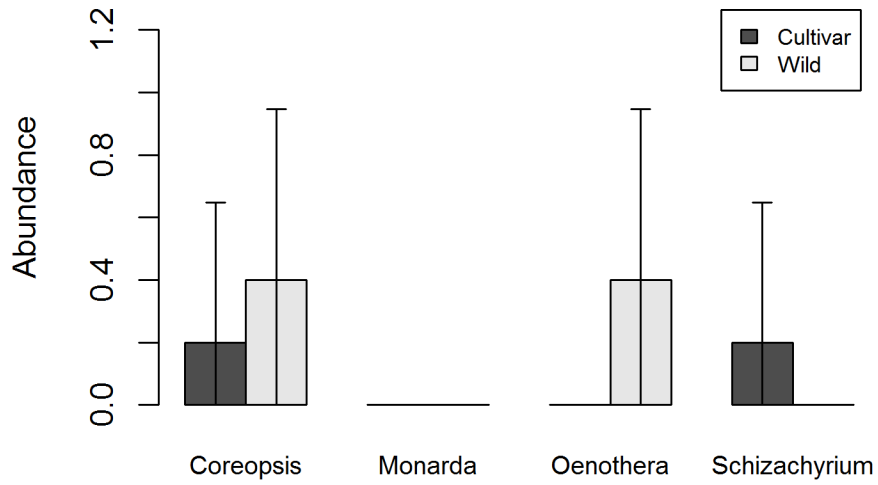
### Osbornellus\_clarus



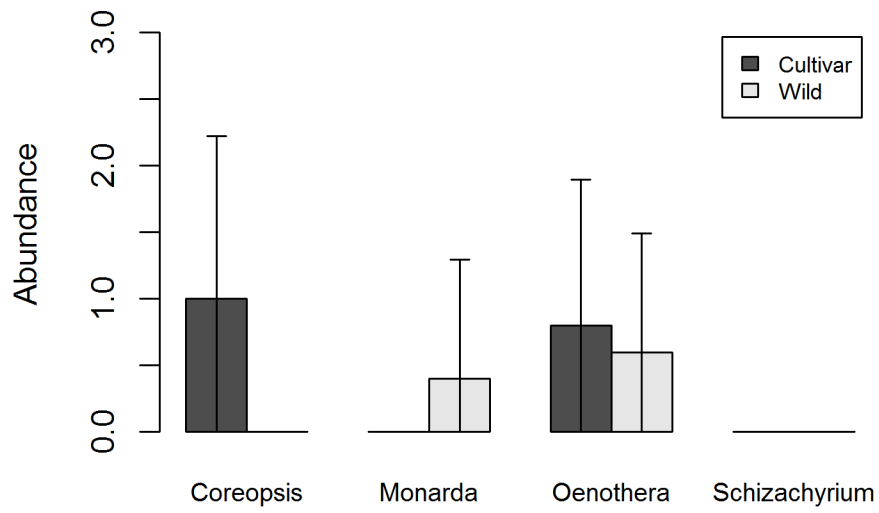
## Paramysidia\_mississippiensis



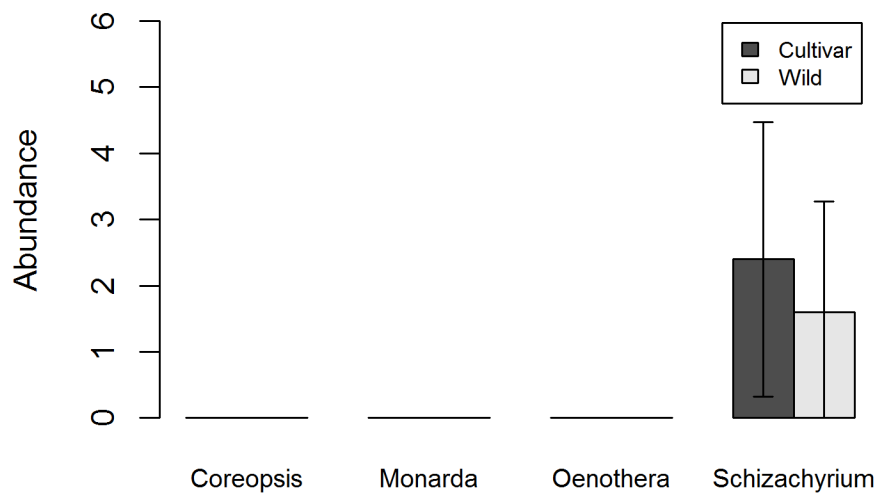
## Paraphlepsius\_tennesus



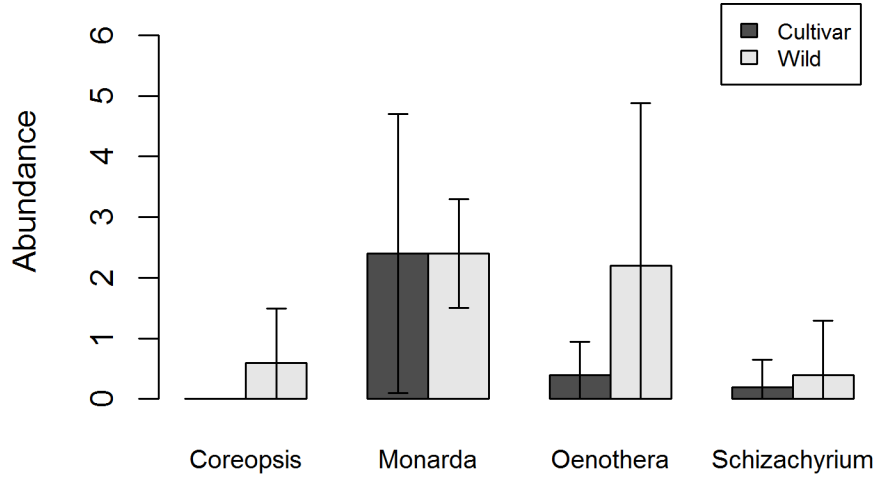
### Paraulacizes\_irrorata



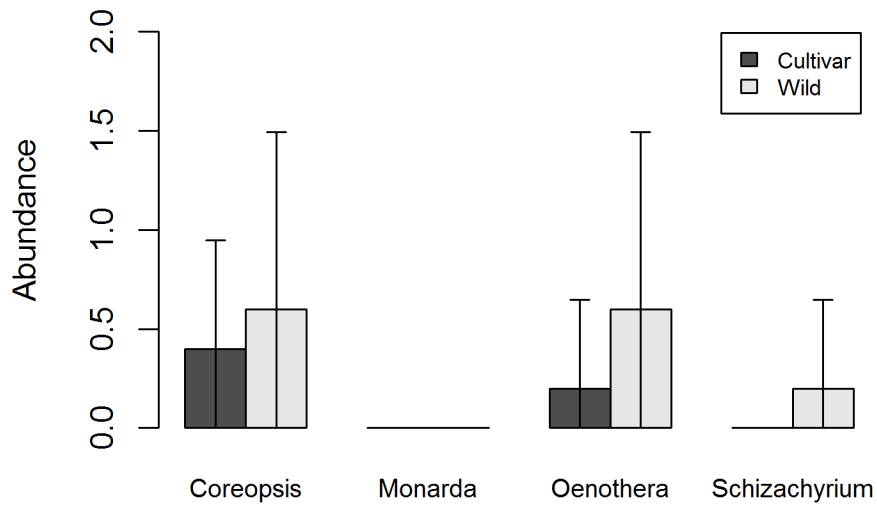
### Paromius\_longulus



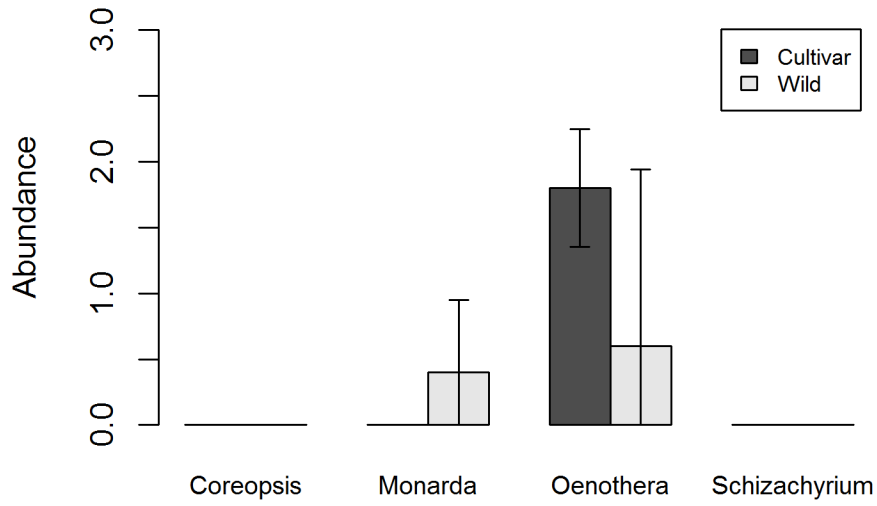
### Phytocoris\_tibialis



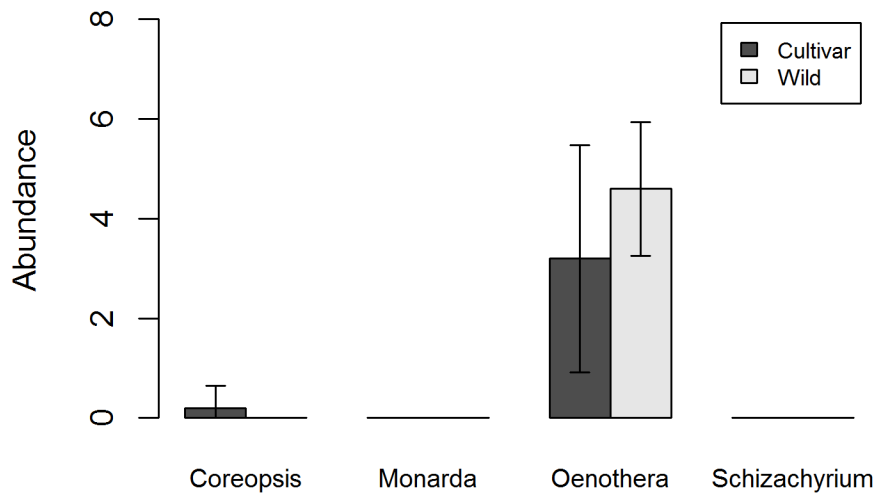
### Pissonotus\_piceus



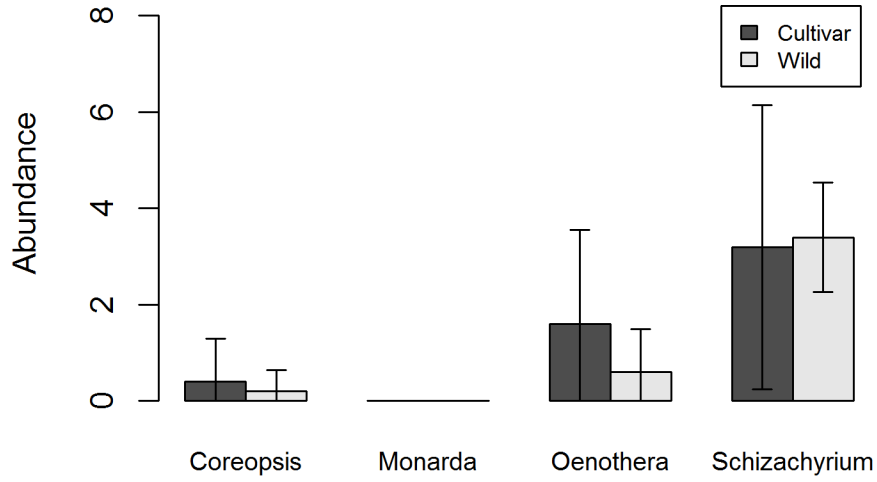
### Plagiognathus\_guttulosus



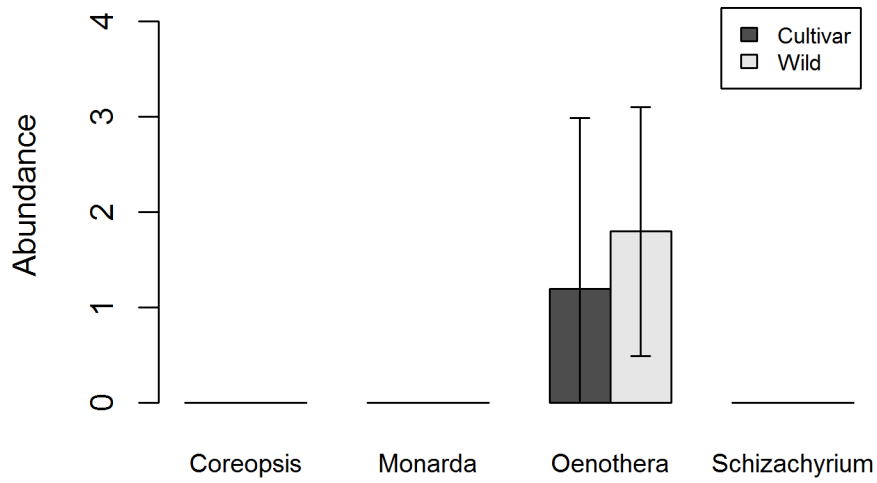
### Prepops\_rubrovittatus



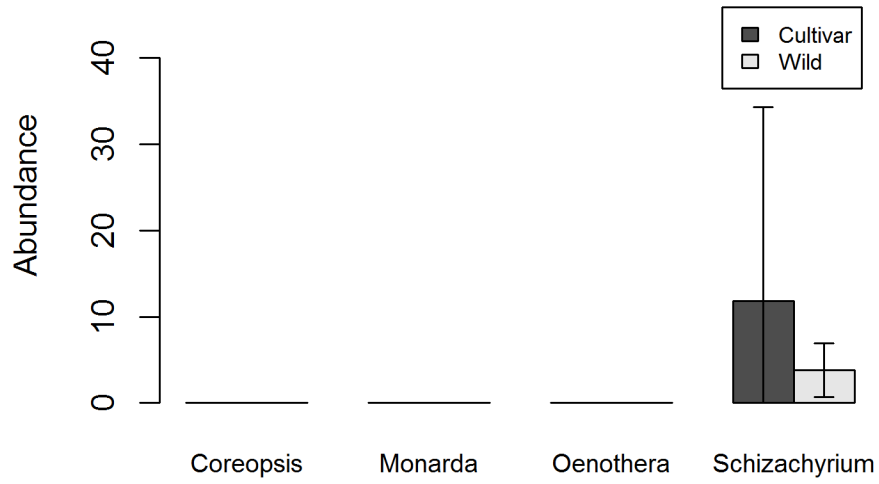
### Prosapia\_bicincta



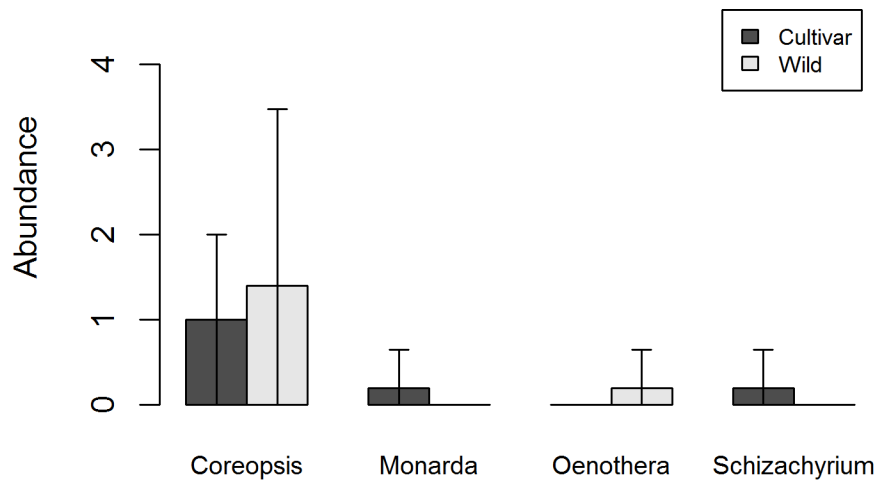
### Ptochiomera\_nodosa



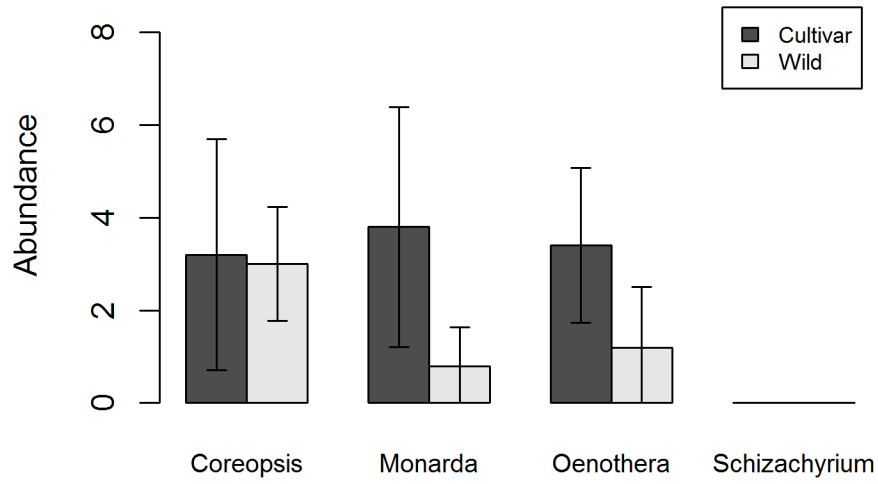
## Saccharosydne\_saccharivora



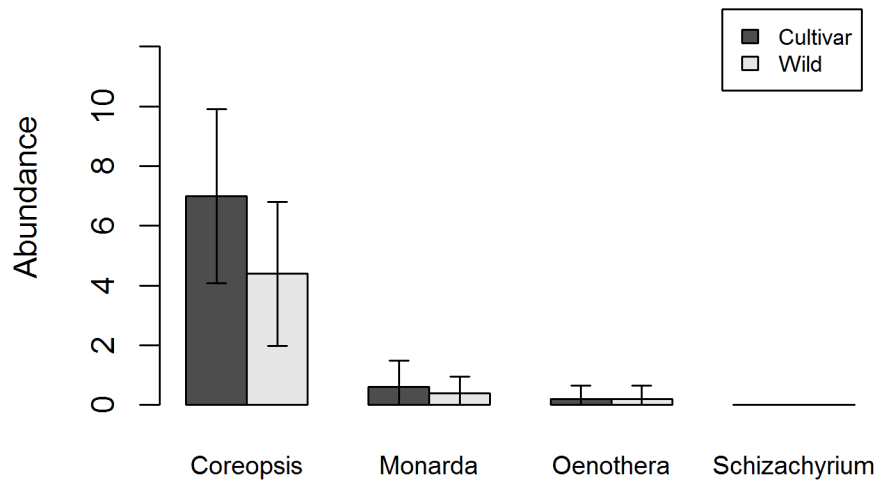
## Scaphoideus\_spp



### Scaphytopius\_acutus

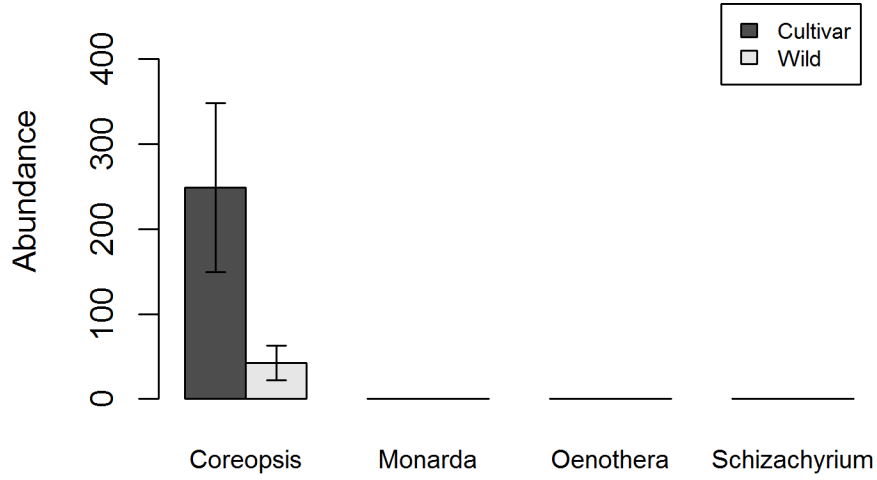


### Scaphytopius\_frontalis

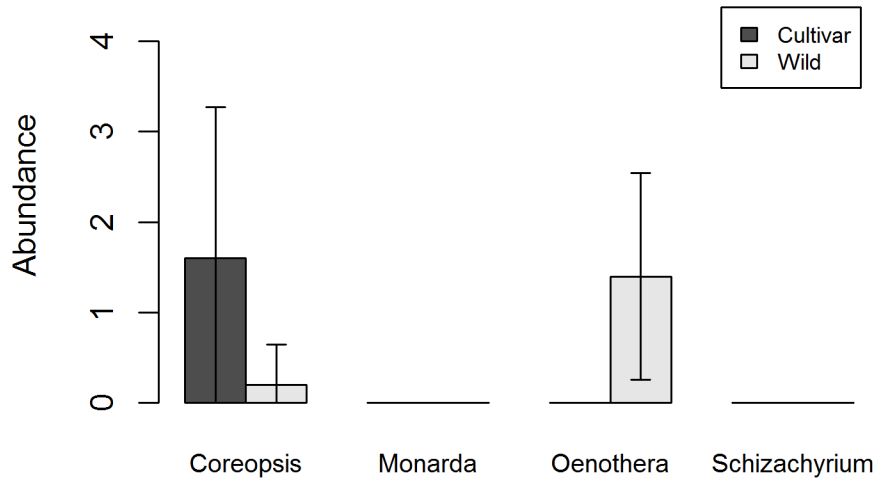




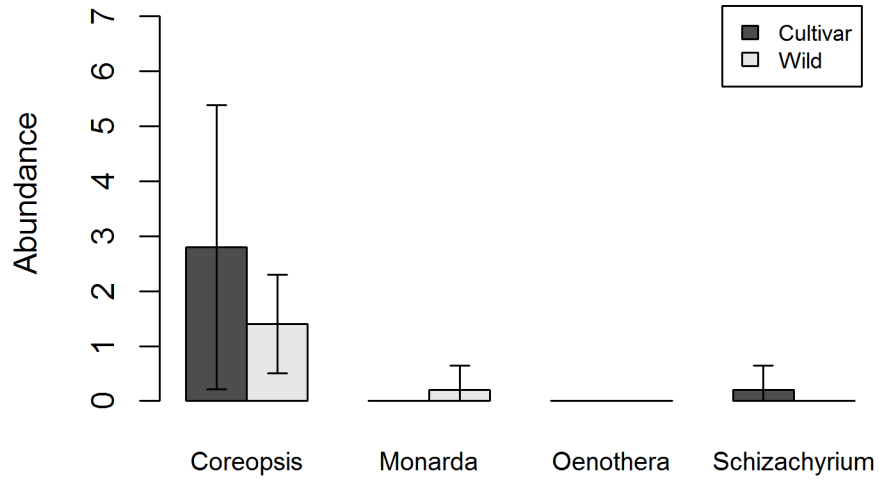
### Sixeonotus\_unicolor



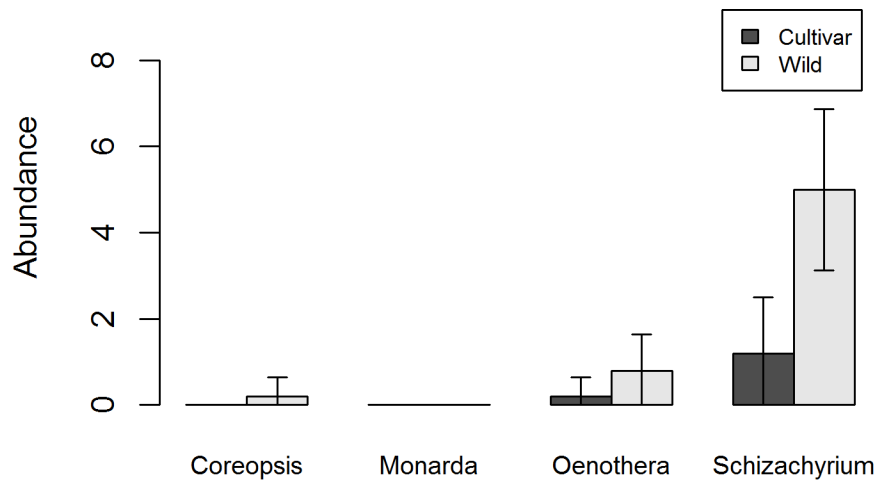
### Spissistilus\_festinus



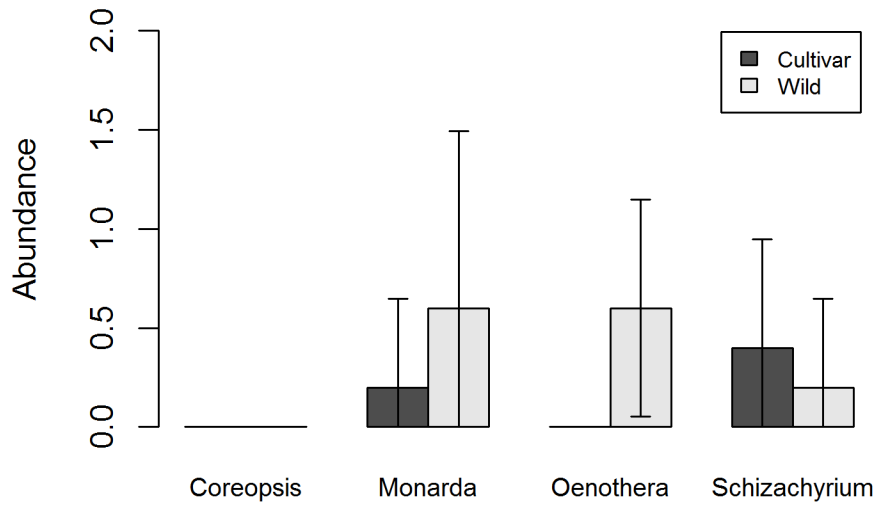
## Texananus\_excultus



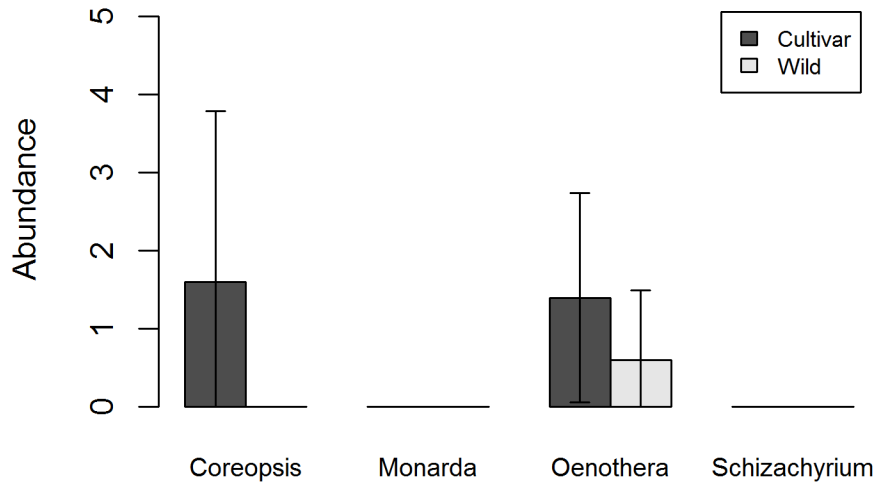
## Tylozygus\_bifida



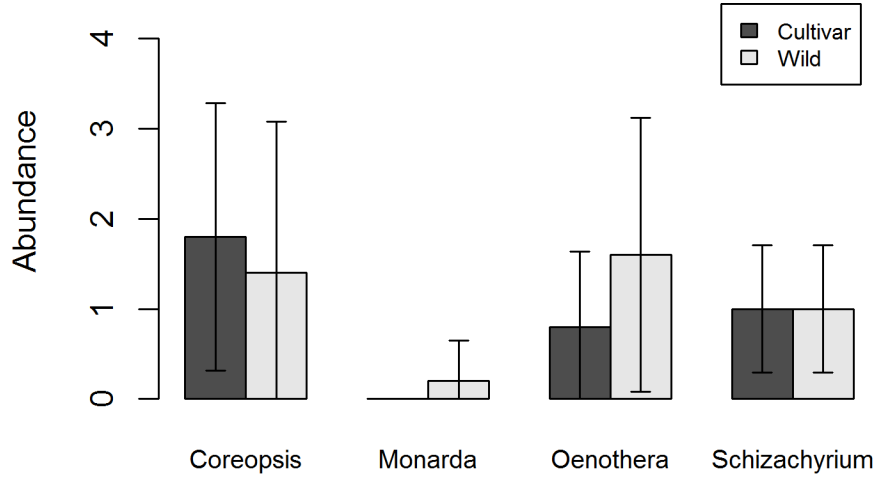
### Typhlocybae\_spp



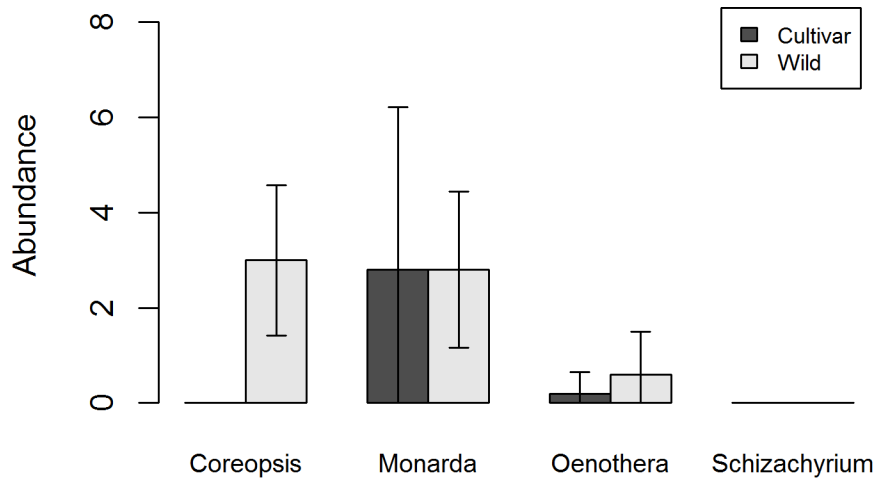
### Xerophloea\_minor



## Xestocephalus\_pulicarius



## Xyonysius\_californicus



## APPENDIX G

### TAXONOMY AND LIFE HISTORIES OF INSECTS

The table below summarizes the taxonomic information, feeding guild, and food plant records of the 65 insect species that were included in the statistical analyses. Some insects had detailed, high quality food plant records available. However, the majority had incomplete or ambiguous records. Moreover, some sources did not distinguish between host plant records, food plant records, and sitting records. Care should be taken in interpreting this life history information, as most insect species likely are able to feed on more plant species than those listed, and some of the plants listed may not be accurate.

<b>Insect Species</b>	<b>Family (and subfamily)</b>	<b>Feeding Guild</b>	<b>Food Plant Records<sup>1</sup></b>	<b>Reference</b>
Cuerna costalis	Cicadellidae: Cicadellinae	xylem	Many species of herbaceous (dicots and monocots) and woody plants	(Tubner and Pollard 1959)
Paraulacizes irrorata	Cicadellidae: Cicadellinae	xylem	Cirsium, Conyza, Lactuca, Silphium, Elymus, and Sorghum	(Mason and Yonke 1971)
Tylozygus bifida	Cicadellidae: Cicadellinae	xylem	Grasses	(DeLong 1948)
Draeculacephala balli	Cicadellidae: Cicadellinae	xylem	Grasses and sedges	(DeLong 1948)
Draeculacephala robinsoni	Cicadellidae: Cicadellinae	xylem	Grasses and sedges	(DeLong 1948)
Draeculacephala antica	Cicadellidae: Cicadellinae	xylem	Grasses and sedges	(DeLong 1948)
Graphocephala versuta	Cicadellidae: Cicadellinae	xylem	Many species of herbaceous plants	(Tubner and Pollard 1959)
Coelidia olitoria	Cicadellidae: Coelidiinae	phloem	Oak, sassafras, and other shrubs	(DeLong 1948)
Xerophloea minor	Cicadellidae: Ledrinae	phloem	Grasses	(DeLong 1948)
Idiodonus brittoni	Cicadellidae: Deltocephalinae	phloem	Shrubs	(DeLong 1948)
Texananus excultus	Cicadellidae: Deltocephalinae	phloem	Grasses	(DeLong 1948)

Paraphlepsius tennesus	Cicadellidae: Deltocephalinae	phloem	None listed	
Scaphoideus spp.	Cicadellidae: Deltocephalinae	phloem	Herbaceous plants	(DeLong 1948)
Osbornellus clarus	Cicadellidae: Deltocephalinae	phloem	Herbaceous plants	(DeLong 1948)
Scaphytopius frontalis	Cicadellidae: Deltocephalinae	phloem	Legumes and other herbaceous plants	(DeLong 1948)
Scaphytopius acutus	Cicadellidae: Deltocephalinae	phloem	Goldenrod, clover, plants in the rose family, and many others	(Nielson 1968; McClure 1980; Fontes et al. 1994)
Deltocephalus flavicosta	Cicadellidae: Deltocephalinae	phloem	Grasses	(DeLong 1948)
Chlorotettix galbanatus	Cicadellidae: Deltocephalinae	phloem	Grasses	(DeLong 1948)
Macrosteles lepidus	Cicadellidae: Deltocephalinae	phloem	Composites or willows	(Oman 1949)
Graminella nigrifrons	Cicadellidae: Deltocephalinae	phloem	Grasses	(DeLong 1948)
Graminella sonora	Cicadellidae: Deltocephalinae	phloem	Grasses	(DeLong 1948)
Balclutha abdominalis	Cicadellidae: Deltocephalinae	phloem	Grasses	(Oman 1949)
Balclutha neglecta	Cicadellidae: Deltocephalinae	phloem	Grasses	(Oman 1949)
Agallia constricta	Cicadellidae: Megophthalminae	phloem	Many species of herbaceous plants, including legumes, grasses, solanaceous plants, smartweeds, etc.	(Nielson 1968)
Agalliopsis novella	Cicadellidae: Megophthalminae	phloem	Alfalfa, clover, and other herbaceous vegetation	(DeLong 1948; Nielson 1968)
Aceratagallia sanguinolenta	Cicadellidae: Megophthalminae	phloem	Mainly clover and legumes, but other herbaceous plants as well	(DeLong 1948; Nielson 1968)
Xestocephalus pulicarius	Cicadellidae: Aphrodinae	phloem	Herbaceous plants among leaf litter and roots	(DeLong 1948; Beirne 1956)
Dikraneura sp.	Cicadellidae: Typhlocybinae	mesophyll	Grasses	(Knight 1968)
Empoasca sp.	Cicadellidae: Typhlocybinae	mesophyll	N/A	
Typhlocybinae spp.	Cicadellidae: Typhlocybinae	mesophyll	N/A	
Erythroneura sp. 2	Cicadellidae: Typhlocybinae	mesophyll	N/A	
Erythroneura sp. 3	Cicadellidae: Typhlocybinae	mesophyll	N/A	
Erythroneura sp. 6	Cicadellidae: Typhlocybinae	mesophyll	N/A	

Saccharosydne saccharivora	Delphacidae	phloem	Andropogon spp., Saccharum, and Sorghum	(Kennedy et al. 2012)
Pissonotus piceus	Delphacidae	phloem	Asters, Polygonum, Ludwigia spp., Liquidambar, and Persicaria	(Wilson et al. 1994; Urban et al. 2010; Kennedy et al. 2012)
Delphacodes andromeda	Delphacidae	phloem	None listed	
Isodelphax basivitta	Delphacidae	phloem	Ludwigia	(Kennedy et al. 2012)
Delphacodes puella	Delphacidae	phloem	Secale, Galinsoga, and Panicum	(Kennedy et al. 2012)
Liburniella ornata	Delphacidae	phloem	Rhynchospora and Carex	(Kennedy et al. 2012)
Anotia burnetii	Derbidae	phloem <sup>2</sup>	None listed	
Anotia bonnetii	Derbidae	phloem <sup>2</sup>	None listed	
Paramysidia mississippiensis	Derbidae	phloem <sup>2</sup>	Sabal and Acer	(Wilson et al. 1994)
Acanalonia conica	Acanaloniidae	phloem <sup>2</sup>	Many species of herbaceous plants	(Wilson et al. 1994)
Prosapia bicincta	Cercopidae	xylem	Grasses, trees, shrubs, and herbaceous plants	(Hamilton 1982)
Lepyronia quadrangularis	Cercopidae	xylem	Trees, brambles, herbaceous plants, and grasses	(Hamilton 1982)
Clastoptera xanthocephala	Clastopteridae	xylem	Prefer asters, but also feed on trees, shrubs, and grasses	(Hamilton 1982)
Spissistilus festinus	Membracidae	phloem	Mostly legumes and asters, but other herbaceous plants as well	(Kopp and Yonke 1973)
Euschistus servus	Pentatomidae	mesophyll, fruits	Many species of herbaceous plants and trees	(Rolston and Kendrick 1961)
Homaemus proteus	Scutelleridae	mesophyll, fruits <sup>2</sup>	Parthenium and Lantana	(Stone and Fries 1986; McClay et al. 1995; Palmer and Pullen 1995)
Neopamera bilobata	Rhyparochromidae	seeds, fruits	Chenopodium, Richardia, Croton, Solidago, and Euphorbia	(Slater and Baranowski 1990)
Paromius longulus	Rhyparochromidae	seeds, fruits	Grasses	(Slater and Baranowski 1990)
Heraeus plebejus	Rhyparochromidae	seeds, fruits	Herbaceous plants	(Slater and Baranowski 1990)
Xyonysius californicus	Lygaeidae	seeds, fruits	Medicago, Flaveria, and Erigeron	(Slater and Baranowski 1990)

Ptochiomera nodosa	Rhyparochromidae	seeds, fruits	Agropyron, Rumex, Plantago, and Euphorbia	(Slater and Baranowski 1990)
Blissus leucopterus	Blissidae	phloem	Grasses	(Slater and Baranowski 1990)
Myodocha serripes	Rhyparochromidae	seeds, fruits	Hypericum, Fragaria, Euphorbia, and other herbaceous plants	(Slater and Baranowski 1990)
Arhyssus nigristernum	Rhopalidae	seeds, fruits	Monarda and other mints	(Schaefer and Chopra 1982)
Prepops rubrovittatus	Miridae	mesophyll	Salix sp.	(Knight 1941)
Sixeonotus unicolor	Miridae	mesophyll	Garden Coreopsis and few-bracted beggarticks	(Wheeler 2001)
Phytocoris tibialis	Miridae	mesophyll	Pycnanthemum sp.	(Knight 1941)
Lygus lineolaris	Miridae	mesophyll, fruits, flowers	Known to feed on more than 300 species, many of which are asterids and rosids	(Young 1986)
Neurocolpus nubilus	Miridae	mesophyll, fruits, flowers	Cephalanthus, Populus deltoides, Gymnocladus, and Salix.	(Knight 1941)
Ceratocapsus punctulatus	Miridae	mesophyll	Phaseolus vulgaris and Bidens pilosa	(Hernandez and Henry 1999)
Halticus bracteatus	Miridae	mesophyll	Trifolium, Phaseolus, Plantago and many others herbaceous plants	(Knight 1941)
Plagiognathus guttulosus	Miridae	mesophyll	Oaks	(Knight 1941)

<sup>1</sup> some records may represent sitting records

<sup>2</sup> inferred feeding guild

### Literature Cited

- Beirne, B. P. 1956. Leafhoppers (Homoptera: Cicadellidae) of Canada and Alaska. Canadian Entomologist 88:1-180.
- DeLong, D. M. 1948. The leaf-hoppers, or Cicadellidae, of Illinois (Eurymelinae-Balcluthinae). Illinois Natural History Survey Bulletin 24:97-376.
- Fontes, E. M. G., H. Habeck, and F. Slansky. 1994. Phytophagous insects associated with goldenrods (*Solidago* spp.) in Gainesville, Florida. Florida Entomologist 77:209-221.



- Hamilton, K. G. A. 1982. The insects and arachnids of Canada Part 10: the spittlebugs of Canada (Homoptera:Cercopidae). Publication N-1740. Agriculture Canada, Ottawa, Ontario.
- Hernandez, L. M., and T. J. Henry. 1999. Review of the *Ceratocapsus* of Cuba, with descriptions of three new species and a neotype designation for *C. cubanus* Bergroth (Heteroptera: Miridae: Orthotylinae). Caribbean Journal of Science 35:201-214.
- Kennedy, A. C., C. R. Bartlett, and S. W. Wilson. 2012. An annotated checklist of the delphacid planthoppers (Hemiptera:Delphacidae) of Florida with the description of three new species and the new genus, *Meristopsis*. Florida Entomologist 95:395-421.
- Knight, H. H. 1941. The plant bugs, or Miridae, of Illinois. Illinois Natural History Survey Bulletin 22:1-234.
- Knight, W. J. 1968. A revision of the holarctic genus *Dikraneura* (Homoptera: Cicadellidae.). Bulletin of The British Museum (Natural History) Entomology 21:99-201.
- Kopp, D. D., and T. R. Yonke. 1973. The Treehoppers of Missouri: Part 2. Subfamily Smiliinae; Tribes Acutalini, Ceresini, and Polyglyptini (Homoptera: Membracidae). Journal of the Kansas Entomological Society 46:233-276.
- Mason, C. E., and T. R. Yonke. 1971. Life history of four *Draeculacephala* species and *Paraulacizes irrorata* (Homoptera: Cicadellidae). Annals of the Entomological Society of America 64:1393-1399.
- McClay, A. S., W. A. Palmer, F. D. Bennett, and K. R. Pullen. 1995. Phytophagous arthropods associated with *Parthenium hysterophorus* (Asteraceae) in North America. Environmental Entomology 24:796-809.
- McClure, M. S. 1980. Role of wild host plants in the feeding, oviposition, and dispersal of *Scaphytopius acutus* (Homoptera:Cicadellidae), a vector of peach X-disease. Environmental Entomology 9:283-292.

- Nielson, M. W. 1968. The leafhopper vectors of phytopathogenic viruses (Homoptera, Cicadellidae) taxonomy, biology and virus transmission. Technical bulletin N-1382. United States Department of Agriculture, Washington, D.C.
- Oman, P. W. 1949. The Nearctic leafhoppers (Homoptera: Cicadellidae): a generic classification and check list. *Memoirs of the Entomological Society of Washington* 3:1-253.
- Palmer, W. A., and K. R. Pullen. 1995. The phytophagous arthropods associated with *Lantana camara*, *L. hirsuta*, *L. urticifolia*, and *L. urticoides* (Verbenaceae) in North America. *Biological Control* 5:54-72.
- Rolston, L.H., and R. L. Kendrick. 1961. Biology of the brown stink bug, *Euschistus servus* Say. *Journal of the Kansas Entomological Society* 34:151-157.
- Schaefer, C. W. and N. P. Chopra. 1982. Cladistic analysis of the Rhopalidae (Hemiptera: Coreoidea) with a list of food plants. *Annals of the Entomological Society of America* 75:224-233.
- Slater, J.A., and R.M. Baranowski. 1990. Lygaeidae of Florida (Hemiptera: Heteroptera). *Arthropods of Florida and Neighboring Land Areas* 14:1-211.
- Stone, J. D., and J. N. Fries. 1986. Insect fauna of cultivated guayule, *Parthenium argentatum* Gray (Campanulatae: Compositae). *Journal of the Kansas Entomological Society* 59:49-58.
- Tubner, W. F., and H. N. Pollard. 1959. Life histories and behavior of five insect vectors of phony peach disease. Technical Bulletin N-1188. United States Department of Agriculture, Washington, D.C.
- Urban, J. M., C. R. Bartlett, and J. R. Cryan. 2010. Evolution of Delphacidae (Hemiptera: Fulgoroidea): combined-evidence phylogenetics reveals importance of grass host shifts. *Systematic Entomology* 35:678-691.
- Wheeler, A.G. 2001. Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists. Cornell University Press, Ithaca, New York.
- Wilson, S. W., C. Mitter, R. F. Denno, and M. R. Wilson. 1994. Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. Pages 7-113 in R.F. Denno and T.J. Perfect, editors. *Planthoppers: their ecology and management*. Chapman and Hall, New York.

Young, O. P. 1986. Host plants of the tarnished plant bug, *Lygus lineolaris* (Heteroptera:Miridae). Annals of the Entomological Society of America 79:747-762.