Test of a Natural Enemy Hypothesis on Plant Provenance: Spider Abundance in Native and Exotic Ornamental Landscapes[1]

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Abstract There is heightened interest in the effects that the provenance of plants in the landscape has on animals inhabiting them. This topic is of great interest for designers of urban ornamental landscapes, which tend to be mosaics of native and exotic plants. Although there is a substantial body of research on insect herbivores, less attention has been paid to arthropod natural enemies. Many commonly grown exotic woody plants were missing from eastern North America for millions of years prior to the arrival of Europeans. Due to the lack of a recent co-evolutionary history with these exotic plants, native natural enemies may be less well able to use the resources provided by them—architectural features and nutritional supplements—than they will those of native plants. Hence, natural enemies will be less numerous and diverse in landscapes dominated by exotic plants. To test this hypothesis, we designed a replicated experiment comprising 0.08-hectare plots planted to congeneric pairs of 16 genera of woody plants from either Eurasia or North America. Spiders attending egg masses of the brown marmorated stink bug, *Halyomorpha halys,* (Stål) (Hemiptera: Pentatomidae) emplaced on leaves of a subset of plant species known to be attacked by this pest, were statistically less abundant in the exotic plots, thus supporting the hypothesis.

Key Words biological control, invasive insect species, natural enemies, spiders, urban ornamental landscapes

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Two features of plants and plant complexes, defensive chemistry and physical structure, are powerful determinants of the identity, abundance, and diversity of herbivorous arthropods and their natural enemies. Many plant groups are characterized by classes of toxins or antifeedants that inhibit herbivore attack (e.g., tannins in *Quercus*, cucurbitacins in Cucurbitaceae, and cardiac glycosides in Apocynaceae). The resulting co-evolutionary "arms race" between plants, with increasingly sophisticated defenses, and herbivores, with better detoxifying enzymes or toxin-evading behaviors, appears to have led to diversification of both insect and plant taxa (Farrell et al. 1992). A key corollary is that herbivores are expected to be more abundant and diverse on plants with which they have a long

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evolutionary history than on exotic plants (Ehrlich and Raven 1964). This expectation is embodied in the Enemy Release Hypothesis that has led some to assume that exotic plants will be relatively free from attack by native insect herbivores (Keane and Crawley 2002). In fact, herbivores vary in host-use traits that have enabled some native insect herbivores to colonize exotic plants (Pearse and Hipp 2009, Strong et al.1984). Nevertheless, at least for some polyphagous North American Lepidoptera, larvae offered exotic plants tended to have poorer survivorship and were much smaller than conspecifics reared on native hosts (Tallamy et al. 2010). Exotic plants also have been found to support less lepidopteran biomass and fewer lepidopteran species than native plants (Burghardt et al. 2010, Zeufle et al. 2008).

By similar reasoning, native natural enemies are expected to be better adapted to survive and reproduce among native than exotic plants. Plants provide predators with living space, attachment points for snares and shelters, cover from prey and predators, and buffering of abiotic factors. A large body of evidence, most of it from natural and agricultural settings, has shown that vegetation structural diversity and host plant chemistry are major determinants of natural enemy abundance and diversity (Alston et al. 1991, Greenstone 1984, Honek 1983, Langellato and Denno 2004, McCormick et al. 2012, Vet and Dicke 1992,). The influence of vegetation diversity and structure on natural enemy complexes in urban landscapes is an emerging area of research (Frank and Shrewsbury 2004, Joseph and Braman 2009, Smith et al. 2006, Sperling and Lortie 2010), but trends appear similar to those in natural and agricultural landscapes, with natural enemy abundance and diversity or both positively correlated with vegetation structural diversity (Shrewsbury and Raupp 2006).

Plants also supply a surprising diversity of nutritional supplements to natural enemies (Lundgren 2009). Predators of many families feed on floral and extrafloral nectar and pollen (Pemberton and Vandenberg 1993, Pollard et al. 1995, Nomiku et al. 2003). Feeding on nectar or pollen raises predator fitness (Limburg and Rosenheim 2001, McMurty and Scriven 1964, Patt et al. 2003, Putnam 1955, Smith and Mommsen 1984, Taylor and Bradley 2009, Taylor and Pfannenstiel 2009, van Rijn and Tanigoshi 1999). Analysis of the literature on the influence of vegetation structure and plant food resources on herbivore and natural enemy diversity and performance has inspired experimentation and influenced practices in the biological control of insect pests (Fiedler et al. 2008, Gurr et al. 2004), including a new focus on native plants (Fiedler and Landis 2007a, 2007b, Frank et al. 2008, Isaacs et al. 2009).

Based on the foregoing discussions of natural enemy adaptations to plant architecture, chemistry, and non-prey food resources, we now propose a Natural Enemies Hypothesis for arthropod–plant trends in relation to plant provenance.

Due to more recent shared evolutionary histories, arthropod natural enemies will be better adapted to native than to exotic plant species assemblages. Consequently, natural enemies will be more abundant and more diverse, and exert more effective biological control of herbivore populations, in native than in exotic landscapes.

Because plant host chemistry and plant structure are such powerful determinants of habitation by arthropods, a stringent test of the Natural Enemies Hypothesis requires explicit control of these variables. In order to minimize the incidence of unwitting architectural and chemical differences that could confound the test of plant provenance, we drew the study taxa from a pool of phylogenetically matched species pairs that have been geographically separated for at least one million years. During a study to evaluate the effects of native and exotic plants on sentinel egg masses of the exotic invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), we observed that spiders frequented clips used to attach the egg masses to plant leaves (Cornelius et al. 2016). This study reports the abundance of spiders in experimental plots and represents part of an ongoing series of investigations testing the Natural Enemies Hypothesis.

Materials and Methods

Plants in the experiment. North American cultivated landscapes include taxa from nearly every floristic region of the globe, yet by virtue of a predominantly temperate climate, these landscapes rely heavily on plants derived from the Holarctic Kingdom, the dominant floristic kingdom of the northern hemisphere. The modern temperate flora is derived from an ancient boreotropical flora that spread during the warm, early Tertiary period through land bridges that connected the northern hemisphere continents and, subsequently, adapted to the cooling climates of the Miocene, evolving into a widespread mixed mesophytic forest (Milne 2006). The floristic break between the New World and Old World gradually grew as the North Atlantic land bridge fragmented in the Eocene between 30 and 40 million years ago (mya), separating North America and Eurasia; whereas, the break with eastern Asia was completed much more recently, during the start of the Pliocene (5 mya) (Milne 2006).

A continuous link between Asian and North American floras was present for most of the last 65 million years that, combined with geologic and climatic changes, has led to various divergence dates for related taxa or even multiple vicariance events within genera of temperate plants (Braun 1955, Donoghue and Smith 2004). For instance, the white pines in this study, *Pinus strobus* L. and *Pinus wallichiana* A.B.Jacks, are both in the traditional subg. *Strobus,* sect. *Strobus*. The split between the purely North American clade of sect. *Strobus* (e.g., *Pinus strobus*) from the clade that gave rise to *P. wallichiana* (Himalayan white pine) is calculated as approximately between 50 and 60 mya (Eckert and Hall 2006). Within the oaks, *Quercus alba* L. and *Quercus robur* L. are both members of sect. *Quercus* (white oaks), a relatively recently evolved section of the genus, originating in the New World and spreading to the Old World in the Oligocene and upper Miocene (from 34 to 20 mya), with the intercontinental divergence dated at approximately 17 mya (Manos and Stanford 2001). For disjunct genera with true sister-species pairs, such as the tulip trees (e.g., *Liriodendron tulipifera* L. and *Liriodendron chinense* [Hemsl.] Sarg.) and trumpet vines (e.g., *Campsis radicans* and *Campsis grandiflora* [Thunb.] K.Schum.), the divergence times are even more recent, at 6.15 ± 3.31 mya and 1–5 mya, respectively.

Altogether, we planted matched species pairs in 16 genera (listed in Table 1 of Cornelius et al. 2016) including only taxa that are available in the nursery trade, so that the results of this research would be relevant to planting and management

Table 1. Indicators of spider presence, summed across treatments and plant species.

Date egg masses emplaced	Live animal	Retreat in clip	Silk on leaf	Exuvium in clip
03 June 2014	3	0	0	0
17 June 2014	1	0	0	0
01 July 2014	5	0	0	0
15 July 2014	10	0	0	0
29 July 2014	3	2	0	0
12 August 2014	4	1	0	0
26 August 2014	3	2	0	0
9 September 2014	3	1	1	1
01 June 2015	1	0	0	0
16 June 2015	4	0	0	0
30 June 2015	12	0	0	0
14 July 2015	8	0	0	0
28 July 2015	10	3	0	0
11 August 2015	11	1	1	0
25 August 2015	3	0	0	0

choices in urban landscapes. The only exception to the one-to-one congeneric match is the turf, because no native turf grasses are adapted to the relatively low summer temperatures and high humidities of the study area.

Locality and design of the experiment. We performed the experiment at the United States National Arboretum (USNA) in Northeast Washington, DC, USA (N38°54′36.84”, W76°58′3.14”) in USDA plant hardiness zone 7a (-17.8 to -15°C). The USNA is uniquely suited for urban study: it is located within a large city; is itself a model urban landscape; and contains hundreds of examples of exotic and native congeners of popular urban landscape plants, including many of those in our experiment. Hence, many herbivores and natural enemies capable of colonizing the experiment are found in the surrounding landscape, as they are in real-world urban residential plots.

The experiment was set up in a randomized complete block design, with one replicate of each treatment — native or exotic — on each of three blocks, to control for location effects due to differences in soil, slope, exposure, and surrounding vegetation mosaic. The specific plant species selected, background behind these selections, and details of plot preparation and maintenance, are provided in Cornelius et al. (2016). The plots measure 25 × 25 m, with the selected trees, shrubs, and turf arrayed to simulate an urban backyard (Fig. 1; see Cornelius et al.

Fig. 1. Satellite image of the pair of native and exotic 25 m × 25 m experimental plots in the Valley block.

2016 for additional details of landscape design). The blocks, named for roads or floristic sections in the USNA, were designated Azalea Road, Valley Road, and Conifers (Fig. 2). At the time data collection began, the plots had been established for three years and most plants had flowered and produced fruits.

Data collection. Four-day observation and specimen collection periods began during the first week of June in 2014 and 2015, and were repeated every other week through the first week of September in 2014 and the last week of August in 2015. At the beginning of each sampling period, 24 individual fresh egg masses (oviposited within the previous 24 h) of the brown marmorated stink bug, *H. halys*, on rectangles of paper towel (approximately 1 cm × 2 cm), were received from a continuous colony maintained at the Invasive Insect Biocontrol and Behavior Laboratory in Beltsville, MD. They were then assigned to one of eight plant species, on each of the three blocks: *Acer saccharum* Marshall*, Cercis canadensis* L., *Hydrangea arborescens* L., or *Prunus virginiana* L. (all native); and *Acer platanoides* L.*, Cercis chinensis* Bunge, *Hydrangea paniculata* Siebold, or *Prunus padus* L. (exotic).

The egg masses were transported to the USNA plots and attached with two 4.8 cm-long wooden clothespins (Darice, Inc., Strongsville, OH) to the abaxial surfaces of one leaf on one individual of each of the eight plant species in all three blocks, between 1.2 m and 1.8 m above the ground on the trees, and in the upper third of the canopy on *Hydrangea*. Each egg mass was visited mid-morning and mid-afternoon on each of the following 2 d, and again on the third following morning. At

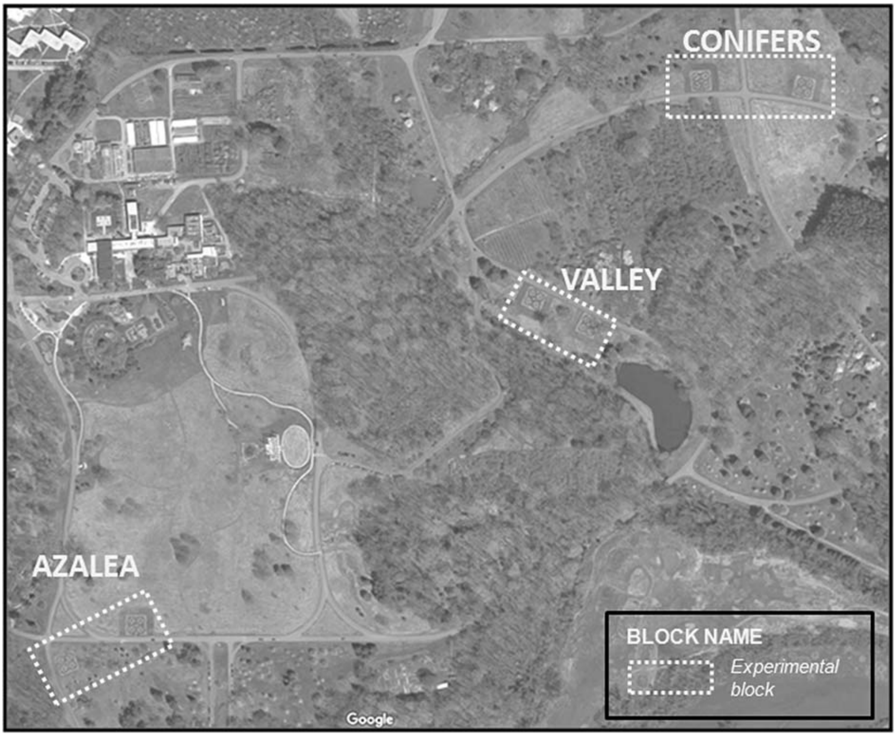

Fig. 2. Satellite image of the United States National Arboretum, indicating the locations of the three blocks of the randomized complete block design.

each visit, both surfaces of the leaf, and the arch formed by the semicircular hole of each jaw of the clip in contact with the leaf, were observed for the presence of live spiders (Fig. 3), retreats, exuviae, and silk lines, as indicators of spider presence during the time since set-up or previous visit. Live spiders were collected when possible, placed into 80% ethanol, and transported to the laboratory for identification. During the second season, the numbers of intact, broken, and collapsed eggs in each mass were determined under high magnification with a dissecting microscope before emplacement in the field and after they were collected. Broken eggs in excess of those found during set-up were scored as chewed by predators, mostly represented by beetles and spiders (although they do suck up extra-orally digested remains of their prey, spiders first break them up with their maxillae, giving them an appearance similar to those of prey broken by classical chewing insect predators [Morrison et al. 2016]). In order to avoid multiple counts of the same individual, only one indicator of spider presence per leaf was counted, unless multiple live individuals were encountered simultaneously on the same leaf.

During the week of 12 August 2014, *H. halys* egg mass production was low and we were short seven egg masses. We assigned the missing plants by means of a table of random numbers, such that no plant species was missed more than once.

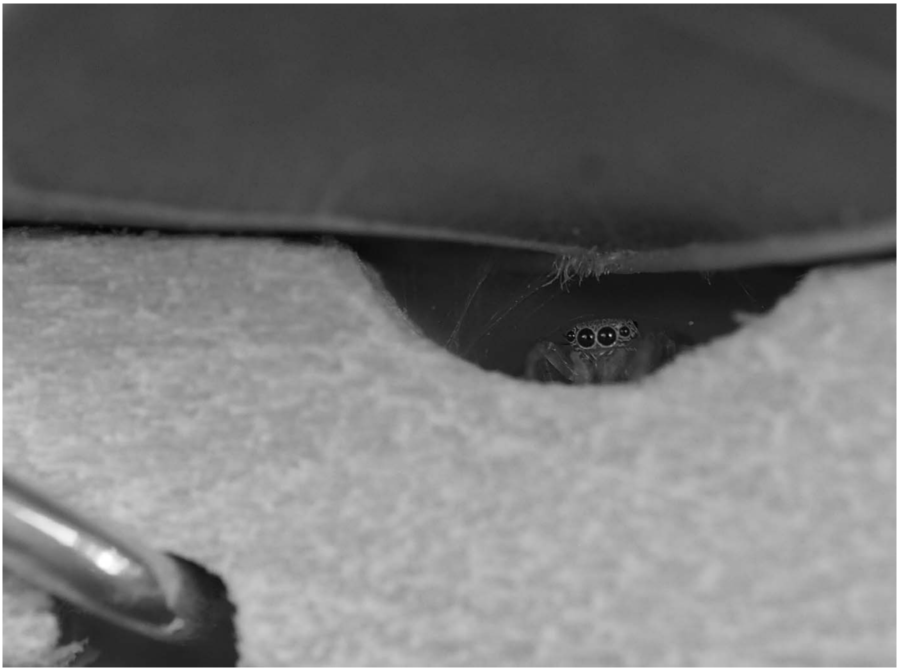

Fig. 3. Juvenile salticid in its retreat in the arch of a clothespin. The base of the arch spans approximately 6 mm.

Additionally, the *Hydrangea* leaf at the Grove site on which an egg mass had been emplaced on 29 August 2014 was discovered on the ground the following day, and that egg mass had to be omitted from the experiment.

Statistical analysis. Spider abundance was measured by counting live spiders, spider retreats, silk lines, and spider exuviae. Statistical analyses were conducted in SAS Version 9.4 (SAS Institute 2013). Data were square-root-transformed before analysis. Statistical analyses were conducted using a linear mixed model (PROC MIXED) with plot (exotic or native) and plant genus (*Acer, Cercis, Hydrangea,* or *Prunus*) as factors and blocks as a random effect. Protected pair-wise comparisons were made of the individual levels of plant genus by using the least significant difference (LSD) test at a 0.05 error rate. The levels of plant genus were classified as a 4 × 2 factorial arrangement with the factors defined as genus (*Acer, Cercis, Hydrangea,* or *Prunus*) and treatment (native or exotic), and data were summed over all census dates.

Results and Discussion

Ninety-four indicators of spider presence, comprising 81 live animals, 10 unoccupied retreats, 1 exuvium, and 2 silk lines, were detected on leaves with sentinel egg masses during a total of 15 weeks of observation during the two seasons of the study (Table 1). The majority of these animals belonged to the

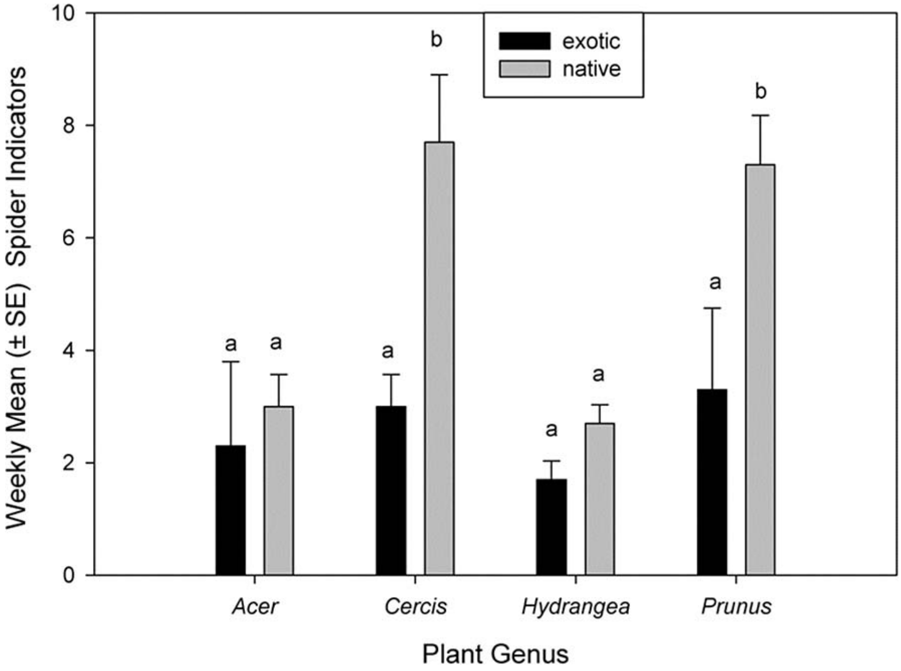

Fig. 4. Mean (± SE) indicators of spider presence on each plant genus in native versus exotic plots. Bars followed by the same letter were not significantly different (least significant difference test: $P > 0.05$).

families Salticidae ($n = 27$) (Fig. 3) and Anyphanidae ($n = 11$), hunting spiders that form purse-like resting retreats on vegetation. There were 5 and 2 individuals, respectively, of the crab spider families Thomisidae and Philodromidae, active hunters not known for spinning retreats. The remaining spider belonged to the web-spinning family Theridiidae. All but one of the collected animals (a philodromid male) were immature, making morphological identification to species impossible. Therefore, we could not, *ipso facto*, use our data to estimate species diversity.

Overall, the incidence of spiders was greater in native than in exotic plots ($F = 10.6$; df = 1, 16; $P = 0.001$) with a mean (± SE) abundance in native plots of 5.167 ± 0.0787 compared with 2.583 ± 0.04994 in exotic plots. There was also an overall significant difference in spider abundance among the plant genera ($F = 4.5$; df = 3, 355; $P = 0.004$) with the incidence of spiders significantly higher on *Cercis* and *Prunus* than *Hydrangea* (LSD test: $P < 0.05$) (Fig. 4). There were more spiders on native plants than on exotic plants for all four genera. However, the factorial analysis indicated that the statistical difference between exotic and native plots was due entirely to *C. canadensis* L. having a statistically higher incidence of spiders than *C. chinensis* ($F = 11.88$; df = 1, 16; $P = 0.003$) and *P. virginiana* L. having a statistically higher incidence of spiders than *P. padus* L. ($F = 8.73$; df = 1, 16; $P = 0.009$) with no significant difference in the number of spiders on either *A. platanoides* L. compared with *A. saccharum* Marshall ($F = 0.24$; df = 1,1 6; $P =$

0.629) or *H. paniculata* Siebold compared with *H. arborescens* L. ($F = 0.55$; df = 1, 16; $P = 0.471$) (Fig. 4). No block effects were seen.

The incidence of spiders in the native plots was twice that in the exotic plots, which supports the abundance portion of the Natural Enemies Hypothesis. That the preponderance of these animals, which were collected on leaves, was hunting spiders is to be expected, because hunting spiders forage on surfaces. Conversely, spinning spiders forage in spaces within and among plants, and tend to be accidentals on surfaces.

Of the 167 egg masses recovered in the 2015 season, 19 had at least 1 chewed egg, but only 1 of those 19 egg masses exhibited any sign of spider presence. This could reflect a preference for other prey, or the inability of juvenile spiders to attack egg masses, both of which have been reported by Morrison et al. (2016). This begs the question of why spiders are attending the egg masses in the first place. One possibility is that they are awaiting the arrival of softer-bodied animals that will be associated with the egg masses, such as parasitoids that may oviposit upon or emerge from the eggs, or other, poorly defended predators.

An alternative explanation is suggested by the fact that the majority of the hunters were found under the arches at the clothespin-leaf interfaces, presumably because they provide shelter, as well as more complex attachment points for retreats and molting. As such, the arches may act as arrestants, delaying the spiders as they traverse the landscape in search of prey. Our recorded abundances may, therefore, differ from ambient absolute abundances, but the measured abundances are quantitatively comparable because the collections were made simultaneously under the same weather conditions in both treatments; the structure of the habitat and microhabitat were virtually identical; and the spiders' taxonomic distributions, at least at the family level, are similar (Fisher's exact test with the three least abundant families grouped, $P = 0.17$).

There is conflicting published evidence for the Natural Enemies Hypothesis. There were no differences in the predation and parasitism rates on sentinel egg masses of the invasive *H. halys* in exotic and native plots or among the four plant genera (Cornelius et al. 2016). Although overall spider abundance was higher in native plots, plant genus had a significant effect. Of the four plant genera tested, there was no statistical difference in spider abundance between exotic and native species pairs for *Acer* or *Hydrangea,* whereas there were more than twice as many spiders on native than exotic plants for the other two plant–species pairs. We do not know why there were more spiders associated with native *Cercis* and *Prunus* than with their exotic congeners. Further studies are necessary in order to elucidate the specific ecological factors that might confer an advantage for native plants over exotic plants in harboring spiders.

The results presented here are of more than theoretical interest. The proportion of Earth's surface occupied by urban landscapes is growing as employment opportunities and the populations dependent on them move from rural areas to cities and suburbs, increasing their importance as providers of ecosystem services (Millennium Ecosystem Assessment 2005). For example, more than 75% of the U.S. population inhabited urban areas in 1994, covering roughly 281,000 km^2 of the coterminous United States, twice the urbanized area just 25 years previously (Nowak et al. 2001). Developing countries are urbanizing even more quickly and are predicted to contain 80% of Earth's human population by 2030 (United Nations

Fund for Population Activities 2007). The increasing role of mechanization and sophisticated technology required to feed the world's growing population will accelerate the loss of jobs in rural areas, driving people to cities and increasing rates of urbanization (Federoff et al. 2010, Godfrey et al. 2010). Hence, the ecosystem services derived by humankind from urban landscapes, along with the costs to maintain them and the pollutants and other detrimental impacts associated with them, will become increasingly important to the health and sustainability of the Biosphere. Further, as the diminution and fragmentation of habitats devoted to other critical activities (e.g., forestry and agriculture) increases, urban areas will also become increasingly important as refugia for organisms essential to the functioning of those systems.

The commercial availability of hundreds of taxa of woody plants offers many choices to homeowners, builders, and urban planners involved in vegetating our urban spaces. Among these choices is whether to plant native or exotic species. Some of the ecosystem services provided by urban plantings, for example provision of biological control services and providing refuges for polyphagous biological control agents active in forest and agroecosystems, could be profoundly affected by these choices. The research reported here suggests that insect biological control by spiders may be one of these services, and that at least for some of the woody taxa used in this experiment, native species may be the better choice.

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