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Insects on urban plants: contrasting the flower head feeding assemblages on native and exotic hosts

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Abstract Exotic plant species very often comprise a large proportion of urban floras. Because herbivorous insects depend on the presence of suitable host plants to maintain their populations, it is imperative to elucidate the relative importance of native and exotic hosts to understand the response of herbivorous guilds to urbanization. By using a plant-herbivore system composed of Asteraceae hosts and flower-head endophagous insects, we investigated whether the diversity and composition of herbivorous insects differs between native and exotic host-plant species in an urban environment. Although we found only seven exotic Asteraceae among the 30 species recorded, the overall abundance of exotics was considerably greater than that of native host plants. Overall, the exotic host species supported a small subset of the herbivore assemblage found on the native ones. The number of herbivore species per host species was significantly higher among the native plants, but we did not find a difference in herbivore abundance. Moreover, the higher taxonomic composition of herbivores on exotic Asteraceae was reduced, being composed of only three genera and two families from a total of 16 genera and six families of herbivores. These results provide support for the idea that plants outside of their original geographic distribution have lower loads of enemies than phylogenetically related native species. Our findings indicate that native host plants in urban areas play a critical role in supporting the native herbivorous insect fauna.

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Introduction

Urbanization is one of the most severe human modifications of the natural landscapes (Grimm et al. 2008), altering markedly both abiotic conditions (e.g., soil properties and microclimate) and resource availability (e.g., space, water and nutrients) for native species. Such alterations mean that species' adaptations to original or neighboring natural habitats do not translate into higher competitive abilities over exotic species. Furthermore, the abundance and composition of species within urban regions is greatly managed and controlled by humans, especially for plants because they are a primary component of urban aesthetics and have been used for gardening and food supply in many urban regions. Consequently, exotic species very often comprise a large proportion of urban floras (Pysek 1998; Santos et al. 2010), decreasing from more toward less urbanized regions (McDonnell and Pickett 1990; McIntyre 2000; McKinney 2010).

Because most herbivorous insects feed on a few closely related plant species (Futuyma and Mitter 1996; Jaenike 1990; Strong et al. 1984), any change in the local set of available host-plant species can strongly affect both insect composition and diversity. Thus, it is of particular interest to ascertain whether exotic plants support similar assemblages of herbivorous insects compared to the native host plants in urban habitats. A better understanding of this point is critical for the formulation of more specific hypotheses regarding plant-insect interactions in urban habitats. Interestingly, there seems to be no general pattern in the response of herbivorous insect assemblages to urbanization gradients, with empirical studies reporting negative, neutral and nil impacts of urbanization on the abundance and diversity of distinct insect taxa and guilds (see McIntyre 2000; McKinney 2010; Raupp et al. 2010 and references therein). Because herbivores depend on the presence of suitable host plants to maintain their populations, it is imperative to elucidate the relative importance of native and exotic hosts to the response of herbivorous guilds to urbanization.

In this study, we used a plant-herbivore system comprised by Asteraceae hosts and flower-head endophagous insects to investigate whether exotic plants are used by herbivorous insects in an urban environment. Asteraceae is the largest plant family in the world and figures among the most common plant families in urban environments (Pysek 1998). A diverse assemblage of endophagous insects feed on flower heads during their larval stage, consuming sap, flowers, ovaries and fruits (Gagné 1994; Headrick and Goeden 1998; Zwölfer and Romstöck-Völkl 1991). Flower-head assemblages are comprised mainly of dipterans (Tephritidae, Agromyzidae and Cecidomyiidae), microlepidopterans (families) and coleopterans (mainly Apionidae in the Neotropics, and Curculionidae in the Holarctic) (Almeida et al. 2006; Fonseca et al. 2005; Gagné 1994; Headrick and Goeden 1998; Prado et al. 2002; Zwölfer and Romstöck-Völkl 1991).

Our aim was to investigate whether the diversity and composition of herbivorous insects differ between native and exotic host-plant species in an urban environment. Specifically, we addressed the following questions: (1) Do native Asteraceae species support a richer assemblage of flower head feeding herbivores than exotic confamilial species? (2) Are higher taxa of herbivores more diverse in native than in exotic host-plant species? and (3) Are the abundance and incidence of host plants equally important for the abundance and richness of herbivores in native and exotic host species?

Material and methods

Study area and sampling procedure

This study was carried out in four green areas (lawns) on the Campus of the State University of Campinas, located in the city of Campinas, State of São Paulo, Brazil (Fig. 1). The local climate is characterized by dry winters and rainy summers, with a mean annual temperature of 21.6°C and annual mean precipitation of 1,378 mm^3. The minimum and maximum distances between any two sites are 300 and 1,150 m. Sites were covered mainly by grasses (*Brachiaria* sp., *Pennisetum* sp. and *Paspalum* sp.), and they used to be mowed practically at the same time (within a three-week time interval) with an average frequency of four times a year.

We sampled each site in three different periods: June and September, 2005, and February, 2006. These months include the peak flowering periods of the most representative tribes of Asteraceae according to previous phenological records in the region (Almeida et al. 2005; Batalha and Mantovani 2000; Batalha and Martins 2004; Fonseca et al. 2005; Marchini et al. 2001). According to literature and personal observation, most exotic Asteraceae flower during 8 months or more, while the flowering ranges of the majority of native Asteraceae are shorter than 4 months. For each individual plant, we randomly collected up to 80 ml of flower heads. We determined the maximum biomass to be removed rather than a minimum because there was great variation in the individual and total biomass of flower heads per individual among plant species, as well as abudance of individuals, with some hosts having only a single recorded individual and a few flower heads, while other had more than 1,000 recorded individuals in the four areas. The abundance of each species within the sites was classified according to the following classes: I) 1; II) 2; III) 3 to 10; IV) 11 to 30; V) 31 to 100; VI) 101 to 300; VII) 301 to 1,000; VIII) > 1,000 individuals. In the laboratory, flower head samples were kept in plastic containers covered with a fine mesh lid, where emergence of adult insects was checked once or twice weekly for 2 months or until emergence rates became insignificant. All insects were reliably identified at least to the genus level, and all host plants identified to species, based on our reference collections and the Unicamp herbarium.

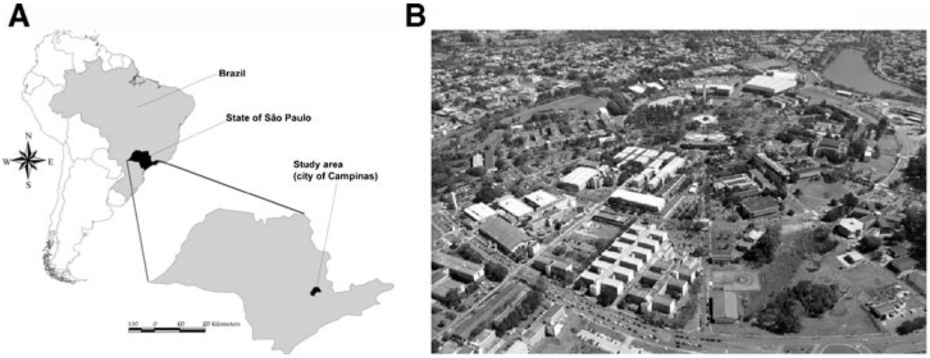

Fig. 1 Geographical location of the city of Campinas (**a**) aerial photography of the main Campus of the State University of Campinas (**b**)

Data analyses

To estimate whether each plant species was available to its assemblage of herbivorous insects, we produced an index of availability (hereafter "availability") for each host species, composed of the multiplication of plant species incidence (the number of areas in which a species was found; ranging from 1 to 4), mean abundance (mean value for the classes of local abundance) and flowering span (number of flowering periods). To evaluate whether native and exotic species differ in their incidences, abundances, flowering ranges and availability, we performed non-parametric randomization tests (NPRT). We found a strong positive linear correlation of weight of sampled flower heads (a measure of sampling effort) with the mean abundance of host plant species ($r_{\mathrm{Pearson}}=0.700$; $P<0.001$) and with host species availability ($r_{\mathrm{Pearson}}=0.930$; $P<0.001$).

The NPRT procedure was also used to test for differences in the following variables between native and exotic host species: (1) abundance of insect individuals per unit weight of flower heads for each host species, (2) number of herbivore species per host plant, and (3) number of herbivore species per unit weight of sampled flower heads per host species. The number of insect individuals per total flower-head weight is a measure of insect density per host plant. In contrast, the number of herbivore species per host plant is relatively small and does not increase linearly with sampling effort. Thus, our correction for sampling artifacts related to differences in sampling effort cannot be interpreted as a suitable measure of herbivore species density per host species (the species density concept sensu Gotelli and Colwell 2001). We used this correction simply to provide a benchmark for the effects of sampling on the contrasts between the number of insects associated to native and exotic Asteraceae. Only plants with at least 1 g of sampled flower heads were used to compare the herbivore assemblages on native and exotic Asteraceae. Finally, we explored the relationships between host plant availability and the abundance and richness of their herbivorous assemblages through Spearman rank correlations. All randomizations were performed with the software Resampling Stats v.3 (Blank 2010).

Results

We found 30 species of Asteraceae (flowering or fruiting) from 29 genera and 11 tribes (Table 1). Among these species, four are native to Asia or Europe (*Crepis japonica*, *Emilia sonchifolia*, *Sonchus oleraceus*, and *Taraxacum officinale*), and three are from North or Central America (*Conyza canadensis*, *Parthenium hysterophorus*, and *Tridax procumbens*). Although exotic species comprised a quarter of the recorded Asteraceae species, both their index of availability and local abundance were significantly higher than those for native Asteraceae (Fig. 2; NPRT: $P=0.014$ and $P=0.024$ for availability and mean local abundance, respectively).

We reared 419 adult insects, comprising 26 species of flower head-feeding endophages belonging to 16 genera and six families (Table 2). All of the insect species were recorded on at least one native host species, but only four of the 26 species were found on the exotic hosts. The number of herbivore species per host species was significantly higher among the native plants (Fig. 3, NPRT: $P=0.023$). This finding did not change when we controlled for differences in sampling effort using the number of insect species per weight of sampled flower head (NPRT: $P=0.034$). Herbivore abundance (adjusted per weight of sampled flower heads) did not differ between native and exotic host-plants (NPRT: $P=0.063$).

Table 1 Native (N) and exotic (E) species of Asteraceae sampled in four green areas on the main campus of the State University of Campinas (Brazil) and the species richness of flower head feeding insects associated with them

Tribe Species	Abbreviation	Status	No. of herbivores
Astereae			
Aster squamatus (Spreng.) Hieron.	Astsqu	N	0
Baccharis dracunculifolia DC.	Bacdra	N	2
Conyza canadensis (L.) Cronquist	Concan	E	0
Cichorieae			
Crepis japonica (L.) Benth	Crejap	E	0
Hypochaeris brasiliensis (Lees.) Benth. and Hook.f.	Hypbra	N	2
Sonchus oleraceus L.	Sonole	E	0
Taraxacum officinale G.H. Weber ex Wiggers	Taroff	E	1
Coreopsideae			
Bidens subalternans DC.	Bidsub	N	2
Eupatorieae			
[a]*Mikania cordifolia* Willd.	Mikcor	N	0
Praxelis clematidea (Griseb) RM King and H Rob.	Pracle	N	4
Gnaphalieae			
Achyrocline satureoides (Lam.) DC.	Achsat	N	0
Gnaphalium spicatum Lam.	Gnaspi	N	2
Helenieae			
Porophyllum ruderale (Jacq) Cass.	Porrud	N	3
Heliantheae			
Ambrosia psilostachya DC.	Ambpsi	N	2
Eclipta prostata L.	Eclpro	N	1
[a]*Galinsoga parviflora* Cav.	Galpar	N	0
Parthenium hysterophorus L.	Parhys	E	0
[a]*Sphagneticola trillobata* (L.C. Rich.) Pruski	Sphtri	N	0
Tridax procumbens L.	Tripro	E	1
Mutisieae			
Chaptalia nutans (L.) Pol.	Chanut	N	3
Plucheeae			
Pluchea sagittalis (Lam.) Cabrera	Plusag	N	2
Pterocauluon sp.	Ptersp	N	0
Senecioneae			
Emilia sonchifolia (L.) DC.	Emison	E	3
Erechtites hieraciifolius (L.) Raf. Ex DC.	Erehie	N	0
Vernonieae			
[a]*Centratherum punctatum* Cass.	Cenpun	N	0
Elephantopus mollis Kunth	Elemoll	N	2
Lepidaploa remotiflora (Rich.) H. Rob	Leprem	N	3
Orthopappus angustifolius (Sw.) Gleason	Ortang	N	4
Vernonanthura ferruginea (Less.) H. Rob.	Verfer	N	3
Vernonanthura phosphorica (Vell.) H. Rob.	Verpho	N	1

[a] These plant species were not included in the analysis as they had less than 1 g of sampled flower heads

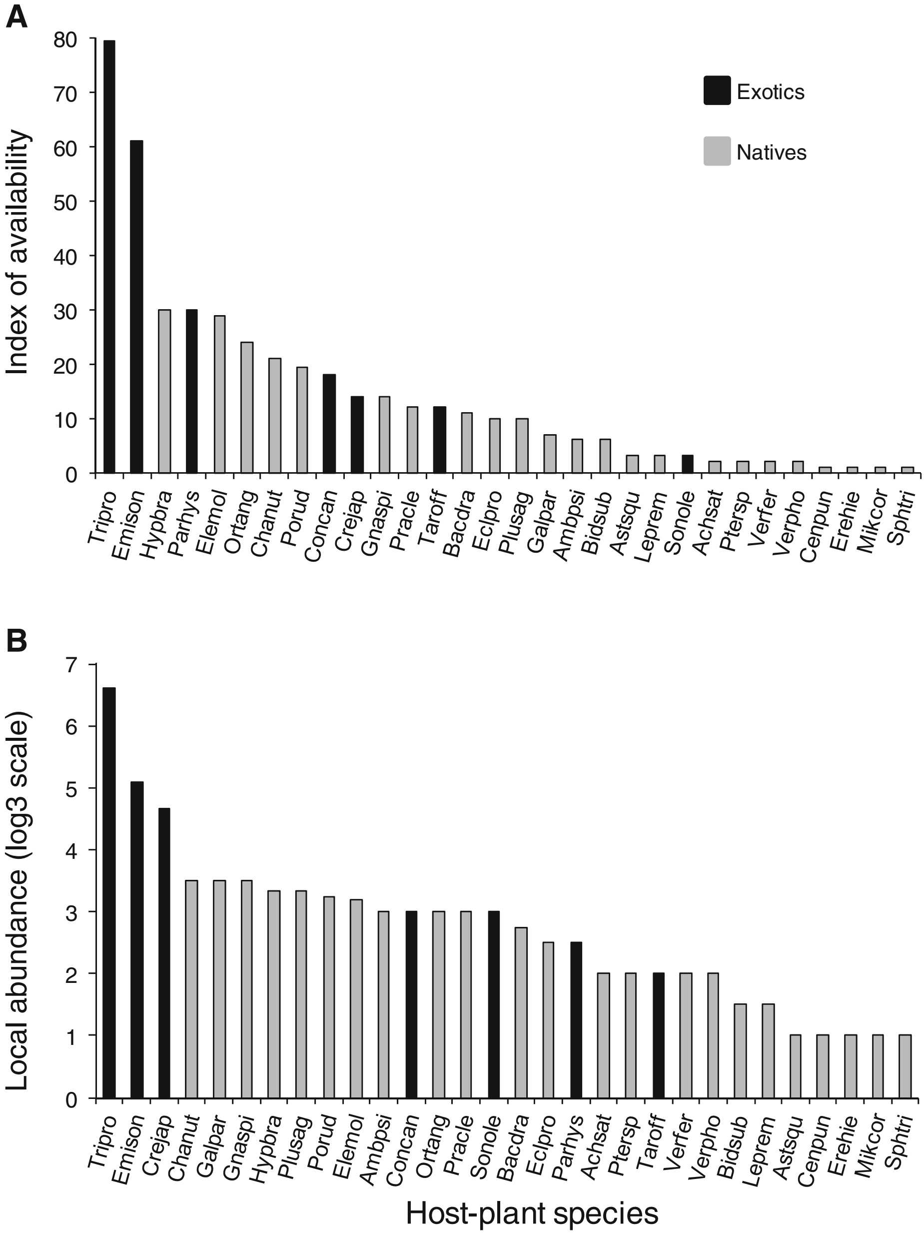

Fig. 2 Rank order of overall plant availability (based on an index of availability) for the 30 Asteraceae species found in four green areas (lawns) of the main Campus of the State University of Campinas. Species' name abbreviations as in Table 1

Overall, the exotic host plants supported a small subset of the herbivore assemblage found on the native plants (Table 2). From the total set of flower head endophages recorded in this study, only three species of agromyzid flies and one species of pyralid moth were recorded consuming flower heads of exotic Asteraceae. Interestingly, these four herbivore

Table 2 Flower head endophagous insects and their respective Asteraceae host plants sampled in four green areas on the main campus of the State University of Campinas (Brazil)

Order Family	Species	Abundance	Native hosts	Exotic hosts
Diptera				
Agromyzidae	*Melanagromyza bidentis* Spencer	4	1	1
	Melanagromyza chaptaliae Spencer	65	2	0
	Melanagromyza neotropica Spencer	9	2	1
	Melanagromyza sp.	12	1	0
	Ophiomya sp.	14	2	2
Cecidomyiidae	*Asphondylia* sp.1	12	3	0
	Asphondylia sp.2	3	2	0
	Asphondylia sp.3	1	1	0
	Asphondylia sp.4	1	1	0
	Asphondylia sp.5	3	1	0
	Asphondylia sp.6	8	1	0
	Clinodiplosis sp.	2	1	0
	Dasineura sp.	9	1	0
Tephritidae	*Dioxyna chilensis* (Macquart)	71	2	0
	Euaresta regularis Norrbom	3	1	0
	Euarestoides sp.	1	1	0
	Neomyopites paulensis Steyskal	34	2	0
	Tetreuaresta sp.	87	2	0
	Tomoplagia gr. *incompleta*	1	1	0
	Tomoplagia heringi	1	1	0
	Trupanea sp.1	10	3	0
	Trupanea sp.2	1	1	0
	Xanthaciura biocellata Thomson	11	2	0
Lepidoptera				
Geometridae	*Synchlora* sp.	1	1	0
Pterophoridae	*Lioptilodes parvus* Walsingham	7	1	0
Pyralidae	*Rotruda* cf. *mucidella*	65	3	2

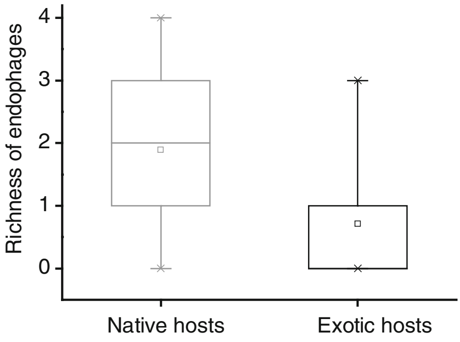

Fig. 3 Median and range of the richness of flower head feeding insects on native and exotic Asteraceae species in an urban environment

species were recorded in the same number or in a higher number of native host plants (always from distinct tribes). The pyralid moth was the only insect species whose abundance was higher on exotic ($n=54$) than on native host plants ($n=10$).

Host plant availability and its related variables (incidence, local abundance and flowering span) showed weak to moderate positive relationships with the richness and abundance of the herbivorous assemblages (Table 3). Comparisons between the correlations for native and for exotic plant species are limited to correlation coefficients because degrees of freedom for the latter is very small. Apart from the number of flowering periods, all other plant related variables showed stronger correlations for the native plants than for the exotic ones (Table 3).

Discussion

We showed that despite being generally more abundant and widespread, exotic Asteraceae species supported a small subset of the assemblage of flower head-feeding insects associated with native confamilial species in an urban environment. Moreover, the higher taxonomic composition of herbivores on exotic Asteraceae was reduced, being comprised of only three genera and two families from a total of 16 genera and six families of herbivores. These results provide support for the idea that plants out of their original geographic distribution have lower loads (abundance and richness) of enemies than phylogenetically related native species (Fenner and Lee 2001; Keane and Crawley 2002), a basic assumption of the "Enemy Release Hypothesis".

Although similar findings have been reported for natural environments (e.g., Fenner and Lee 2001), richer herbivore assemblages on native host plants is not a given. In fact, some studies have found no differences (Frenzel and Brandl 2003; Zuefle et al. 2007) or higher richness of herbivorous insects on exotic plants (Novotny et al. 2006). These contrasting results may be due to the feeding specialization of the studied herbivorous guild and the phylogenetic relatedness between native and exotic plants. If the native assemblage of herbivores is mostly comprised of specialist insects exploiting closely related plant species, then most exotic plants will be consumed by no (or few) native herbivores. However, if the studied herbivorous guild is comprised of generalist insects capable of feeding on most plants from the same family or order, then there is no reason to expect higher herbivore richness on native plants. Actually, exotic plants could support a richer herbivore assemblage if their defenses are less effective against the phytophagous insects when

Table 3 Spearman rank correlations of the abundance and richness of flower head feeding insects with host plant variables related to the spatial and temporal availability of flower heads. Comparisons between the set of correlations for native and exotic plants are restricted to their correlation coefficients

Plant status	Herbivores	Sampled flower heads (g)	Mean local abundance	Incidence	No. of flowering periods	Index of availability
All plants	Abundance	0.631***	0.449*	0.347 ns	0.576***	0.545**
($n=26$)	Richness	0.614***	0.364*	0.246 ns	0.512**	0.447*
Only natives	Abundance	0.763***	0.594**	0.503*	0.693***	0.760***
($n=19$)	Richness	0.769***	0.505*	0.390 ns	0.666***	0.673***
Only exotics	Abundance	0.571 ns	0.477 ns	0.454 ns	0.692 ns	0.570 ns
($n=7$)	Richness	0.478 ns	0.362 ns	0.376 ns	0.700 ns	0.478 ns

ns non-significant; *$P<0.05$; **$P<0.01$; ***$P<0.001$

compared with native plants that have long coevolutionary histories with their herbivores (see Raupp et al. 2010; Gandhi and Herms 2010).

Tallamy (2004) pointed out that the capacity of native insects to discriminate between hosts becomes reduced if exotic plants are found in greater abundance. Consequently, the use of exotic plants by native herbivores would become more frequent. In this study, the availability of exotic flower heads to the endophagous insects was considerably higher than that of native flower heads, but only a small subset of the flower head feeding insects were found on the exotic Asteraceae. Although our results did not provide support for this hypothesis, we found that the majority of generalist herbivores (three agromyzids from a total of five species of this family and a single pyralid species) were capable of using the exotic Asteraceae. Thus, Tallamy's (2004) discrimination hypothesis probably applies for generalist insect fauna and studies focusing on insect guilds that are mostly composed of typically specialist herbivores rarely will support this discriminatory effect. If this is a widespread pattern, then the importance of host-plant abundance as one of the main determinants of local insect richness (Frenzel and Brandl 2003; Marques et al. 2000; Marquis 1991) may not apply for urban environments.

Ectophagous (external feeders) insects are supposed to be less specialized than endophages because they are free of intimate adaptations to internal plant environment (Cornell and Kahn 1989; Gaston et al. 1992; Lewinsohn et al. 2005). Most species of flower head endophages, for instance, are specialists, consuming plant species from the same genus or subtribe (Gagné 1994; Prado and Lewinsohn 2004). This is especially the case for Cecidomyiidae and Tephritidae, the most representative insect families on flower heads of Asteraceae in the Neotropics (Almeida-Neto et al. 2011; Lewinsohn 1991). Microlepidopterans and agromyzid flies seem to be less specialized, being frequently found on different tribes of Asteraceae (Braun et al. 2008; Lewinsohn 1991). Not by coincidence, the only flower head endophages that we found on exotic Asteraceae were three agromyzids and one pyralid moth (Table 2). In a comparison of the flower head fauna associated with 13 species of Asteraceae, Fenner and Lee (2001) found only one herbivorous species on a single host species in New Zealand (exotic distribution) and ten herbivores on the native distribution of these plant species (Britain). On the other hand, Zuefle et al. (2007) did not include internal feeders (gall-makers, stem borers or leaf-miners) and found no difference in the ratio of specialist to generalist insects found in native, non-native and alien plants species.

Time since introduction has been shown to be another important determinant of the number of native herbivore species associated with exotic plants (Andow and Imura 1994; Brändle et al. 2008; Carpenter and Cappuccino 2005; Frenzel and Brandl 2003). We hypothesize that time since introduction is particularly important for more generalist herbivorous insects, because monophages or highly specialist herbivores will rarely use plants that are not closely related to their original hosts. Thus, for most flower head endophagous species, time since introduction would be of minor importance compared to phylogenetic proximity.

Here we found that native plants have, on average, twice as many herbivore species than the exotic ones. If our findings remain qualitatively unchanged in other urban plant herbivore systems, then we surmise that urban ecosystems are characterized by low biomass transfer efficiency from plants to herbivores. This supposition is based on two assumptions: (1) the more diverse the consumers (i.e. more species), the larger the range of consumed resources, and (2) the more specialized a consumer, the more efficiently it converts food into growth or production of offspring. A more diversified, and more specialized, herbivore fauna on native plants has the potential for higher complementarity in appropriating plant biomass, as well as stabilizing the aggregate effect of herbivory on plants (Hooper et al. 2005). Note also the high abundance of generalist flower-head feeders on exotic hosts, contrary to what has been found for leaf-feeders in Canada (Hill and Kotanen 2010). This can increase their population density and bring more pressure on native hosts. Potentially, urban communities may thus experience destabilization of their interaction structure and degradation of biodiversity-related ecosystem processes, akin to the loss of rare non-target native hosts as a consequence of biological weed control (Louda et al. 2003).

In conclusion, as long as studies in diverse geographic regions and with different taxonomic and ecological groups are not carried out, the effects of the urbanization of natural landscapes on the structure of the interactions between plants and insects cannot be generalized. The present study adds important information to the understanding of insect-plant interactions in human-modified landscapes by comparing herbivorous insect assemblages on native and exotic host plants in an urban environment. Specifically, our findings indicate that native host plants in urban areas play a critical role in supporting the native fauna of herbivorous insects.

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