

Host-Plant Specialization Mediates the Influence of Plant Abundance on Host Use by Flower Head-Feeding Insects

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Abstract

Among-population variation in host use is a common phenomenon in herbivorous insects. The simplest and most trivial explanation for such variation in host use is the among-site variation in plant species composition. Another aspect that can influence spatial variation in host use is the relative abundance of each host-plant species compared to all available hosts. Here, we used endophagous insects that develop in flower heads of Asteraceae species as a study system to investigate how plant abundance influences the pattern of host-plant use by herbivorous insects with distinct levels of host-range specialization. Only herbivores recorded on three or more host species were included in this study. In particular, we tested two related hypotheses: 1) plant abundance has a positive effect on the host-plant preference of herbivorous insects, and 2) the relative importance of plant abundance to host-plant preference is greater for herbivorous species that use a wider range of host-plant species. We analyzed 11 herbivore species in 20 remnants of Cerrado in Southeastern Brazil. For 8 out of 11 herbivore species, plant abundance had a positive influence on host use. In contrast to our expectation, both the most specialized and the most generalist herbivores showed a stronger positive effect of plant species abundance in host use. Thus, we found evidence that although the abundance of plant species is a major factor determining the preferential use of host plants, its relative importance is mediated by the host-range specialization of herbivores.

Key words: Compositae, diet breadth, fruit fly, host plant selection, information-processing (or neural-constraints) hypothesis

Understanding the factors that influence the oviposition behavior of herbivorous insects is critical to identify the major drivers of host-plant use (Jaenike 1990). The choice of egg-laying sites is particularly important for insects that feed and develop internally in their host plants (i.e., endophages), because their immature stages face strong movement limitations and cannot usually move to other plant individuals, conspecific or not, or even to better sites within the same host. Both intrinsic and extrinsic factors can influence the oviposition behavior of adult herbivorous insects. Examples of the former include species traits such as body size, feeding mode, and host-plant specialization (Gaston et al. 1992, Novotny and Basset 1999, Liu et al. 2012), whereas extrinsic factors include host-plant abundance, plant phenology, competition with other herbivores, and risk of attack by natural enemies (Southwood 1973, Bernays and Graham 1988, How et al. 1993, Wright and Samways 1999).

For herbivores that lay eggs on a single plant species (i.e., monophages), host-plant selection depends on the ability of adult females to identify their host species among patches of nonhost species, as

well as to select adequate individuals from within the plant population in terms of offspring performance. Nonmonophagous herbivores, furthermore, have to search for and evaluate the quality of oviposition sites among different host species (Janz and Nylin 1997). This additional requirement means that on average, the nonmonophagous adult female must process more information to make decisions as accurate as those made by co-occurring monophagous females (Bernays et al. 2004). If this demand of information processing is extensible to a continuous host specialization spectrum, more generalist herbivores have to process more information per unit time to make decisions on host choice (Bernays 1999, 2001). However, because there is an upper limit to the amount of information that can be processed and stored by insects, their ability to evaluate the relative quality of a given host-plant species is not expected to be as accurate as the ability of a more specialized herbivore using the same host plant. This is a core assumption of the information-processing (or neural-constraints) hypothesis (Levins and MacArthur 1969, Futuyma 1983, Bernays and Wcislo 1994), which

postulates that generalist herbivores are less efficient in making their host-plant choices than specialists. This hypothesis has been supported by both empirical (Bernays and Funk 1999, Janz 2003, Egan and Funk 2006) and theoretical (Tosh et al. 2009) results.

The efficacy of an egg-laying decision is often evaluated by offspring performance, which in turn, depends on host-plant quality for the development of the immature stages (Thompson 1988, Gripenberg et al. 2010). Therefore, in the absence of other factors, females should lay eggs preferentially on higher quality host plants and show a consistent preference ranking for different host plant species. In larger spatial scales, this consistent ranking implies that if plant A is preferred over plant B in a given site, this preference should hold in all (or at least most) sites within a region or landscape. However, as factors influencing oviposition behavior can vary from site to site, offspring performance is not necessarily the sole or the best criterion for egg-laying decisions in terms of the overall fitness of adult females (Waddell and Mousseau 1996, Janz and Nylin 1997, Scheirs et al. 2004). An extrinsic factor that can play an important role in determining host-species preference is a plant's abundance relative to other sympatric potential host species.

The higher the abundance of a given host-plant species, the greater the probability of it being encountered by herbivorous insects through a passive sampling process (Jaenike 1990, Kuussaari et al. 2000, Cunningham et al. 2001, West and Cunningham 2002). Moreover, higher densities can promote preferential use by herbivorous insects by reinforcing previous experiences (Bernays 1999) and facilitating the discrimination of host-plant species (Fox and Lalonde 1993, Bernays 2001). In addition, using more abundant host-plant species instead of rare ones can reduce the overall cost of oviposition in terms of energy and time spent searching for a specific resource (Bernays 1999, 2001). This cost can be particularly high for herbivores with a broad host range, because they must select and evaluate a large number of potential hosts. In this situation, the detection of relevant information can be facilitated by visual or chemical stimuli, both of which are influenced by the abundance of the host plant (Bernays 1999, 2001).

Although both host-plant abundance and identity are expected to influence host selection by adult females, the relative importance of each factor is likely to be mediated by host-plant specificity. If neural constraints impose a higher cost for generalist rather than for specialist herbivores that search for a specific host-plant species, then the relative importance of host-plant abundance in influencing host preference is presumed to be higher for generalist than for specialist herbivores. In the present study, we used Asteraceae plants and the endophagous insects that develop in their flower heads as a study system to investigate the interplay between plant identity and plant abundance in influencing the pattern of host-plant use by herbivorous insects. By using insect herbivores recorded on three or more host species and with distinct host ranges, we also evaluate how feeding specialization modulates the relative importance of plant identity and plant abundance. In particular, we tested two related hypotheses: 1) plant abundance has a positive effect on the host-plant preference of herbivorous insects, and 2) the relative importance of plant abundance to host-plant preference is greater for herbivorous species that use a wider range of host-plant species.

Materials and Methods

Study System

The flower heads of Asteraceae are used as a food source and microhabitat for a diverse insect fauna (Zwölfer 1988, Lewinsohn 1991).

In Brazilian Asteraceae, the most common and diverse groups of flower head endophages belong to five families of Lepidoptera (Tortricidae, Pterophoridae, Pyralidae, Gelechiidae, and Blastobasidae), three families of Diptera (Tephritidae, Agromyzidae, and Cecidomyiidae), and one family of Coleoptera (Apionidae) (Lewinsohn 1991, Almeida et al. 2006, Almeida-Neto et al. 2011). Plants and insects were sampled from April to May 2003 in 20 Cerrado areas located in three neighboring counties in the State of São Paulo in southeastern Brazil. In each area, we counted the abundance of each host-plant species in 15 transects randomly allocated in relation to the edge of each area. Each transect had an area of 30 by 5 m² and was arranged perpendicular to the perimeter of the areas. We collected roughly 80 ml of flower heads per individual plant and whenever available, sampled flower heads from at least 20 individuals of each Asteraceae species.

In the laboratory, the flower head samples were kept in plastic containers covered with a mesh lid. Adult herbivore emergence was checked at least weekly for a period of 2 mo. Additional details on the sampling methods are presented in Almeida-Neto et al. (2011).

Host-Plant Range and Host-Plant Preference

In each area, the preference of each herbivore species for a given host-plant species was estimated by the number of adult individuals of each herbivore species that emerged from that host, divided by the total dry weight of sampled flower heads of the plant species (ind/g) (herbivore abundance). Relative host-plant abundance was calculated as the density of each host species (ind/ha) divided by the total Asteraceae density in each area.

The overall host-plant specialization of each endophagous species was calculated as the total phylogenetic diversity (PD; Faith 1992) of its set of host-plant species in all communities. The phylogenetic diversity of a set of species is defined as the sum of branch lengths in the minimum spanning path of the phylogeny connecting all species in the set (Faith 1992). We produced a phylogeny for the host plants by combining the information from a composite tree of the entire Asteraceae family (Funk et al. 2005, 2009) for most of the genera, with the taxonomy as a surrogate for phylogenetic relationships of nodes for which no information was available. When even the taxonomy was unable to provide relationships, unresolved nodes were left as polytomies. Species were also attached as polytomies deriving from each genus. The greater the phylogenetic diversity of the host-plant set recorded for an insect species, the more generalist the insect. We chose to use the phylogenetic diversity value without null model comparisons (cf. Jorge et al. 2014), since here we are interested in the total phylogenetic history of hosts included in a given herbivore's diet.

We considered only the herbivore species that occurred in at least three study areas with a minimum abundance of three individuals in each area. Also, only herbivores with at least three host species recorded in this study were included. Using these criteria, we retained a total of 11 herbivore species (Table 1).

Statistical Analysis

First, we tested the hypothesis that local host-plant abundance has a positive influence on the selection of host-plants by herbivorous insects due to their increasing preference for the more abundant plant species. For each herbivore species, we adjusted a linear model in which the local herbivore abundance on each host-plant species (ind/g) was related to the relative local density of each host-plant species (ind/ha) and with the species identity of each host plant (i.e., host species). By including host species identity in the model, we

Table 1. List of the 11 herbivore species analyzed in this study, including their taxonomic affiliation, incidence (number of areas with ≥ 3 recorded individuals), their mean density per site (ind/g of dried flower heads), and their host-plant breadth measured as the phylogenetic diversity (PD) of the host plants and as the number of host species consumed by each herbivore

Herbivore species	Taxonomic affiliation (order, family)	Incidence (no. of sites)	Mean abundance (ind/g)	Host-plant PD	No. of host species
<i>Apion</i> sp.	Coleoptera, Apionidae	5	1.395	1.161	3
<i>Melanagromyza bidentis</i>	Diptera, Agromyzidae	8	0.348	2.494	6
<i>Melanagromyza</i> sp.	Diptera, Agromyzidae	4	0.646	3.207	3
<i>Cecidochares connexa</i>	Diptera, Tephritidae	11	0.669	1.161	4
<i>Cecidochares</i> sp.	Diptera, Tephritidae	15	2.881	1.276	5
<i>Neomyopites paulensis</i>	Diptera, Tephritidae	14	0.788	1.563	5
<i>Xanthaciura biocellata</i>	Diptera, Tephritidae	16	0.677	2.218	7
<i>Xanthaciura chrysur</i>	Diptera, Tephritidae	16	1.699	2.241	7
<i>Xanthaciura</i> sp.	Diptera, Tephritidae	17	9.981	1.471	7
<i>Recurvaria</i> sp.	Lepidoptera, Gelechiidae	3	0.394	3.563	3
<i>Adaina bipunctata</i>	Lepidoptera, Pterophoridae	6	0.614	1.759	4

The herbivores were sorted according to their phylogenetic and taxonomic relatedness.

Table 2. Overall and partial r -square values from the linear models relating plant identity and abundance and host-plant use for each herbivore species

Herbivore species	Overall model		Partial r -squares for		
	R^2	P -value	Plant identity	Plant abundance	Shared effect
<i>Apion</i> sp.	0.690	0.004	0.271	0.384	0.035
<i>Melanagromyza bidentis</i>	0.177	0.287	0.115	0.001	0.061
<i>Melanagromyza</i> sp.	0.779	0.011	0.626	0.492	-0.340
<i>Cecidochares connexa</i>	0.477	<0.001	0.063	0.083	0.331
<i>Cecidochares</i> sp.	0.300	0.003	0.169	0.113	0.018
<i>Neomyopites paulensis</i>	0.271	0.008	0.193	0.036	0.042
<i>Xanthaciura biocellata</i>	0.332	0.001	0.267	0.094	-0.030
<i>Xanthaciura chrysur</i>	0.280	<0.001	0.106	0.122	0.052
<i>Xanthaciura</i> sp.	0.369	<0.001	0.226	0.154	-0.011
<i>Recurvaria</i> sp.	0.934	0.002	0.160	0.672	0.102
<i>Adaina bipunctata</i>	0.131	0.743	0.025	0.036	0.070

P -values for the overall models are also presented. The herbivores were sorted according to their phylogenetic and taxonomic relatedness.

controlled for species-specific factors (such as defensive compounds or volatile profile), which can influence the preference of herbivores for the host species. By using local relative abundances, we aimed to monitor the possible effects of differences in total abundances among areas.

To test the second hypothesis that the positive influence of local plant abundance on host-plant preference is stronger for generalist than specialist herbivores, we partitioned the variance resulting from the linear models for each species. This variance partition analysis produced partial regression determinants (partial r^2) exclusively associated with plant abundance and plant identity. Thus, we obtained a partial r^2 for the effect of host-plant abundance (R_{ab}) on the preference of each herbivore species for their host plants. We also obtained a r^2 value for the joint effects of host-plant abundance and identity that cannot be dissected (R_{shared}). The hypothesis that host-plant abundance is more important for generalist herbivores than for specialist herbivores was then tested by two regression analyses, with the host-plant range of each species as the predictor variable and the R_{ab} for that species as the response variable in one model, and the sum of R_{ab} and R_{shared} as the response variable in the other. We then tested for the existence of a quadratic relationship in both models and used the Akaike information criterion (AIC) to evaluate it against the linear regression fit. All

analyses were performed in the R environment (R Core Team 2014), using the *picante* package for specialization measures (Kembel et al. 2010). Graphs of the abundance and identity effects were generated using the *effects* function of the *effects* package (Fox 2003).

Results

For eight out of the eleven herbivore species, significant effects of relative plant abundance and plant identity on the host use were observed (Tables 2 and 3; Figs. 1 and 2). An exclusive positive effect of relative plant abundance on host use was observed for two herbivore species, the tephritid flies *Cecidochares connexa* (Macquart, 1848) and *Xanthaciura chrysur* (Thomson, 1869) (Tables 2 and 3; Fig. 1). Only the tephritid fly *Neomyopites paulensis* (Steyskal) showed an exclusive preference for certain host-plant species for reasons other than relative plant abundance (Tables 2 and 3; Fig. 1). Only two herbivore species, the moth *Adaina bipunctata* (Möschler, 1890) and the agromyzid fly *Melanagromyza bidentis* (Spencer, 1966), showed no consistent response either to plant identity or to abundance across sites (Table 2).

The effect of plant identity on the host preference of herbivore species was mostly characterized by a preferential use of a single host

Table 3. Effects of plant identity and plant abundance on host-plant choice by endophagous herbivores in flower heads of Asteraceae

Herbivore species	Host-plant identity (t)												Host-plant abundance (t)
	ts	ch	cc	cl	co	cp	cg	cs	mc	vm	gp	tv	
<i>Apion</i> sp.			3.031				-1.148		-1.630				3.695
<i>Melanagromyza bidentis</i>			0.199		0.762	0.528	0.094	0.820		0.236			0.857
<i>Melanagromyza</i> sp.									2.796		-4.209	1.915	3.949
<i>Cecidochares connexa</i>					-0.842	0.394	1.860	-1.691					2.387
<i>Cecidochares</i> sp.			-0.227	2.736		-3.083	-0.554	-0.897					2.843
<i>Neomyopites paulensis</i>			-1.539		-0.296	3.056	-1.426	0.417					1.547
<i>Xanthaciura biocellata</i>	1.321	3.480	-1.816		-0.114	-1.444	-2.051	-1.662					2.863
<i>Xanthaciura chrysura</i>		-1.861	0.975		1.305	1.667	-1.516	0.535	-0.969				3.686
<i>Xanthaciura</i> sp.		-2.401	0.647	-0.785	2.763	1.092	-2.466	2.377					4.199
<i>Recurvaria</i> sp.			3.131				-2.990			0.869			7.145
<i>Adaina bipunctata</i>		0.608			0.738	0.941	0.922						0.477

(t): estimated t-values for the effects of plant identity and plant abundance on each herbivore species. Significant values are highlighted in bold. The herbivores were sorted according to their phylogenetic and taxonomic relatedness.

ts, *Trichogonia salviaefolia* Gardner; ch, *Campuloclinium chlorolepis* (Baker) R.M.King & H.Rob.; cc, *Chromolaena chaseae* (B.L.Rob.) R.M.King & H.Rob.; cl, *Chromolaena laevigata* (Lam.) R.M.King & H.Rob.; co, *Chromolaena odorata* (L.) R.M.King & H.Rob.; cp, *Chromolaena pedunculosa* (Hook. & Arn.) R.M.King & H.Rob.; cg, *Chromolaena pungens* (Gardner) R.M.King & H.Rob.; cs, *Chromolaena squalida* (DC.) R.M.King & H.Rob.; mc, *Mikania cordifolia* (L.f.) Willd.; vm, *Vernonanthura membranacea* (Gardner) H.Rob.; gp, *Gochnatia pulchra* Cabrera; tv, *Trixis verbasciformis* Less.

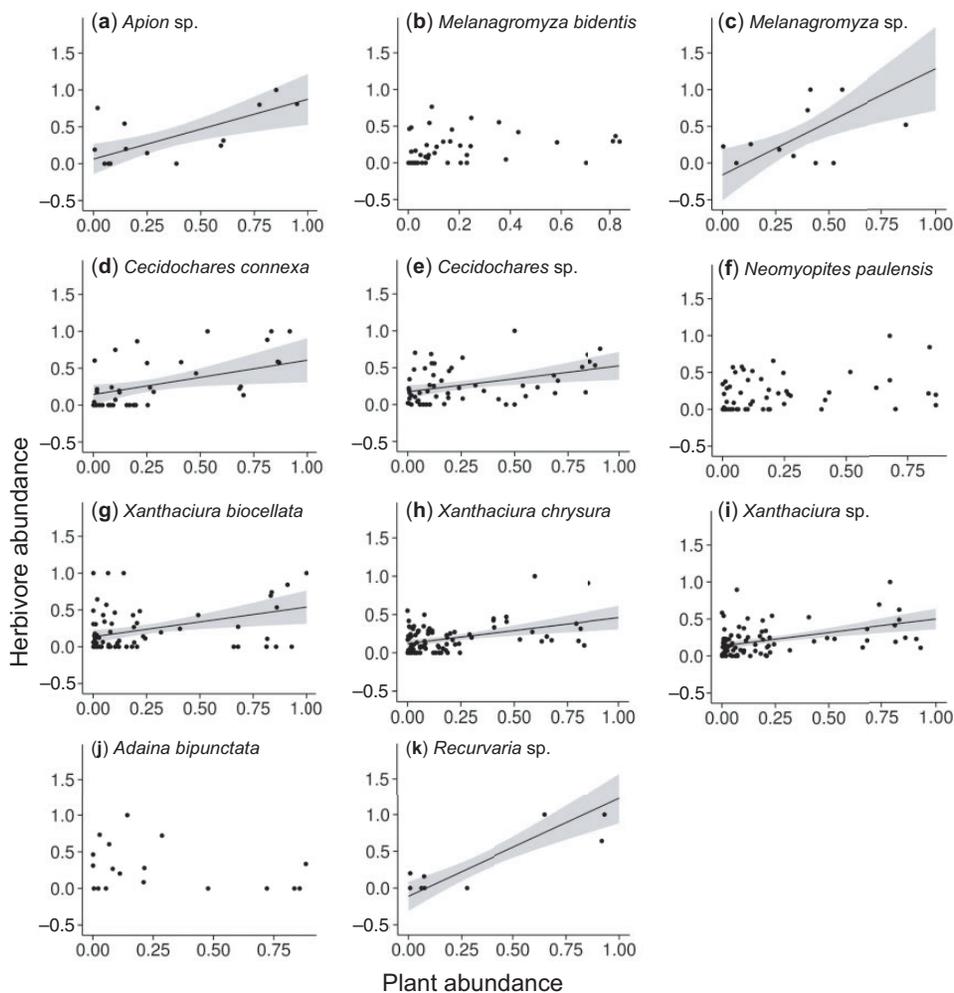


Fig. 1. (a–k) Relation between relative herbivore abundance (ind/g) and host-plant abundance expressed as the relative density of each host-plant species (ind/ha rescaled by the maximum). Points are observed values, lines are model predictions (when significant), and grey bands their 95% confidence intervals. The herbivores were sorted according to their phylogenetic and taxonomic relatedness.

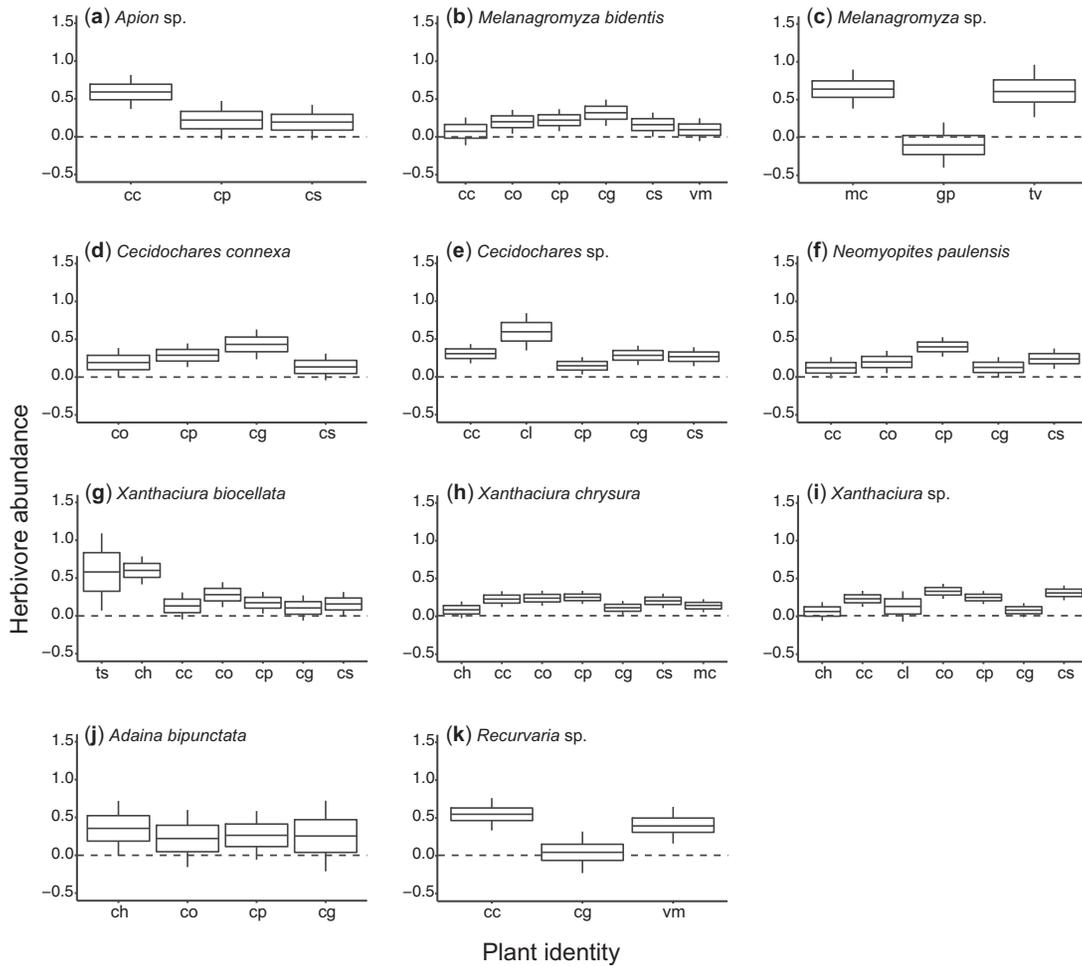


Fig. 2. (a–k) Herbivore preference for each host plant species, expressed as model estimates for mean local herbivore relative abundances (proportion of individuals) on each host, after removing the effects of plant abundance by setting all abundances to the mean value. Central lines in boxes are mean estimated effects and bars are 95% confidence intervals. Higher values indicate that, all abundances being equal, the mean proportion of individuals in that host plants is higher. ts, *Trichogonia salviaefolia*; ch, *Campuloclinium chlorolepis*; cc, *Chromolaena chaseae*; cl, *Chromolaena laevigata*; co, *Chromolaena odorata*; cp, *Chromolaena pedunculosa*; cg, *Chromolaena pungens*; cs, *Chromolaena squalida*; mc, *Mikania cordifolia*; vm, *Vernonanthura membranacea*; gp, *Gochnatia pulchra*; tv, *Trixis verbasciformis*. The herbivores were sorted according to their phylogenetic and taxonomic relatedness.

species (Table 3; Fig. 2). The only exception was *Xanthaciura* sp. (Tephritidae), which showed a preference for two congeneric plant species. In addition, six out of the seven herbivores that responded significantly to plant identity showed a negative response to one or two host-plant species (Table 3; Fig. 2), meaning that they use those plants with a lower frequency than expected by host abundance.

Contrary to our expectations, we found a U-shaped rather than a positive linear relationship between the host-plant range of the herbivore species and the contribution of relative plant abundance to the herbivores' preference for their host plants (Table 4; Fig. 3). This result was observed with the partial r^2 of host-plant abundance singly (Fig. 3a) or together with the joint effect of plant abundance and plant identity (Fig. 3b). Therefore, both the more specialist and the more generalist herbivores showed a stronger positive response to plant abundance in their egg-laying decisions than those herbivore species with intermediate levels of specialization.

Discussion

This study shows that both host-plant identity and host-plant abundance can play a significant role in determining the host choice of

Table 4. Comparison between the quadratic, linear, and null fits (AIC and Δ AIC) for regressions between host-plant range of each species and the r -square components: partial r -square exclusive to host-plant abundance (R_{ab}) and the sum of the partial r -square exclusive to host-plant abundance (R_{shared}), and partial r -square shared between abundance and identity effects ($R_{ab} + R_{shared}$)

Variables	Models	AIC	Δ AIC
R_{ab}	Quadratic	-15.557	0.000
	Linear	-2.453	13.104
	Null	0.690	16.247
$R_{ab} + R_{shared}$	Quadratic	-10.143	0.000
	Null	0.911	11.055
	Linear	1.939	12.082

endophagous herbivore species. The effect of plant identity can be regarded most simply as a consistent preference (or avoidance) for one or more host species among the studied sites, regardless of variations in their relative abundance. This effect actually integrates a set of characteristics of the host plants (e.g., plant chemistry, phenology, and morphology) that are detected by the herbivore and govern

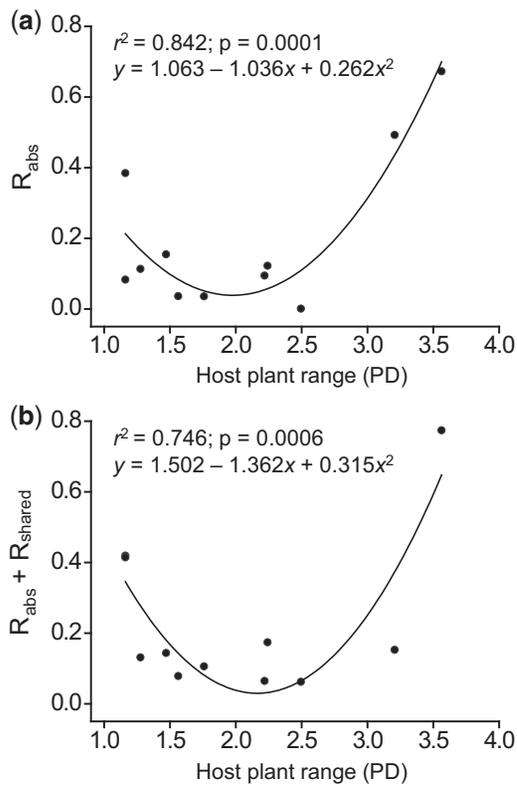


Fig. 3. Relationship between the importance of plant abundance, as measured by the variance partition, in host plant choice for each herbivore and their host range. An insect's host range was calculated as the total phylogenetic diversity of its set of host-plant species. (a) Partial r -square exclusive to host-plant abundance (R_{abs}). (b) The sum of the partial r -square exclusive to host-plant abundance (R_{abs}) and partial r -square shared between abundance and identity effects (R_{shared}). The lines represent the best model according to AIC values.

the selection of the host plant, producing a preference hierarchy or ranking. On the other hand, the effect of host-plant abundance was also relatively site-specific, depending not only on the abundance of each host-plant species, but also on its relative abundance compared to all available hosts. Given the separate effects of plant identity and plant abundance, they can reinforce each other when a herbivore's preference hierarchy and the local abundance ranks are the same. Alternatively, if both hierarchies differ, the prevailing effect is expected to depend on the magnitude of variation in host-plant-abundance and host-plant quality, which in turn, are also expected to depend on the host-plant breadth of the herbivore species.

The relationship between host-plant abundance and herbivore preference was positive, supporting the hypothesis that more abundant host-plants are more likely to be used than less abundant co-occurring host-plant species. The positive effect of host-plant abundance on herbivore preference has been shown in many herbivore species from different guilds and taxonomic groups (e.g., Bernays 1988, Bernays and Graham 1988, Kuussaari et al. 2000). Likely explanations for this positive effect identified in our study should focus on adult female behavior rather than on the immature stages, because the endophagous larvae that feed in the flower heads develop from the egg to the adult stage within a single flower head. From the viewpoint of egg-laying female insects, differences in host-plant abundance can be perceived as differences in visual and olfactory stimuli (Bernays 2001, Cunningham 2012). In some situations,

a species that is better ranked among the herbivore's preferences may be supplanted by a lower ranked but locally more abundant host species (Singer et al. 1989). This effect might explain why in this study *Chromolaena squalida*, a lower ranked host of the tephritid fly *Xanthaciura* sp., was more preferred by *Xanthaciura* sp. than the preferred host *Chromolaena odorata*, as the former host was six times more abundant than the preferred host in one of the sampling areas. Cunningham et al. (2001) proposed an additional benefit based on the notion that the suitability of the host for larval development varies with the abundance of host species. They suggested that the induction of food preferences could lead to the increased survival of descendants placed on conspecific host plants. In time, the most abundant host plants would become more suitable for larval development.

Although most herbivore species in this study shared three or more host plant species with at least one of the other herbivores, only two species (*Apion* sp. and *Recurvaria* sp.) showed a significant preference for the same host species (Table 3). This finding suggests that host-plant abundance does not affect all herbivores in the same way, and also that the herbivore species respond to different stimuli and constraints when making their egg-laying decisions. In addition, the preference hierarchy can differ even among those herbivores that share most of their host plants (Singer et al. 1989, Bernays 2001). Such differences would be favored, for instance, if the indirect effects of competition on adult fitness are greater than the benefits of oviposition in more nutritious host-plant species.

This study shows that host-plant breadth mediates the importance of plant abundance on the use of distinct plant species. However, the results show more complex effects than a linear increase in the effect of host abundance on the host-plant choice of more generalist herbivores. Herbivores with intermediate levels of host-plant specialization were weakly influenced by host-plant abundance, whereas the most specialist and most generalist herbivores showed moderate to strong changes in host selection due to host-plant abundance. One possible explanation for the significant effect of host abundance on host choice by the more specialized herbivores is that the use of alternative host plants entails little additional cost, because phylogenetically closer plants tend to be similar in morphology, nutritional quality, and chemical defenses (Barrett and Heil 2012). These results generally agree with the greater match between preference and performance observed for species with an intermediate degree of diet specialization in a recent meta-analysis (Gripengberg et al. 2010). Thus, we present further evidence that herbivore diet breadth modifies the relationship between host-plant use and plant abundance or, conversely, that local plant abundance modulates the expression of relative preference for different hosts within the genetically fixed spectrum of potential host-plant species.

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