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EFEITO DO ISOLAMENTO FILOGENÉTICO SOBRE A RIQUEZA E COMPOSIÇÃO DE INSETOS HERBÍVOROS EM PLANTAS EXÓTICAS

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Sumário

Resumo

A substituição de plantas nativas por plantas exóticas invasoras ou introduzidas pode ter impactos significativos sobre a fauna de insetos herbívoros.Este impacto pode ocorrer tanto diretamente, por meio de mudanças no sucesso reprodutivo e no tamanho populacional de insetos herbívoros que consomem as plantas exóticas, quanto indiretamente, através da alteraçãona disponibilidade de plantas hospedeiras nativas. O presente trabalho está dividido em duas partes. No primeiro capítulo, avaliei o efeito do isolamento filogenético sobre a riquezae composição de espécies de insetos herbívoros em plantas exóticas. Além disso, examinei possíveis diferenças na resposta ao isolamento filogenético de plantas exóticas entre assembleias de herbívoros compostas exclusivamente por insetos endófagos einsetos exófagos. No segundo capítulo, avaliei o efeito do isolamento filogenético das plantas hospedeiras sobre a especialização média das faunas de insetos herbívoros associadas às plantas hospedeiras. Além disso, também analisei se o efeito do isolamento filogenético das plantas hospedeiras difere entre as plantas nativas e exóticas. Tomados em conjunto, os resultados dos dois capítulos exemplificam como a riqueza, a composição e a especialização dos insetos herbívoros respondem ao isolamento filogenético de suas plantas hospedeiras.

Abstract

The replacement of native plants by introduced or invasive exotic plants may have significant impacts on the fauna of herbivorous insects. These impacts can occur both directly, through changes in reproductive success and population size herbivorous insects that consume the exotic plants, and indirectly through changes in the availability of native host plants. This study is divided into two parts. In the first chapter, I evaluated the effect of phylogenetic isolation on the richness and composition of species of herbivorous insects on exotic plants. In addition, I also examined possible differences in response to phylogenetic isolation of exotic plants between herbivore assemblages made up exclusively of endophagous and exophagous insects.In the second chapter, I evaluated the effect of phylogenetic isolation of host plants on the mean specialization of herbivorous insects fauna associated with host plants. In addition,I also analyzed the effect of phylogenetic isolation of host plants differs between native and exotic plants. Taken together, the results of the two chapters exemplify how the richness, composition and specialization of herbivores respond to phylogenetic isolation of their host plants.

INTRODUÇÃO GERAL

A ocorrência de espécies exóticas em habitats naturais é considerada uma das principais ameaças para a biodiversidade (Cohen e Carlton. 1998; Mack et al. 2000). As plantas exóticas podem exercer efeitos sobre espécies nativas tanto por meio de ação direta (e.g., competição por espaço, luz ealelopatia) quanto indireta (e.g., efeitos sobre os herbívoros via redução de plantas nativas) (Lau e Strauss 2005). Assim, plantas exóticas podem substituir espécies de plantas nativas, modificando a diversidade e a estrutura das comunidades vegetais e, por consequência, alterando a comunidade de insetos herbívoros associados às plantas hospedeiras (Tang et al. 2012). A substituição de espécies nativas por plantas hospedeiras exóticas pode ter efeitos importantes sobre a ecologia e evolução das interações inseto-planta (Cox 2004).

Diferenças na riqueza de insetos herbívoros entre plantas hospedeiras exóticas podem ser influenciadas por características químicas, morfológicas ou fenológicas dessas plantas em relação às plantas nativas (Harvey e Fortuna 2012). Além disso, fatores como o tempo de introdução, tamanho da área de ocorrência e complexidade estrutural da planta, também podem determinar a riqueza de insetos herbívoros associados às plantas exóticas (Brändle et al. 2008; Spafford et al. 2013). Alguns estudos têm demonstrado que plantas exóticas filogeneticamente mais distantes da flora nativa podem abrigar uma menor riqueza de insetos herbívoros (Connor et al. 1908; Spafford et al. 2013). Isso ocorre possivelmente porque o isolamento filogenético é uma medida indireta da dissimilaridadequímicas e morfológica de uma planta em relação às demais (da Roset al. 1993). Algumas evidências sugerem que restrições filogenéticas no uso de plantas hospedeiras exóticas fazem com que a dissimilaridade na composição de insetos herbívoros seja maior sobre plantas exóticas que são mais isoladas filogeneticamente das plantas nativas (Gossner et al. 2009). Por outro lado, plantas nte tendem a ser consumidas por herbívoros menos especializados (Vianatteet al. 2010). Tais insetos apresentam adaptações morfológicas, fisiológicas e comportamentaiscapazes de burlar as defesas das plantas exóticas (Bezemeret al. 2014). Para um inseto especialista usar uma planta hospedeira isolada filogeneticamente, o inseto deve reconhecer a planta como alimento e ser capaz de sobreviver nela. Portanto, espera-se que herbívoros especialistas que se adaptaram às defesas físicas e químicas das plantas hospedeiras isoladas filogeneticamente sejam menos propensos a colonizar outras espécies de plantas, sendo portantoespecialistas desses hospedeiros isoladas.

Variações na riqueza e a composição de insetos herbívoros sobre plantas exóticas também são relacionadas ao habito alimentar dos insetos (Jobinet al. 1996). Insetos endófagos (i.e., aqueles que se alimentam no interior das estruturas das plantas) são mais especializados sobre suas hospedeiras que insetos exófagos (i.e., aqueles que se alimentam de estruturas externas das plantas) (Gaston et al. 1992; Forister et al. 2014). De fato, alguns estudos têm revelado que insetos endófagos são raramente encontrados nas plantas exóticas em áreas em que tais plantas foram introduzidas (Memmott et al. 2000; Cripps et al. 2006). Já os insetos exófagos, por apresentarem uma dieta comparativamente mais generalista,geralmente estariam mais pré-adaptados à inclusão de plantas exóticasem sua dieta (Tallamy 2004).

Na presente dissertação, avaliei as interações entre insetos herbívoros e suas plantas hospedeiras, com um enfoque sobre plantas exóticas. O sistema composto por insetos herbívoros e suas plantas hospedeiras nativas e exóticas é um bom modelo para estudos ecológicos e evolutivos. Meu objetivo foi investigar como a riqueza e composição dos insetos herbívoros responde aos efeitos do isolamento filogenético das plantas hospedeiras exóticas, e como a especialização dos insetos herbívoros também filogenético das plantas hospedeiras (exóticas e nativas) nas assembleias locais. No primeiro capítulo avaliei o efeito do isolamento filogenético sobre a riqueza e composição de insetos herbívoros em plantas exóticas. Além disso, analisamos se o efeito do isolamento filogenético das plantas exóticas sobre a riqueza e a dissimilaridade na composição de insetos herbívoros apresenta diferença entre as assembleias compostas exclusivamente de insetos herbívoros endófagos ou exófagos. No segundo capítulo, avaliei o efeito do isolamento filogenético das plantas hospedeiras sobre a especialização dos insetos herbívoros. Nesse capítulo, também examineipossíveis diferenças no efeito do isolamento filogenético de plantas hospedeiras nativas e exóticas.

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CAPÍTULO I

O isolamento filogenético de plantas afeta a dissimilaridade –mas não a riqueza– de insetos herbívoros em hospedeiras exóticas

host plants affects the dissimilarity but not the
s of herbivore species

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Herbivorous insects are highly dependent of their host plants and the introduction of exotic plants can affect the native herbivorous insect fauna because they do not have a shared evolutionary history with them. We test the effect phylogenetic isolation on species richness and species composition similarity of herbivorous insects on exotic host plants species. In addition, we tested for differences in the effect of the phylogenetic isolation of exotic host plants on the species richness and species composition dissimilarity between assemblages composed exclusively of exophagous or endophagous herbivore insects. The richness of insect herbivores was not affected by the phylogenetic isolation of the exotic plant species. This lack of effect of phylogenetic isolation was not significantly affected when comparing between exophagous and endophagous assemblages with their host plants. However, the mean phylogenetic isolation was a good predictor of the dissimilarity in the composition of insect herbivores on exotic plants phylogenetically isolated from native plants. Contrary to our expectation, the effect of phylogenetic isolation on dissimilarity in the composition of insect herbivores was higher to exophages than endophagous insect assemblages. However, when the Jaccard index was used, we did not find differences between exophage and endophage assemblages. Our findings show that phylogenetic isolation and degree of intimacy of insect herbivores can be important factors to understand the relationship between herbivores and exotic plant species.

Key words: species richness, β diversity, exotic plants, phytophagous insect

Exotic plant species have become an increasingly significant part of local and regional floras due to deliberate introduction, their invasion capacity, or both factors. The displacement of native plants by exotic plants has occurred mainly in human-dominated landscapes, where levels of habitat disturbance and modification generally tend to be high (DôAntonio and Vitousek 1992; Vitousek et al 1997; Taylor and Irwin 2004). The increasing abundance and richness of exotic plant species can promote the local extinction of native plants thus acting either additively or synergically with disturbance in the modification of the original diversity and structure of plant assemblages (Vitousek et al 1996; Pimentel et al. 2000; Vilà et al. 2011). In addition to their effects on co-occurring native plant species, exotic plants have also been shown to have a strong influence on the insect herbivore assemblages that depend on their host plants for food and shelter (Tallamy 2004; Lau and Strauss 2005).

Exotic plant species have been shown to be consumed by fewer herbivore species than native sympatric plants (Jobin et al. 1996;Prochek et al. 2008;Perre et al. 2011; Helden et al. 2012; but see Liu and Stiling 2006). Among the very exotic plant species there is usually large variation in the number of associated herbivorous insects, implying that specific species-to-species comparisons between native and exotic plant species do not necessarily reflect the magnitude of difference in herbivore species richness between native and exotic plant assemblages. However, although a certain set of attributes of exotic plant species consistently explain the species richness of the herbivorous insects associated with them across different habitats, most studies have focused mainly on evaluating the differences in species richness and herbivory damage between native and exotic plants (Novotny et al. 2003; Dietz et al. 2004; Carpenter and

). Little is known about what factors determine the richness and faunal composition of herbivores on exotic plant species.

The morphological, chemical, and phenological features that distinguish exotic plants from native plant species are the major factors explaining why they tend to be used, on average, by a smaller fraction of herbivorous insects than native plants (Harvey and Fortuna 2012; Bezemer et al. 2014). Additional explanations for lower herbivore richness on exotic plants compared to native plants are time since introduction (Brändleet al.2008), range size, and plant architectural complexity (Spafford et al. 2013). Because differences in plant traits tend to be more pronounced among phylogenetically distant species, it has also been hypothesized and observed that the more phylogenetically isolated an exotic plant is, the lower the species richness of the herbivores on it will be (Connor et al. 1980;Spafford et al. 2013). Consequently, insect herbivores are generally expected to preferentially accept exotic plants that are phylogenetically close to native plants (Pearse and Hipp 2014). In a seminal study, Connor et al. (1980) showed that for Strongôs (1974a,b) species-area curves for herbivorous insects on exotic trees, the regression residuals increased when the exotic trees were more highly related to native trees. Because more phylogenetically isolated exotic plants are expected to be used by a very small fraction of herbivore insects, phylogenetic isolation might also lead to higher dissimilarity in herbivore species composition on exotic plant species that are more phylogenetically isolated from the native plants (Gossner et al. 2009).

Variation in the richness and composition of insect herbivores on exotic plant species may also depend largely on the guilds of herbivores under investigation (Brändle et al.2008; Jobin et al. 1996). Insects that feed internally on vegetal tissues (i.e., endophagous herbivores) tend to be more specialized on their host plant species (i.e., exophages) (Gaston et al. 1992; Forister et al. 2014). Many studies have shown that endophagous insects are rarely found on exotic host plants in their introduced range (Memmott et al. 2000; Cripps et al. 2006; Hansen et al. 2006). In some cases, endophagous insects may be even completely absent in recently colonized areas (Memmott et al. 2000).

In the present study, we evaluate the extent to which there is a negative effect of phylogenetic isolation on the species richness and species composition dissimilarity of herbivorous insects on exotic host plants species. In addition, we tested for differences in the effect of the phylogenetic isolation of exotic host plants on the species richness and species composition dissimilarity between assemblages composed exclusively of exophagous or endophagous herbivore insects. Our hypotheses are the following: (1) greater phylogenetic isolation in relation to the native plant species leads to a reduction in species richness and to higher species composition dissimilarity in the herbivorous insects on exotic plant species; and (2) the effects of phylogenetic isolation on both the species richness and species dissimilarity of herbivores are more pronounced in plant-herbivore assemblages made up exclusively of endophagous rather than exophagous insects.

METHODS

Data compilation

We carried out a comprehensive search for plant-herbivore assemblages in the SciVerse Scopus, Portal Capes, and Google Scholar databases between 2011 and 2013 using the following combinations of keywords: (plant*) AND (herbivor*) AND (network* OR interaction* OR web*) AND (survey* OR list*). Only plant-herbivore assemblages that met the following criteria were included in this study: 1) the presence es, allowing for the comparison of the composition of herbivorous insects of each exotic plant in relation to the pool of native plants; 2) the occurrence of at least three exotic plant species; and 3) the occurrence of exotic plant species with different levels of richness of herbivore species (at least three categories of herbivorous richness), allowing for at least a minimum degree of variation in the herbivorous richness for each plant-herbivore assemblages in our analysis. From a total of 6,550 articles, only 14 plant-herbivore assemblages met our criteria (Supplementary 1).

Plant status and herbivore feeding mode

To categorize the plant species as native or exotic, we used plant databases available for each country where the plant-herbivore assemblages were sampled (Supplementary Material 2). Plant species was determined only at genus level (i.e., species identified in ñsp.ò), and they were categorized as exotic or native to each country according their genus status. Unidentified plant species, which could not be placed into any category, were excluded from the analyses. The excluded plants represent 11% of the 504 plant species (native, exotic, and unknown) recorded in the 14 plant-insect assemblages. We assumed that all assemblages were composed predominantly of native insects because native plant species were more prevalent than exotic plants in the selected plant-herbivore assemblages. In addition, the regional pools of native herbivorous insects were certainly much greater than the regional pools of exotic herbivorous insects.

Each local plant-herbivore assemblage was made up only of endophagous or exophagous insect species. We categorized as endophages those herbivores that feed concealed within plant tissues (e.g., gall makers, leaf miners). Free-living insects able to

., leaf chewers, phloem suckers) were classified as exophages. .

Phylogenetic data

We constructed a phylogenetic hypothesis for all 451 recorded plant species (exotic and native) using Phylomatic (Webb and Donoghue 2005) based on a maximally resolved supertree of plants following the classification proposed in APG III (2009). The resulting phylogeny was calibrated, and its branch lengths were estimated using the*bladj* algorithm of Phylocom 4.2 (Webb et al. 2011). Node ages to calibrate the phylogeny were taken from Wikström et al. (2001). This calibrated phylogeny was used to calculate the phylogenetic distance (in millions of years) among species using the *cophenetic* function in the R package *ape* (Paradis et al. 2004). We then calculated the mean phylogenetic isolation of each exotic plant species from its co-occurring native plant species.

Data analyses

The herbivore species richness associated with each host plant species was obtained by counting the number of insect species associated with each exotic plant species. The mean dissimilarity in the species composition of the herbivore fauna for each exotic host plant in relation to the pool of native host plants was calculated using the Jaccard and Simpson indexes. The Jaccard dissimilarity index is calculated as 1-a/(a+b+c), where ñaò is the number of species found in both samples (i.e., both host species), ñbò is the number of species exclusively found in exotic host plants, and ñcò is the number of species exclusively found in native host plants. The Jaccard dissimilarity index accounts for differences in both species richness and species replacement n dissimilarity index (βsim) was calculated as min(b,c)/(min(b,c)+a), where ñaò is the number of species present in both samples, and ñbò and ñcò are the numbers of species occurring in only one sample or the other. The Simpson index is not affected by differences in species richness; thus, it accounts only for species replacement (Koleff et al. 2003). For these calculations, we used R Packages *vegan* for the Jaccardôs index (Oksanen et al. 2013) and *betapart*forthe Simpson index (Baselga et al. 2013).

We used generalized linear mixed models (GLMM) to test the effects of mean phylogenetic isolation and the level of intimacy of the herbivores with their hosts (i.e., wether they were endophages or exophages) on species richness and the mean dissimilarity of insect herbivores on exotic plant species. Mean phylogenetic isolation, intimacy level were considered the fixed effects, and the identity of each local assemblage was entered into the model as a random effect. In the model to analyze the herbivorous species richness associated with each exotic plant, we also included the local species richness of the herbivores recorded in each assemblage as a covariate. We used a Poisson error structure (count data) in the models for herbivore species richness, and we used a binomial error structure (proportion data) for species composition dissimilarity of the herbivore associated with each exotic plant species. These models were built using the *glmer* function in the *lme4* package (Bates et al. 2014) in R (R Core Team 2014).

RESULTS

We used 14 plant-insect assemblages of which seven were composed exclusively of exophages and seven were composed exclusively of endophages. In n orders of insects were Hemiptera (56 species), Lepidoptera (28 species), and Diptera (12 species.).

The herbivorous insect richness recorded on each exotic host plant species was not significantly affected by the mean phylogenetic isolation of exotic plant species from the recorded set of native host plant species ($z = -1.74$, $p = 0.08$; Table 1). This lack of effect was not related to degree of intimacy of herbivores with their host plants ($z = -0.58$, $p = 0.56$; Table 1).

The dissimilarity of herbivore species composition significantly increased as the phylogenetic isolation of exotic species in relation to the native plant species increased. This positive effect was found using both Jaccard ($z = 2.05$, $p = 0.04$, Table 1, Fig. 1a) and Simpson ($z = 3.70$, $p < 0.001$; Table 1, Fig. 1b) dissimilarity indexes. On the other hand, we did not find differences between exophage and endophage assemblages when using the Jaccard index ($z = 1.94$, $p = 0.05$, Table 1), but when using the Simpson index we found higher values of mean dissimilarity in assemblages of exophagous insects ($z = 2.17$, $p = 0.03$; Table 1, Fig. 1b).

DISCUSSION

Contrary to our expectation, more phylogenetically isolated exotic plant species did not show a lower richness of herbivorous insects. This result contrasts with those of previous studies, which found that exotic plants phylogenetically isolated from native plants harbor a lower number of insect herbivore species (e.g. Spafford et al. 2013). Also contrary to our expectation, these results mean that there is evidence of a monotonic decrease in herbivore species richness as the mean phylogenetic isolation of the exotic host plants increases. If there is a threshold for phylogenetic distance that limits the consumption of exotic host plants by most herbivores, mainly by more ble that phylogenetic isolation has a very limited effect on the variation in the number of herbivore insects associated with exotic plant species. Similarly, we also did not found no effect of exotic phylogenetic isolation on herbivore species richness when compared assemblages of endophages and exophages. Note that because we included only exotic plant species that were consumed by at least one herbivore species, our findings say nothing about the effect of phylogenetic isolation on the likelihood of a given exotic plant species being attacked by at least one native herbivore.

This study shows that the phylogenetic isolation of exotic host plants in relation to the native plant assemblages is an important factor determining the extent to which the composition of insect species consuming a given exotic plant species is similar to the herbivore fauna associated with the native host plants. In agreement with our initial prediction, we found that the composition dissimilarity of insect herbivores on exotic host plants tends to increase as the phylogenetic isolation of exotic plants increases. This finding corroborates those of other previous studies, such as the study by Gossner et al. (2009) on the species of Heteroptera associated with exotic trees in Germany. Phylogenetic isolation is supposed to affect the establishment of insect herbivores on exotic host plants in different ways. The species composition of the herbivore fauna associated with more phylogenetically isolated exotic plants would have a distinct pool of insect herbivores, composed of the generalist insect herbivores able to overcome the physical, chemical and morphological barriers of the exotic plants. This effect, in turn, could lead to an increase in the species composition dissimilarity of the herbivores consuming the exotic host plants that are more phylogenetically isolated from the native flora (Gossner et al. 2009).

phagous herbivore assemblages showed different responses to exotic host plants. Contrary to our initial prediction, we found higher species composition dissimilarity among exotic hosts for exophagous than for endophagous assemblages. We hypothesize that the regional pool of exophagous and endophagous herbivore insects could play a role in explaining this result. If consuming exotic host plants imposes fewer constraints on exophagous than on endophagous insects, then it is likely that a larger fraction of exophagous insects from the regional pool are able to colonize habitats occupied by their novel exotic host plants. As these herbivores from the regional pool were not part of the local insect pool, their colonization means that exotic hosts are consumed by herbivores that are not able to consume the native co-occurring plants.

By feeding and developing internally in the vegetal tissues, endophagous herbivores have to deal continuously with physiological and morphological barriers of their host plants (Cornell 1989). Therefore, the endophagous feeding mode imposes higher costs in terms of adaptation to the chemistry and structure of their novel exotic host plants (Frenzel and Brandl 2003). For this reason, endophagous herbivore insects able of including exotic host plant species in their diets likely have evolve behavioral and physiological adaptations to overcome physical and chemical defenses, and colonize exotic host plant species.If the endophagous herbivorous insect fauna on exotic host plants is subset found in the native plants, then exotic host plants shared with the native plant species a major proportion of herbivore species. This will lead a high similarity in the endophagous herbivorous insect fauna on exotic host plants.

This study highlights the importance of phylogenetic isolation on the colonization of exotic host plants by herbivorous insects. In particular, we show that phylogenetic isolation does not play a significant role in determining the species h exotic hosts, but it does in determining the extent to which the composition of herbivores on exotic species differs from the herbivorous fauna associated with native host plants. In addition, this study reveals that the level of intimacy of herbivores with their host plants can be important for understanding the relationship between herbivores and exotic plant species. Our findings could have important practical implications. For instance, invasive exotic host plants that are more phylogenetically isolated from native plants are more likely to escape from natural enemies in their new areas (Yguel et al. 2011). As a consequence, populations of exotic species that are more phylogenetically isolated can also grow faster, making their management more difficult.

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in a generalized linear mixed model (GLMM) with Poisson Family and log link for richness of insect herbivores; Binomial Family and logit link for Jaccard and Simpson dissimilarity index.

Response variable	**Explanatoryvariable**	**Std. Coef.**	**z value**	***P* value**
Richness of insect herbivores	Mean phylogenetic isolation	-0.07	-1.74	0.08
	Degree of intimacy	-0.03	-0.58	0.56
	Total richness	-0.06	-0.96	0.34
Jaccardôsdissimilarity	Meanphylogeneticisolation	0.16	2.05	0.04
	Degreeofintimacy	1.39	1.94	0.05
Simpsonôsdissimilarity	Meanphylogeneticisolation	0.13	3.70	< 0.001
	Degreeofintimacy	3.02	2.17	0.03

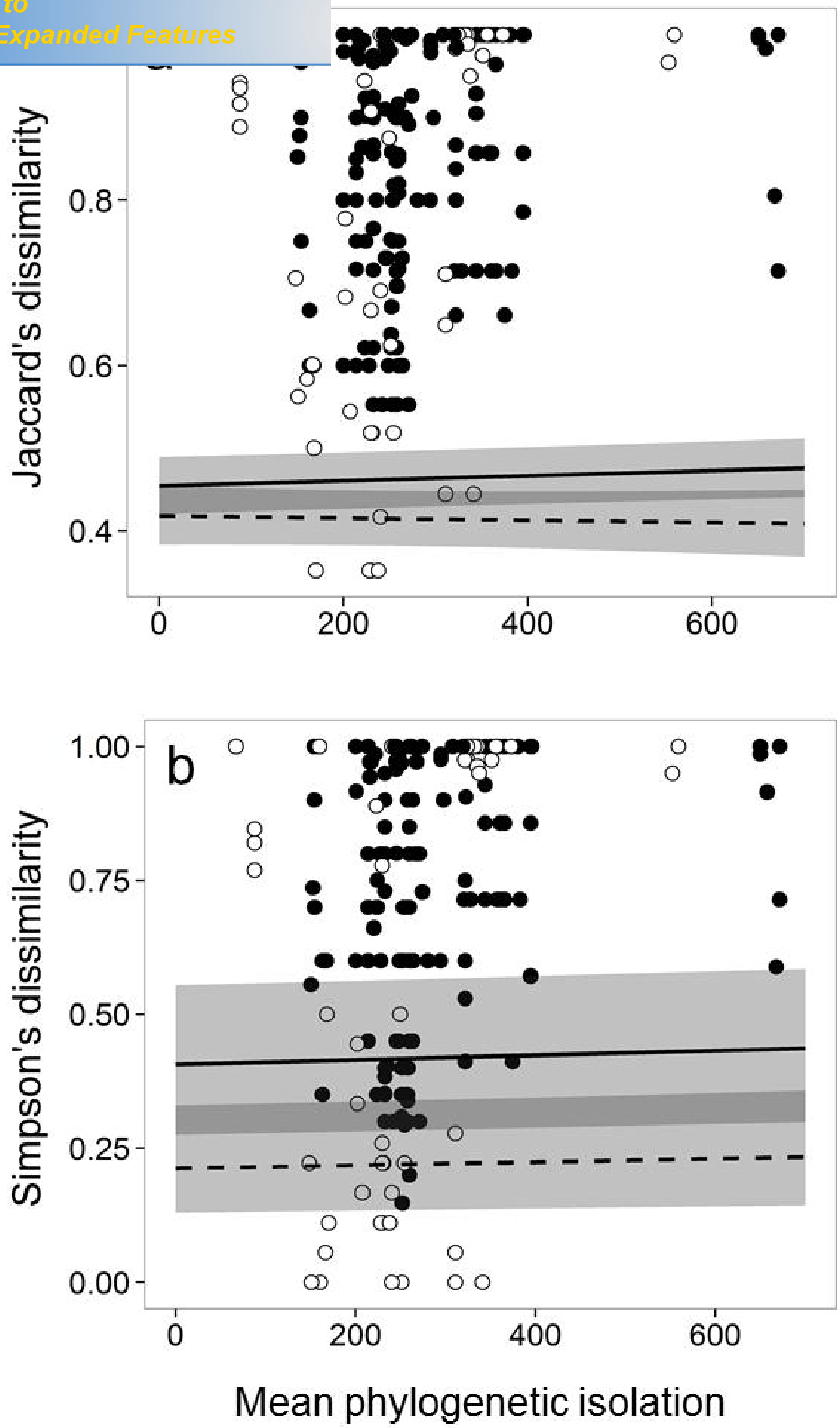

Figure 1. Relationship between mean phylogenetic isolation and dissimilarity of insect herbivore species on exotic host plant species.Filled circles and continuous line represent exophagous insects. Empty circles and dotted line represent endophagous insects. Gray bands represent the modelôs 95 % confidence intervals.

List of references of the 14 local plant-herbivore assemblages used in this study.

Code	References
Cavalleri 2005	Cavalleri, A. 2005. Comunidades de Tripes (Insecta: Thysanoptera) em flores e ramos, com ênfase em Asteraceae, no Parque Estadual de Itapuã, Viamão, RS. Master Thesis, Porto Alegre, Brazil.
Delfino et al. 2008	Delfino, M.A. and Buffa, L.M. 2008. Afidosen plantas ornamentales de Córdoba, Argentina (Hemiptera: Aphididae). Neotropical Entomology 37: 74-80.
HennemanandMemmot 2001	Henneman, M.L. and Memmot, J. 2001. Infiltration of a Hawaiian community by introduced biological control agents. Science 293: 1314-1316.
Kollár 2011	Kollár, J. 2011. Gall-inducing arthropods associated with ornamental woody plants in a City Park of Nitra (SW Slovakia). Acta entomologicaserbica 16: 115-126.
Leal 2008	Leal, M.R. 2008. Dinâmica populacional das moscas-das-frutas (Diptera: Tephritidae) e introdução de *Diachasmimorphalongicaudata*Ashmead (Hymenoptera: Braconidae) para controle da praga na região norte do estado do Rio de Janeiro. Master Thesis, Seropédica, Brazil.
Lopes and Basso 1974	Lopes. O.J.; Link. D. and Basso. L.V. 1974. Pentatomídeos de Santa Maria ï lista preliminar de plantas hospedeiras. Revista Centro Ciências Rurais 4: 317-322.
Perontiand Sousa-Silva 2002	Peronti, A.L.B.G. and Sousa-Silva, C.R. 2002. Aphids (Hemiptera: Aphidoidea) of ornamental plantsfrom São Carlos, São Paulo state, Brazil. Revista de Biología Tropical 50: 137-144.
Perreet al. 2011	Perre, P.; Loyola, R.D.; Lewinsohn, T.M. and Almeida-Neto, M. 2011. Insects on urban plants: contrasting the flower head feeding assemblages on native and exotic hosts. UrbanEcosystem 14: 711-722.

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Uramotoet al. 2004	Uramoto, K.; Walder, J.M.M. and Zucchi, R.A. 2004. Biodiversidade de moscas-das-frutas do gênero *Anastrepha* (Diptera. Tephritidae) no *campus* da ESALQ-USP, Piracicaba, São Paulo. Revista Brasileira de Entomologia 48: 409-414.

List of online database and sources used in the determination of exotic and native plant status.

Country	Online database or Source	Access date
Argentina	http://www.floraargentina.edu.ar/espsin.asp	22-Apr-13
Brazil	http://floradobrasil.jbrj.gov.br/jabot/listaBrasil/PrincipalUC/PrincipalUC.do	17-Apr-13
Hawaii	http://plants.usda.gov/du/DistributionUpdate.html	19-Apr-13
India	Reddy CS (2008) Catalogue of invasive alien flora of India. Life Science Journal 5:84-89	9-May-13
Slovakia	Jarolímek I. (2012): *Inventory of the alien flora of Slovakia*. Preslia 84: 257ï 309	21-Apr-13

CAPÍTULO II

Especialização local de insetos herbívoros em plantas hospedeiras: uma comparação entre o efeito do isolamento filogenético de plantas nativas e exóticas

faunas on host plants: contrasting the effect of
tion between native and exotic plants

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Plants are consumed by a variety of herbivorous insects, with plant species being used either by specialized insects, generalist insects or a combination of both. In theory, such host plant insect faunas are determined by host plant phylogeny. Moreover, specialization of host plant insect faunas also depends on the plantôs origin (native or exotic). Here, we test the effect of phylogenetic isolation of host plants on the specialization of herbivore faunas across local assemblages. In addition, we tested for differences of such effect between native and exotic host plants. We show that the mean phylogenetic isolation of host plants is positively related with the specialization of their herbivore faunas. In addition, this effect was not significantly different between native and exotic plants. Our findings show that phylogenetic isolation of host plants is an important factor in explaining the specialization of local herbivore faunas regardless of the plantsô origin.

Key words: herbivory, phylogeny, phytophagous insect, plant-insect interactions, plant origin

The vast majority of herbivorous insects are highly specialized in the range of host plant species they consume, exploiting a small set of hosts for their own nutrition or that of their offspring (Jaenike 1990; Lewinsohn et al. 2005, Forister et al. 2014). Factors that promote or constrain the specialization of herbivorous insects on their host plants remain poorly understood for most insect groups and habitat types. Some studies suggest that the diet specialization of insect herbivores has evolved in concert with only one or a few host plant species (Barone 1998; Novotny et al. 2002a; Novotny et al. 2010). Such restrictions in host plant use require an evolutionary time-scale, during which herbivorous insects can develop behavioral and physiological adaptations (Tallamy 2004). The tendency towards specialization on just one or a few host plant species decreases on plant lineages that have accumulated a diverse array of characteristics to defend against herbivorous insects (Ehrlich and Raven 1964; Farrell and Mitter 1994).

Phylogenetically related plant species are more likely to share similar physical, chemical and phenological characteristics than phylogenetically distant plant species (Rasmann and Agrawal 2011). As a result, most herbivorous insect species are better able to colonize novel host plants that are more closely related to their original host plants (Agrawal and Kotanen 2003; Roques et al. 2006; Viallatte et al. 2010). In fact, several studies have documented that phylogenetically isolated host plants are colonized by fewer species of insect herbivores than phylogenetically close plant species (Connor et al. 1980; Gossner et al. 2009; Spafford et al. 2013). In addition, phylogenetically isolated plants tend to host less specialized herbivores (Viallatte et al. 2010). Such insects have evolved specialized adaptations to circumvent or detoxify the plantsô defenses through a combination of morphological, physiological, and behavioral

For a specialist insect to use a phylogenetically isolated host plant, the insect must recognize the plant as food and be able to survive on it. Therefore, specialist herbivores that have adapted to the physical and chemical defenses of phylogenetically isolated host plants are predicted to be less likely to colonize other plant species, and thus they should be specialists of those isolated hosts.

The sharing of evolutionary historyis also expected to influence the specialization of herbivores on host plants, particularly when comparing hosts that evolved together with herbivores (natives) with hosts of alien origin (exotics). In addition to the previously mentioned factors regarding phylogenetic isolation, the fact that exotic plant species and native herbivores have not evolved in the same habitats and conditions can further complicate the use of exotic plants as hosts (Memmott et al. 2000). Specialist insects are generally expected to preferentially accept exotic plants that are phylogenetically close to native plants (da Ros et al. 1993; Jobin et al. 1996). Given the close similarity in biological characteristics between the plants, the exotic plants become appropriate hosts for the specialized herbivores of their native relatives (da Ros et al. 1993). On the other hand, exotic plants that are distantly related to native the plants are more likely to have novel traits that limit the colonization of specialist insects (Ness et al. 2011). This could lead to a reduction in the diversity of insect herbivores occurring on exotic host plants in relation to native hosts, due to the loss of specialist insects (Liu and Stiling 2006) and, consequently, to a lower specialization of insect herbivores on exotic host plants.

In the present study, we compared the effects of plant origin (native vs. exotic) and phylogenetic isolation on the mean specialization of the herbivore faunas using co-occurring host-plant species. Our hypotheses were the following: (1) plant species exhibiting high phylogenetic isolation host a more specialized set of insect herbivores

...netic isolation; and (2) the effect of phylogenetic isolation on host plant specialization is less pronounced in exotic plants than in native plants, with exotic plant species harboring less specialized herbivores than their native counterparts.

METHODS

Data compilation

We carried out a comprehensive search of plant-herbivore assemblages in the literature using SciVerse Scopus, Portal Capes and Google Scholar databases with the following combinations of keywords: (plant*) AND (herbivor*) AND (network* OR interaction* OR web*) AND (survey* OR list*). We only included assemblages with at least three exotic plant species. Overall, 30 local plant-herbivore assemblages were selected from 21 studies (Supplementary Material 1). The latitudinal distribution of the plant-herbivore assemblages ranged from 49.3° N to 37.5° S (Fig.1), and their altitudes ranged from 9 to 1430 m.a.s.l. (Supplementary Material 2)

Plant status

We categorized the origin status of the host plant species as natives (naturally occurring in the region) or exotics (occurring via introduction or invasion) for each local plant-herbivore assemblage. First, we checked the synonym using The Plant List Database (http://www.theplantlist.org). Then, we accessed the plant databases available for each country from which samples were drawn (Supplementary Material 3). We also used additional information, such as the Missouri Botanical Garden (www.missouribotanicalgarden.org), Invasive Species Specialist Group databases (www.issg.org)and Global species (www.gobalspecies.org), databases to refine our ecies where they were sampled. Host-plant species not determined to the species level were categorized as exotic or native depending on the origin status of the plant genus. Unidentified plant species (13% of all host-plant species) were excluded from the analyses.

Phylogenetic data

A working hypothesis for the phylogenetic relationships among all 582 plant species recorded in our assemblages (exotic and native) was constructed with Phylomatic software (Webb and Donoghue 2005) using the APG III supertree (2009). Branch lengths of the resulting phylogenetic tree were adjusted using the *bladj* algorithm in Phylocom 4.2 (Webb et al. 2011) based on node ages taken from Wikström et al. (2001) to calibrate the phylogeny.Phylogenetic distances (in millions of years) between all species pairs were then calculated using the *cophenetic* function in the R package *ape* (Paradis et al. 2004). We calculated the mean phylogenetic isolation between each focal species and all other species within each plant-herbivore assemblage.

Measuring host-plant specialization

To assess the specialization of herbivorous insects on their host-plant species for each plant-herbivore assemblage, we calculated Blüthgen et al.ôs (2006) specialization index *dô*. Thisindex is a standardized measure of the Kullback-Leibler distance, which measures the specialization of a species based on the frequency of the total number of interactions. The *dô* index ranges from zero to one, where zero indicates maximum generalization and one indicates maximum specialization. We first calculated a global *dô*for each herbivore insect species for each plant-herbivore assemblage. Then, we bivorous insects associated with each host-plant species in the assemblage. Specialization indices were calculated using the *bipartite* package (Dormann et al. 2009) in R 3.1.0 (R Core Team 2014).

Data analyses

We applied linear mixed models (LMM) to test the effect of mean phylogenetic isolation and plant status on the mean specialization of herbivorous insects associated with host plants. To build the LMMs, the mean phylogenetic isolation and plant status were set as fixed effects, whereas the local assemblage was set as a random effect. This model was built using the *lmer* function, which is part of the *lme4* package (Bates et al. 2014), available in R software version 3.1.0 (R Core Team 2014).

RESULTS

A total of 518 herbivorous species and 582 host plant species (241 exotic species and 361 native species) were recorded in the plant-herbivore assemblages. The total numbers of insect herbivores associated with exotic and native host plants were 177 and 429, respectively. The local species richness of herbivores varied from 5 to 91 species (21.5 ± 23.8).

We detected an effect of host-plant phylogenetic isolation on the mean specialization of associated herbivorous fauna ($t = 2.70$, $p = 0.007$), with more phylogenetically isolated host-plant species harboring more specialized insect herbivores (Table 1, Fig. 2). However, we did not find differences in the effect of host-plant phylogenetic isolation on the mean specialization of herbivorous fauna when comparing between native and exotic plants ($t = -0.14$, $p = 0.89$; Table 1).

This study compared the local host-plant specialization of the herbivore faunas on native and exotic plant species while controlling for the effect of plant phylogenetic isolation. In contrast with previous studies (Liu and Stiling 2006), we found no evidence that exotic host-plant species are consumed by less specialized herbivorous insects than co-occurring native plant species. Our results also showed that the more phylogenetically isolated a host-plant species is, the more specialized its associated insect herbivores are.

For a proper interpretation of our findings, it must be considered that we compared the mean specialization of the herbivore faunas on native and exotic plants rather than the extent to which exotic host-plant species are consumed by specialist or generalist herbivores. The lack of difference in host-plant specialization between herbivores associated with native and exotic plant species could result from the fact that both sets of host-plants are mostly consumed by generalists or, alternatively, that both are mostly consumed by specialist herbivores.

The positive association between higher phylogenetic isolation from co-occurring plants and an increase in the mean host specialization of the herbivore fauna contrasts the study by Viallatte et al. (2010), which showed that more phylogenetically isolated trees had less specialized herbivores. Gossner et al. (2009) found that phylogenetically isolated host plants shared no or only a few herbivore species with other co-occurring plant species. This result can be interpreted as evidence of a higher host plant specialization of herbivores on phylogenetically isolated plants. In addition, specialized herbivorous insects are not expected to incorporate plant into of their diets that are phylogenetically distant from their original host species. As a consequence, phylogenetic isolated host-plant species are more likely to harbor host-specialist rich lineages. If a phylogenetic isolated host plant is closely related to the original host of an insect, a specialist herbivore may expand its host range and colonize a new niche (Dalin and Björkman 2006). Moreover, phylogenetically isolated host plants may have chemical defenses that are similar to those of a native host plant; thus, they may become appropriate hosts for the adapted local specialists (Tallamy 2004), because novel host plants are most likely to share the chemical defenses of a native species if they are closely related to that species (Ehrlich and Raven 1964).

Overall, we have demonstrated that the phylogenetic isolation of host plants can be a determinant factor in explaining the specialization of insect herbivores towards their host plants. This result highlights the importance of understanding how specialist insects respond to variations in their host plantsô phylogenetic relationships. Future investigations should be made to assess how specialist insects respond not only to phylogenetic isolation but also to other factors, such as morphological and chemical traits, range size, and abundance of host plants.

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cts model assessing the effect of mean phylogenetic isolation and plant origin (native vs. exotic) on the meanhost specialization of associated herbivore faunas.

Explanatoryvariable	Std. Coef.	t-value	*P*-value
Meanphylogeneticisolation	0.100	2.70	0.007
Plantorigin	-0.005	-0.14	0.890

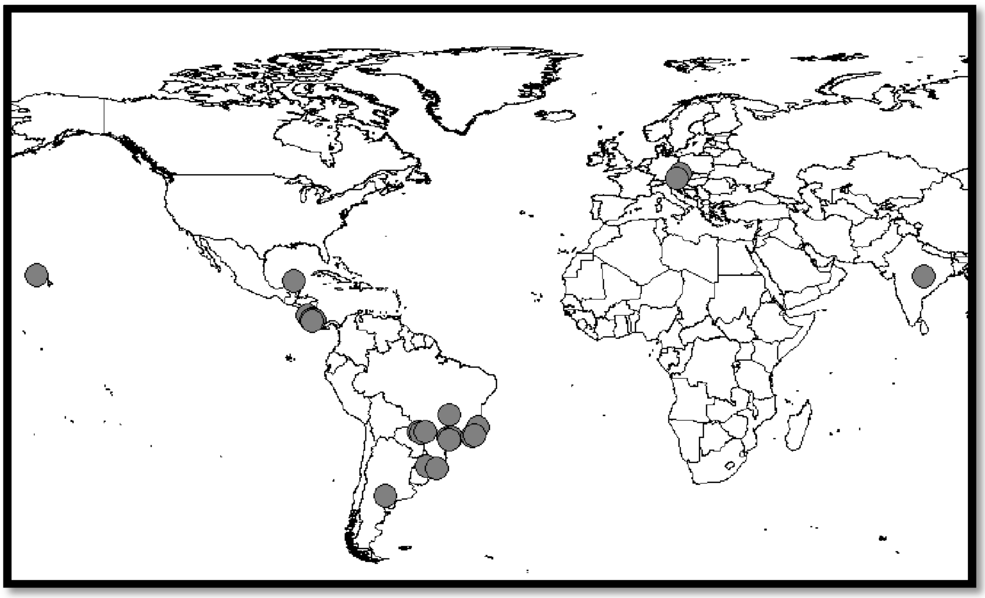

Figure 1. Global distribution of the 30 herbivore-plant assemblages used in this study.

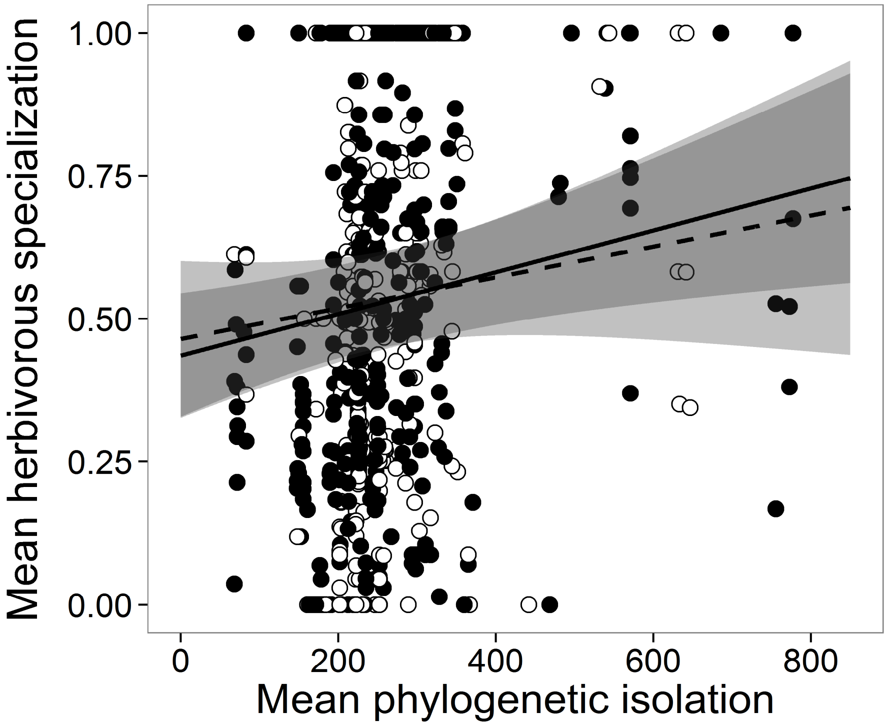

Figure 2. Relationship between plant phylogenetic isolation and mean specialization of their herbivore faunas. Filled circles and continuous line represent the native plants. Empty circles and dotted line represent the exotic plants. Gray bands represent the modelôs 95 % confidence intervals.

List of references of the 30 local plant-herbivore assemblages used in this study.

Code	References
BorgeandBasedow 1997	Borge, M.N.R. and Basedow, T. 1997. A survey on the occurrence and flight periods of fruit fly species (Diptera: Tephritidae) in a fruit growing area in southwest Nicaragua. 1994/95. Bulletin of Entomological Research 87: 405-412.
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HennemanandMemmot 2001	Henneman, M.L. and Memmot, J. 2001. Infiltration of a Hawaiian community by introduced biological control agents. Science 293: 1314-1316.
Hernandez-Ortiz et al. 2006	Hernandez-Ortiz, V.; Delfín-González, H.; Escalante-Tio, A. and Manrique-Saide, P. 2006. Hymenoptera parasitoids of *Anastrepha* fruit flies (Diptera: Tephritidae) reared from different hosts in Yukatan. Mexico. The Florida Entomologist 89: 508-515.
Kollár 2011	Kollár, J. 2011. Gall-inducing arthropods associated with ornamental woody plants in a City Park of Nitra (SW Slovakia). Acta entomologicaserbica 16: 115-126.
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Perontiand Sousa-Silva 2002	Peronti, A.L.B.G. and Sousa-Silva, C.R. 2002. Aphids (Hemiptera: Aphidoidea) of ornamental plantsfrom São Carlos, São Paulo state, Brazil. Revista de Biología Tropical 50: 137-144.
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Pinentet al. 2011	Pinent, S.M.J.; Romanowski, H.P.; Redaelli, L.R. and Cavalleri, A. 2011. Thysanoptera: plantas visitadas e hospedeiras no Parque Estadual de Itapuã, Viamão, RS. Brasil. Iheringia 95: 9-16.
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Latitude and longitude (decimal degrees), altitude (approximate altitude), records in the plant-herbivore assemblages. References of the assemblage original studies are listed in the Supplementary 1.

Code	Country	Latitude	Longitude	Altitude (m)
BorgeandBasedow 1997	Nicaragua	11	-86	445
Cavalleri 2005	Brazil	-30.45	-51.08	129
Delfino et al. 2008	Argentina	-37.872	-64.784	474
Embrapa 2007	Brazil	-15.817	-47.567	1075
HennemanandMemmot 2001	Hawaii	22	-159	771
Hernandez-Ortiz et al. 2006	Mexico	20.3	-89.7	38
Leal 2008 (1)	Brazil	-21.8	-41.3	9
Leal 2008 (2)	Brazil	-21.3	-40.933	10
Leal 2009	Brazil	-21.3	-40.933	10
Lopes and Basso 1974	Brazil	-29.683	-53.783	131
Mejías 2009 (1)	Costa Rica	10.1306	-84.2345	1430
Mejías 2009 (2)	Costa Rica	10.0779	-84.5408	896
Mejías 2009 (3)	Costa Rica	9.8994	-84.8788	18
Mejías 2009 (4)	Costa Rica	9.67878	-84.8793	30
Mejías 2009 (5)	Costa Rica	9.93255	-84.0464	1224
Mejías 2009 (6)	Costa Rica	9.50095	-84.6136	85
Memmontet al. 1994	Costa Rica	10	-85	283
Perontiand Sousa-Silva 2002	Brazil	-22.015	-47.891	830
Perreet al. 2011	Brazil	-22	-47.069	876

[illegible]	Brazil	-30.367	-51.033	20
StarýandHavelka 2008 (1)	CzechRepublic	49.513	14.931	537
StarýandHavelka 2008 (2)	CzechRepublic	49.513	14.931	537
StarýandHavelka 2008 (3)	CzechRepublic	49.513	14.931	537
Tipleet al. 2011	India	21.65	80.65	319
Uchôa et al. 2003 (1)	Brazil	-20.527	-55.837	170
Uchôa et al. 2003 (2)	Brazil	-20.65	-55.331	173
Uchôa et al. 2003 (3)	Brazil	-20.437	-54.082	308
Uramotoet al. 2004	Brazil	-22.708	-47.633	546
Uramotoet al. 2008	Brazil	-19.1	-39.75	60

List of online database and sources used in the determination of exotic and native plant status.

Country	Online database or Source	Access date
Argentina	http://www.floraargentina.edu.ar/espsin.asp	22-Apr-13
Brazil	http://floradobrasil.jbrj.gov.br/jabot/listaBrasil/PrincipalUC/PrincipalUC.do	17-Apr-13
Costa Rica	http://darnis.inbio.ac.cr/ubis/FMPro?-db=UBI&-lay=Weball&-format=findmore.html&-view	20-Apr-13
Hawaii	http://plants.usda.gov/du/DistributionUpdate.html	19-Apr-13
Mexico	http://www.conabio.gob.mx/invasoras/index.php/Especies_invasoras_-_Plantas	20-Apr-13
Nicaragua	http://www.tropicos.org/NameSearch.aspx?projectid=7	20-Apr-13
Czech Republic	Pysek P, S adlo J and Mandák B (2003c) Alien þora of the Czech Republic, its composition, structure and history. In: Child LE, et al (eds) Plant Invasions: Biological Threats and Management Options, pp 113ï 130. Backhuys Publishers, Leiden, The Netherlands	21-Apr-13
Czech Republic	Sadlo J, Chytrý M, &Pyġek P (2007) Regional species pools of vascular plants in habitats of the Czech Republic. Preslia 79:303-321	21-Apr-13
CzechRepublic	Pyġek P, et al. (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. Preslia 84: 155ï 255	21-Apr-13
India	Reddy CS (2008) Catalogue of invasive alien flora of India. Life Science Journal 5:84-89	9-May-13
Mexico	Williams JK (2010) Additions to the alien vascular flora of Mexico, with comments on the shared species of Texas, Mexico, and Belize. Phytoneuron 3: 1-7	20-Apr-13
Mexico	Villaseñor, J. L. y Espinosa-García, F.J. (2004). *The alien flowering plants of Mexico.* DiversityandDistributions 10: 113-12	20-Apr-13
Slovakia	Jarolímek I. (2012): *Inventory of the alien flora of Slovakia*. Preslia 84: 257ï 309	21-Apr-13

CONCLUSÕES GERAIS

Os resultados do presente estudo destacam a importância do isolamento filogenética na colonização de plantas hospedeiras exóticas por insetos herbívoros. Em particular, demonstram que o isolamento filogenético não desempenha um papel significativo na determinação do número de espécies de herbívoros associado às plantas hospedeiras exóticas, mas determina a composição de herbívoros associados às espécies exóticas que diferem da fauna herbívora associada às plantas hospedeiras nativas. Além disso, este estudo revela que o grau de intimidade de herbívoros com as suas plantas hospedeiras pode ser importante para a compreensão da relação entre herbívoros e espécies de plantas exóticas. Por outro lado, o isolamento filogenético de plantas hospedeiras também é importante para explicar a especialização dos insetos herbívoros em relação às plantas hospedeiras, destacando a importância de compreender como insetos especialistas respondem a variações nas relações filogenéticas de suas plantas hospedeiras.