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ORIGINAL ARTICLE

Host diversity and environmental variables as determinants of the species richness of the parasitoids of leaf-cutting ants

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ABSTRACT

Aim Because of the obligatory relationship between endoparasitoids and their hosts, we presume that hosts exert strong selection pressure on parasitoids. One prediction is a positive relationship between host diversity and parasitoid richness. This relationship could be the product of resource availability which could lead to more opportunities for speciation, or could represent shared responses to the environment by both groups.

Location Argentina and Paraguay.

Methods We sampled a 1800-km transect to test for a correlation between the richness of leaf-cutting ant hosts and their phorid parasitoids. Regression models were used to assess if host and environmental variables could explain phorid species richness at nest, hectare and locality spatial scales. We used canonical correspondence analysis (CCA) to explore if there were similar responses of phorid species to particular host and environmental variables at different spatial scales, and partial CCA to separate the relative importance of both groups of variables.

Results Phorid richness was positively correlated with host richness. Host richness/abundance accounted for 20–53% of the variation in parasitoid richness at the hectare and locality scales of analysis, with most of the variation accounted for by ant abundance. We were not able to assess the prediction at the nest scale as only one phorid species was found at most nests. Climatic variables did not explain phorid species richness once host variables were in the models. Partial CCA showed that host-related variables accounted for most of the variance associated with phorid species ordination at the nest and hectare scales, but not at the largest grain, the locality, where climatic variables were more important. However, most phorid species did not show particular positions along the climatic gradient.

Main conclusions The association between parasitoid richness and host richness and abundance, and the overall weak associations with environmental variables, suggest that these host variables are key factors influencing parasitoid speciation.

Keywords

Argentina, Attini, climatic variables, decapitating flies, endoparasitoids, Formicidae, Paraguay, Phoridae, spatial scales, symbiosis.

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INTRODUCTION

Parasitoids have an obligatory relationship with their hosts, using them as their only food for development. For this reason, host richness should influence parasitoid richness, and it is reasonable to expect a positive relationship between the richness of both groups. A positive relationship could be mainly related to host influence. Leaving aside an effect of coevolution, as more resources offer more opportunities for consumers to diversify (Hutchinson, 1959; Knops *et al.*, 1999;

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Siemann *et al.*, 1999), host abundance and richness could be important in determining consumer richness.

There are examples of positive relationships between both host richness and abundance and the richness of their parasitoids (Sheehan, 1994; Haddad *et al.*, 2001; Tylianakis *et al.*, 2006). However, these studies considered hosts and parasitoids pooled from very different taxonomic groups, leading to results representing mixtures of processes due in part to phylogenetic differences. A possible way to circumvent that problem is to study host–parasitoid associations within limited clades. Stireman & Singer (2003), for example, evaluated the factors determining parasitoid species richness in a group of tachinid flies that use Lepidoptera as hosts. They found that host family, a surrogate of host phylogeny, had little relationship to parasitoid richness and suggested that co-radiations of host and parasitoid taxa were unlikely, as the tachinids had wide host ranges. However, they found that host abundance was one of the most important factors accounting for fly parasitoid richness. Another study of tachinids found that almost 69% of the variation in parasitoid richness was explained by host abundance (Sheehan, 1994).

A relationship between parasitoid and host species richness could also be a result of similar responses of parasitoid and host species to the environment. For example, Hawkins & Porter (2003) found that plant and butterfly richness were correlated in California. However, after accounting for environmental variation those variables were no longer correlated, suggesting that resource diversity did not have a direct influence on the diversity of butterflies. Those results highlight the importance of considering climatic variables, and not just resource-related variables, in an effort to explain consumer richness.

Our perception of biodiversity changes according to the scale at which it is measured (Rahbek, 2005). It is widely believed that richness at the local scale is related to coexistence mechanisms driven by interspecific interactions, whereas at the landscape or intermediate scales, factors related to performance in certain habitats are more relevant; additionally, at regional scales the position of the community along environmental gradients can be important (Spiesman & Cumming, 2007). Therefore, using a multi-scale approach to analyse species richness gives a more complete understanding of the hypotheses and predictions based on biodiversity (Ricklefs & Schluter, 1993).

Studies of insect host–hymenopteran parasitoid relationships, from behavioural, ecological and evolutionary perspectives, have allowed the development of a solid and integrated theoretical framework for this type of interaction (Godfray, 1994; Hawkins & Sheehan, 1994; Whitfield, 1998). Many patterns have been discovered at the community (Godfray, 1994; Hawkins & Sheehan, 1994; and references therein) and biogeographical (Janzen, 1981; Hawkins, 1990) levels. However, it is not clear if the same patterns and explanatory mechanisms apply to non-hymenopteran parasitoids, as the latter have diverse phylogenetic origins. Therefore, studies of non-hymenopteran parasitoids provide an opportunity to generalize our knowledge of the parasitoid habit (Feener & Brown, 1997).

Dipteran parasitoids in the family Phoridae are a very diverse group (Disney, 1994). At least several hundred species use ants as hosts, and more surprisingly they parasitize adult ant workers, a life history that is not frequent in other parasitoids. Some of these species are parasitoids of leaf-cutting ants (Formicidae: Myrmicinae: Attini); using a piercing ovipositor they insert an egg inside the body of foraging workers. The larva eats the internal tissues of the ant, killing it, and pupates inside or outside the body of the ant (Feener & Moss, 1990; Erthal & Tonhasca, 2000; Tonhasca *et al.*, 2001; Bragança & Medeiros, 2006).

The ants typically follow marked trails over which they carry the fresh leaf pieces that they have cut. These leaf fragments are processed by the ants into small fragments and used as a substrate to cultivate a fungus that is principally fed to their larvae and queen (Weber, 1966; Hölldobler & Wilson, 1990). Despite this uniformity in behaviour, there is inter-specific variation in how nests are constructed, the number of workers per colony and nest densities. Leaf-cutting ants belong to the genera *Atta* and *Acromyrmex*; *Atta* species have colonies with millions of workers, enormous nests and conspicuous foraging trails, whereas *Acromyrmex* species colonies have thousands of workers, smaller nests and less obvious foraging trails (Beckers *et al.*, 1989; Hölldobler & Wilson, 1990). There are only three species of *Atta* in Argentina (Farji-Brener & Ruggiero, 1994) and five in Paraguay (Fowler, 1985). However, around 15 species of *Acromyrmex* are known in Argentina and more than 16 in Paraguay (Wild, 2007). The leaf-cutting ants represent a monophyletic clade (Wetterer *et al.*, 1998), and the phorids that frequently attack them are in three genera (Borgmeier, 1931), thus reducing potentially confounding effects of multiple evolutionary pathways and ecological characteristics.

In this study our objective was to determine if there was a positive relationship between phorid parasitoid and ant host species richness and/or abundance, also evaluating environmental variables as possible determinants of phorid richness. We examined the prediction at three spatial scales by sampling at nests, hectares and localities along a transect in Argentina and Paraguay, using explanatory variables measured at each scale. To evaluate if there were groups of phorid species responding to the same independent variables we used canonical correspondence analysis (CCA).

MATERIALS AND METHODS

Study sites, sampling design and variables measured

We sampled leaf-cutting ants and their parasitoids at 14 localities from western Paraguay (20°37′ S, 59°52′ W) to the centre of Argentina (36°40′ S, 59°41′ W), with a minimum distance between localities of 60 km, a maximum distance of 430 km and a transect length of 1800 km (Fig. 1). We selected the sampling area to include a gradient of leaf-cutting ant richness (Farji-Brener & Ruggiero, 1994), and extended the

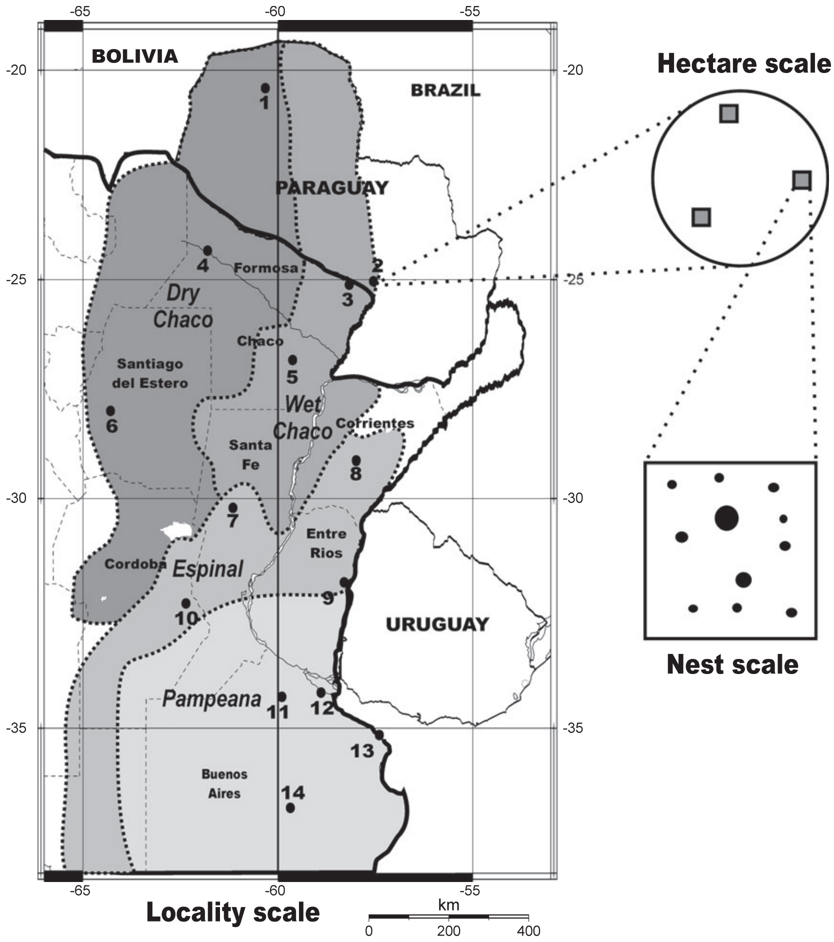


Figure 1 Map showing sampling localities for leaf-cutting ants and their phorid parasitoids, and expanded figures on the right showing the other two spatial scales with three hectares per locality and three nests per ant species at each hectare (for more details see text). Phytogeographical provinces are in italics and political provinces sampled in Argentina are in bold. Locality references are: 1, Defensores del Chaco National Park; 2, Benjamin Aceval; 3, Pilcomayo National Park; 4, Formosa Natural Reserve; 5, Chaco National Park; 6, La María; 7, San Cristóbal; 8, Mercedes; 9, El Palmar National Park; 10, Noetinger; 11, Carmen de Areco; 12, Otamendi Natural Reserve; 13, El Destino Reserve, Magdalena; 14, Azul.

transect north into Paraguay to get a greater environmental gradient. In addition, sampling sites were chosen so as to have low human disturbance, at least without agricultural use, and most sampling localities were in protected areas. Sampling was carried out during summer, autumn and spring from December 2003 to December 2004.

To account for different responses of parasitoid species richness to explanatory variables according to spatial scale, we sampled at three hierarchical scales, changing the grain but not the extent. The nest scale represents the microhabitat, the hectare is an intermediate scale and the locality indicates a regional scale (Fig. 1). At the nest scale we sampled parasitoids by searching for 30 min along ant foraging trails and over nest entrances. We collected phorids using an aspirator. If a nest had more than one foraging trail, we sampled two or three of them for 30 min each, during the morning and afternoon, unless the nests were inactive.

We collected environmental variables at the nest scale (Table 1). At the beginning and end of each 30-min phorid survey we measured light intensity. Some fire ant phorid species were found more frequently in full sun (high light intensity), and other species were found more frequently in shaded conditions, suggesting that light intensity provides an indirect measure of the effect of solar radiation on the microhabitat (Folgarait *et al.*, 2007). For the entire sampling period we placed a data logger on each nest (Hobo Pro Series) that recorded temperature and relative humidity every 2 min to obtain those variables at the microhabitat of nests when phorids were present.

To obtain host variables at the nest scale we counted the ants returning to the nest on a foraging trail for 1 min at the beginning and end of the 30-min phorid surveys (Table 1). We also counted the number of active foraging trails and measured the diameter of each nest as an indirect measure of colony size. Leaf-cutting ant species vary in the number of workers that forage, the number of foraging trails in use and nest density, and any of these factors could influence the availability of ants as a resource for parasitoids. Therefore, we classified ant species based on a cluster analysis using the mean values of nest sizes, the mean number of foraging trails and average ant activity per minute in the foraging trails. We obtained three clusters: (1) 'Ac.L' included *Acromyrmex* spp. with small colony sizes and low foraging activities (*Acromyrmex rugosus*, *Acromyrmex balzani*, *Acromyrmex fracticornis*, *Acromyrmex subterraneus* and *Acromyrmex striatus*); (2) 'Ac.H' that included *Acromyrmex* spp. with large nest sizes and higher ant activity on foraging trails (*Acromyrmex ambiguus*, *Acromyrmex crassispinus*, *Acromyrmex heyeri*, *Acromyrmex hispidus*, *Acromyrmex lobicornis* and *Acromyrmex lundii*); and (3) 'Atta', containing the largest nests and greatest foraging activity (*Atta*

Table 1 Variables used at each spatial scale for the analyses of the determinants of the richness of phorid parasitoids of leaf-cutting ants, with dependent variables in italics and independent variables in bold. Variables that explained some variation in phorid species richness or ordination are abbreviated within brackets.

Host's nest scale	Hectare scale	Locality scale
Presence of phorids	*Phorid species number*	*Phorid species number*
Light intensity (lux): average lux measured at the beginning and at the end of each nest sampling	**Sampling period average mean temperature (Tmean)***	**Annual average mean temperature (AnTmean)§**
Average mean temperature (Tmean): throughout all samplings recorded at a nest	**Sampling period average maximum temperature***	**Annual average precipitation (AnPrec)§**
Minimum temperature: registered throughout all samplings recorded at a nest	**Sampling period average minimum temperature***	**Annual average maximum temperature§**
Maximum temperature: registered throughout all samplings recorded at a nest	**Sampling period thermal amplitude***	**Annual average minimum temperature§**
Average thermal amplitude: difference between the maximum and minimum average temperature throughout all samplings recorded at a nest	**Vapour pressure deficit***,†	**Annual average vapour pressure deficit**
Average relative humidity (RHmean): throughout all samplings recorded at a nest	**Sampling period average relative humidity (RHmean)***	**Annual vapour pressure deficit amplitude (AnVPDamp)**
Minimum relative humidity: registered throughout all samplings recorded at a nest	**Sampling period minimum relative humidity (RHmin)***	**Average precipitations from the three driest months**
Maximum relative humidity: registered throughout all samplings recorded at a nest	**Sampling period maximum relative humidity***	**Average number of frosts per year**
Relative humidity average amplitude (RHamp): difference between the maximum and the minimum average relative humidity	**Sampling period relative humidity amplitude***	**Phytogeographical province**: Pampas (1), Espinal (2) and Chaco (3)‡
Ant availability: categorical variable to account for the size of the ant nest (see Materials and Methods for categories of this variable)	**Maximum temperature registered 2 months before phorid sampling**	**Ant species richness (ant.spp)**¶
Ant activity: average of the initial and final ant activity per minute in the foraging trails	**Minimum temperature registered 2 months before phorid sampling**	**Ant nests per locality****
Foraging trails with ant activity: number of foraging trails with ants foraging in each nest	**Precipitation accumulated 2 months before sampling**	**Ant abundance**: see Materials and Methods for a description
	Presence (1, reference category)–**Absence** (0) **of *Atta*** (Atta)‡	
	Ant species richness (ant.spp)	
	Ant nests density per hectare	
	Ant abundance: see Materials and Methods for a description	
	Type of habitat: grassland (1, reference category), forest (0) (**habitat**)‡	

*Average values for 4–13 days, depending on the time spent sampling at each hectare.

†Calculated as 0.6108 * $\mathrm{EXP}^{(17.27\ *T°C/(T°C\ +\ 237.3))}$ − 0.6108 * $\mathrm{EXP}^{(17.27\ *T°C\ \text{dew point}/(T°C\ \text{dew point}\ +\ 237.3))}$.

‡Numbers represent the codes entered for each category in the regression analysis.

§Average values for 10–20 years, depending on the locality.

¶All the species recorded at one locality.

**Number of nests on all the hectares sampled (see Materials and Methods).

vollenweideri and *Atta saltensis*). We used this classification as a categorical variable to account for the availability of ants as hosts for phorids at the nest scale (Table 1).

At each locality we delimited three 1-ha plots, each separated by at least 600 m. As leaf-cutting ants' foraging trails can reach 200 m (L. Elizalde, pers. obs.), we assumed that nests separated by 600 m did not interact; thus we considered the plots as independent replicates. Plots were selected after locating at least one leaf-cutting ant nest with parasitoids. Within each hectare we searched extensively for all leaf-cutting ant nests to obtain a measure of nest density. In each hectare we chose three mature nests of each ant species, when available, to conduct the 30-min surveys at the nest scale. At those localities where both natural grassland and forest were present, we delimited three plots in each habitat type because nests of some species were found more frequently in open areas and others mostly in shaded areas. Therefore, each plot represented a sampling unit at the hectare scale and the sum across hectares represented each replicate at the locality scale.

To take into account variation in the number of ants foraging for food, we corrected nest density at the hectare and locality spatial scales. For each ant species, we obtained an activity per species factor, multiplying average ant activity in each foraging trail by average number of active trails per nest. At each hectare, we multiplied that factor by the nest density recorded for each species; then we added those values for each hectare. In this way we obtained a variable of ant abundance, or more precisely, of ants foraging per minute, regardless of ant species in each hectare and available as prey for phorids. Adding those values over all hectares from a locality gave us an estimate of the number of ants per minute in each locality. We rescaled the activity per species by dividing it by 100, so that each unit corresponds to an increase in 100 ants per minute per hectare or locality, according to scale. We called this variable ant abundance (Table 1).

We recorded temperature and relative humidity with a data logger placed in the centre of each hectare under trees or bushes, during the time we sampled the nests in each locality. These data represented the climatic variation that the adult phorid experienced when we sampled in a hectare or locality. We obtained annual climatic variables from meteorological stations located near the sampling localities (from the National Meteorological Services of Argentina and of Paraguay). We averaged those data over months and years (between 10 and 20 years depending on the locality) and obtained measures of its variation, characterizing each locality by its historical climate (Table 1).

Ant species were identified using the keys of Bonetto (1959), Gonçalves (1961) and Fowler (1985) and, when necessary, we corroborated specimens with museum collections and ant taxonomists. For the phorids we used the available keys (Brown, 1997; Disney *et al.*, 2006, 2009; Brown *et al.*, 2010), and received the expert opinion of Dr Henry Disney (Department of Zoology, University of Cambridge). Reference specimens of both ants and phorids were deposited in the Museum Bernardino Rivadavia (Buenos Aires, Argentina).

Data analyses

We used species accumulation curves and species richness estimators to assess sampling completeness of phorid species for the entire transect, using the phorid abundance at the nests as a measure of sampling effort (Colwell & Coddington, 1994; Gotelli & Colwell, 2001).

At the nest scale we did not model phorid richness, because 89.3% of the nests with phorids had only one species. To analyse the influence of host and climatic variables on parasitoid richness at the hectare and locality scales we employed Poisson regressions, as Poisson error structures are appropriate for non-negative discrete data such as species richness (Medellín *et al.*, 2000; Mac Nally & Fleishman, 2002; Guisan & Hofe, 2003). In total, the dataset included 42 hectares, of which 22 were in grasslands and 20 were in forests; and 12 localities, with 4 in Chaco, 4 in Espinal and 4 in the Pampeana phytogeographical province. At the locality spatial scale, we could not include the two localities from Paraguay in the analyses because in two hectares sampled in each locality the phorids collected were not parasitoids of leaf-cutting ants or were males (there are no available keys as to identify males).

As sampling effort was not uniform, because we sampled more where more ant species were present, we corrected this uneven sampling using rarefaction at the hectare and locality scales. We used the Mao Tao estimator, implemented in the software EstimateS version 8.0.0 (http://viceroy.eeb.uconn.edu/EstimateS), to calculate sample-based rarefaction (Colwell *et al.*, 2004). Sampling was reduced in each hectare or locality in order to include 11 or 27 sampling periods of 30 min, respectively. Numbers were chosen for being sampling periods where two phorid species were recorded in a hectare or locality. Then, we rounded off to the nearest integer the corresponding phorid richness and used it as the dependent variable in the Poisson regressions.

Phorid richness data were underdispersed at the hectare and locality spatial scales as the deviance was lower than the degrees of freedom (Agresti, 2002). Underdispersion was probably due to the lack of zeros in our data sets (Winkelmann & Zimmermann, 1995), because we included only the hectares and localities with at least one phorid species. Although there is no clear methodology for dealing with underdispersion, one available option is to use quasi-Poisson models (for example Hambäck *et al.*, 2007).

We included in the models the variables alone and in combination with other variables, and in quadratic form. If an explanatory variable was significant and the model including it was better according to a log-likelihood ratio test, we kept that variable in the final model. To compare the effects of the factors affecting phorid richness in the final models (i.e. host versus environmental variables) we used if necessary the standardized coefficients of independent variables from the quasi-Poisson models. These standardized coefficients were calculated by multiplying the coefficient of an independent variable by its standard deviation, as suggested for similar generalized linear models (logistic regression; Agresti, 2002). Thus, a variable with higher absolute value of the standardized coefficient will have greater effect on phorid richness. As a measure of variance accounted for by the model we obtained pseudo-R^2 values (Heinzl & Mittlböck, 2003).

To explore the relationship of the parasitoid species to host and environmental variables at the different spatial scales, we used CCA. We ran CCA analyses at each of the three spatial scales; the dependent matrix contained parasitoid species as columns, and the nests, hectares or localities where they were present as rows, according to each scale. We also performed the analyses with a phorid species abundance matrix but the results were very similar; thus we present only the results of the presence–absence matrix. The independent matrix contained standardized climatic and corresponding host data for each scale (see Table 1). We did not include three rare phorid species and kept only those variables that had variance inflation factor (VIF) values lower than 10 or were significant using permutation tests (Oksanen *et al.*, 2006). In addition, we analysed the matrices with partial CCA, which allowed us to control for variables that can act as covariates in the species matrix. This analysis was used to separate the effect of two types of variables and provided information on the relative importance of host versus climatic variables on the responses of parasitoid species (Legendre & Legendre, 1998). We performed the analyses in the R environment (R Development Core Team, 2006), using the Vegan package (Oksanen *et al.*, 2006).

RESULTS

We collected a total of 15 phorid species along the entire transect, and the species accumulation curve approached an asymptote. The nonparametric incidence-based coverage estimator gave a mean species richness of 18.6 species. Thus, we considered that our sample was sufficient. Indeed, after this sampling we spent a year sampling in the locality with highest phorid richness (San Cristóbal) and found three more species not recorded during the sampling along the transect (Elizalde, 2009). A list of the phorid and host species collected at each locality is provided in Appendix S1 in Supporting Information.

The richness of phorids and ants was positively correlated across localities (Spearman's $\rho = 0.8$, $P < 0.01$). However, localities with low ant richness did not necessarily have the lowest phorid richness (Appendix S1). We distinguished phorid richness according to ant genus because phorids that were parasitizing *Atta* were not collected parasitizing *Acromyrmex*, and vice versa. For the *Acromyrmex* hosts, ant richness was always higher than or equal to phorid richness, with the exception of Carmen de Areco; and for the *Atta* system, ant richness was always lower than or equal to phorid richness, except in Defensores del Chaco National Park (Appendix S1).

Determinants of parasitoid richness

Hectare scale

The quasi-Poisson model for phorid species richness at the hectare scale included the number of ant species and ant abundance, and explained 31% of the variance (Table 2). Although ant abundance was marginally significant and a log-likelihood test showed that including it in the model was also marginally necessary ($P = 0.08$), we decided to leave it in the model as the variation accounted for was higher in this model that in the one with ant richness only (27%). An increase in one ant species resulted in a 1.16 increase in the odds of having another phorid species; in addition, with each increase in 500 ants on foraging trails per minute (e.g. the estimated mean number of leaf-cutting ants foraging per minute in an hectare was 515, SD = 455), the odds of collecting a new phorid species increased 1.02 times. None of the environmental variables had an effect on phorid richness when alone in the models (all $P > 0.3$). The variables indicating habitat type, the presence of *Atta* and nest density were significant when included alone in the models, but when considered simultaneously with host richness or ant abundance they were non-significant ($P > 0.1$).

Locality scale

One of the quasi-Poisson models for phorid species richness at the locality scale explained 23% of the variation and contained only the number of ant species as the explanatory variable. For this model, an increase in one ant species resulted in a 1.14 increase in the odds of collecting one phorid species (Table 2, Model 1). Model 2 explained 53% of the variation and included ant abundance as a host variable instead of ant richness (Table 2). Each increase of 1500 ants foraging in the locality per minute (e.g. estimated mean number of ants foraging per minute in each locality was 1425, SD = 1014) increased the odds of collecting a new phorid species by 1.08. When ant abundance was in the model, ant species richness was not significant, and a log-likelihood test showed that ant

Table 2 Quasi-Poisson regression models for rarefied species richness of phorid parasitoids of leaf-cutting ants at the hectare scale (deviance = 9.04, dispersion parameter = 0.25, d.f. = 39) and at the locality scale (Model 1: deviance = 4.80, dispersion parameter = 0.48, d.f. = 10; Model 2: deviance = 2.91, dispersion parameter = 0.28, d.f. = 10).

	Parameter	Standardized coefficient	Coefficient ± SE	Odds	*z*-value	*P*
Hectare scale	Intercept		0.007 ± 0.118		0.063	0.95
	Ant richness	0.17	0.148 ± 0.052	1.157	2.822	< 0.01
	Ant abundance*	0.12	0.004 ± 0.002	1.004	1.791	0.08
Locality scale						
Model 1	Intercept		0.42 ± 0.26		1.58	0.14
	Ant richness		0.13 ± 0.06	1.14	2.16	0.05
Model 2	Intercept		0.543 ± 0.144		3.78	0.003
	Ant abundance*		0.005 ± 0.001	1.005	3.91	0.003

*Represents 100 ants foraging per minute (see Materials and Methods).

species richness was not necessary to the model. Environmental variables were not significant once host variables were in the models.

Phorid species responses to host and climatic variables

The CCA analyses generated an ordination of phorid species that was consistent, in general, among the spatial scales. Partial CCA analyses, in addition to separating the effect of host or environmental variables on phorid species ordination, allowed us to determine the response of phorid species to environmental variables alone, once the effects of host variables were included in the analysis.

Nest scale

Variables related to temperature (mean temperature), relative humidity (RH; its mean and amplitude) and host availability for phorids explained 28.7% of the variation among phorid species ($P < 0.01$). The first three axes of the biplot accounted for 47%, 24.7% and 17.4% of the explained variance, respectively (Fig. 2a). The variation explained in phorid species ordination of partial CCA by climatic variables (constrained variation) was 9.6%, while the variation explained by host availability (conditioned variation) was 19% ($P < 0.01$; Fig. 2b).

At the nest scale we found that some phorid species were associated with gradients in mean and amplitude of relative humidity, mean temperature, and light intensity, with *Myrmosicarius longipalpis* and *Apocephalus penicillatus* in the wettest, coolest and darkest conditions, while *Myrmosicarius cristobalensis*, *Apocephalus necdivergens* and *Eibesfeldtphora cumsaltensis* occurred in the driest and hottest conditions. *Eibesfeldtphora trilobata*, *Myrmosicarius crudelis* and *Myrmosicarius gonzalezae* were associated with humid conditions and intermediate temperatures, whereas *Myrmosicarius catharinensis* and *Apocephalus setitarsus* were associated with hot but less humid conditions, and with high light intensity. Appendix S2 shows for each phorid species the values for the most important variables recorded at the nest scale when parasitoids were ovipositing.

Hectare scale

The CCA explained 42% of the variation in phorid species ($P < 0.01$) and included variables related to climate (mean temperature, mean and minimum relative humidity), habitat type and host-related variables (the presence of *Atta* and ant richness). The first three axes of the biplot accounted for 39.5%, 25.3% and 15.1%, respectively, of the variance explained by the CCA (Fig. 2c). Partial CCA with host-related variables as covariates showed that 19.6% of the variance was explained by climatic variables (constrained variation) and 22.6% by the host variables (conditioned variation). There was a temperature and relative humidity gradient in the biplot of the partial CCA (Fig. 2d), and in general the results were similar to those found at the nest scale. However, *Apocephalus setitarsus* and *M. crudelis* changed their relative positions along the gradient. Some species were associated with specific habitat types, with *M. catharinensis* in grasslands and *M. longipalpis*, *Apocephalus penicillatus*, *M. crudelis* and *E. cumsaltensis* primarily in forest.

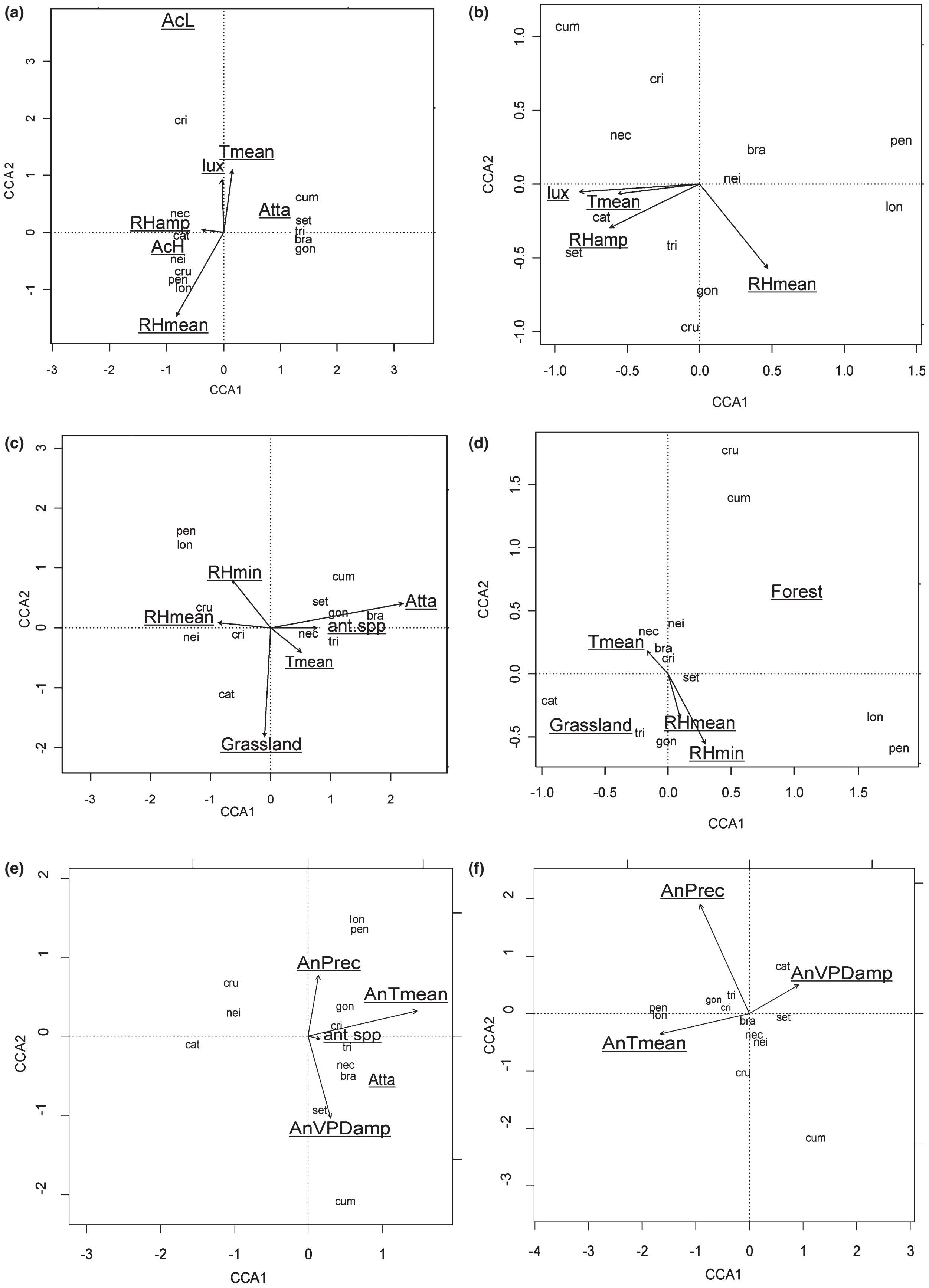
Locality scale

The ordination with historical climatic variables, i.e. annual mean precipitation, amplitude in vapour pressure deficit and mean temperature, plus host-related variables such as richness and the presence of *Atta* explained 66.3% of the variation in phorid species ordination ($P = 0.01$). The first three axes of the biplot accounted for 39.4%, 29% and 16%, respectively, of the variance explained (Fig. 2e). Partial CCA (Fig. 2f) showed that host and climatic variables accounted for 29% and 37%, respectively, of the variation in species ordination. There was a mean annual temperature gradient in phorid species, with *M. longipalpis* and *Apocephalus penicillatus* in the hottest and *M. catharinensis* in the coolest extremes. The amplitude of the vapour pressure deficit generated the opposite gradient. Annual mean precipitation showed that *E. cumsaltensis* was associated with localities with lower mean precipitation (Fig. 2f).

DISCUSSION

As predicted, we found a positive relationship between host and parasitoid richness. This correlation was tested at the locality scale, for which our regression models indicated that host richness and host abundance were determinants of parasitoid richness. We found similar results at the hectare scale. Although we were not able to test the same at the nest scale, a logistic regression for the presence–absence of phorids over host nests showed the importance of host abundance in increasing the odds of finding phorids (Elizalde, 2009). Overall, these results showed that among the variables that are probably related to phorid speciation, host variables seem more important than climate. This result is not surprising, as endoparasitoids require for their existence the presence of an appropriate host. However, this does not mean that climatic variables are unimportant for phorids. In fact, it is reasonable to speculate that phorids are limited in their spread, and therefore their geographic range, by climate (Folgarait *et al.*, 2005), as suggested by the greater contributions of climatic than host variables in the partial CCA at the locality scale.

With our data we cannot ascertain conclusively the mechanism that generated the observed phorid richness. However, in all cases, ant abundance was very important. It should be noted that ant nest density per se did not explain phorid richness, but the composite variable of ant abundance did. This is because *Atta* nests are huge constructions with millions of workers, but with low density. On the other side, this genus represents a fixed resource in space (they are territorial and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move their nest with very low frequency, if at all, during the life of the colony) and time (a colony can live for several years), increasing its reliability as hosts. Therefore, the resource availability hypothesis can account for phorid richness. It is necessary to highlight, however, that there were ant species that contributed disproportionately more to host abundance (such as *Atta* species or *Acromyrmex* classified in the group with big nests) in a hectare or locality, providing a link between host species identity and our host abundance measure. Kelly & Southwood (1999) found a positive relationship between consumer species richness and resource availability when focusing on groups of herbivore insects that were a mixture of generalists and specialists. They explained this by suggesting that insects have higher probabilities of finding abundant resources. For phorids, patches with high numbers of ants should be more attractive to ovipositing females, assuming they can find their host at a distance (Morrison & King, 2004). Thus, abundant hosts can support more generalist parasitoids as they are more easily found. In addition, an abundant host would also support more species of specialist parasitoids because the risk of extinction of those populations tends to be lower. All of these mechanisms could favour specialization on the abundant host species, and speciation of the phorids. In general, it seems that ant abundance is important with respect to broad patterns as there are few phorid parasitoid species associated with ants with relatively small colonies, and most are associated with ants having large colonies (Disney, 1994), such as *Atta* and *Acromyrmex* species. In fact, we found *Trachymyrmex* ants in 47% of the localities we sampled but we never found phorids associated with them, even when their nest density was very high (L.E. & P.J.F. unpublished results); this genus is intermediate in colony size and morphology between the inferior Attini and the leaf-cutting ants (Hölldobler & Wilson, 1990).

Although we did not evaluate the flip side of the relationship, i.e. the possibility that phorid parasitoids are influencing host richness, via top-down processes, it seems unlikely in this system. One top-down process would be a reduction in the number of host species through the elimination of certain species in an area because of high parasite pressure. However, the few studies of parasitism rates of leaf-cutting ant phorids reported very low percentages (Tonhasca, 1996; < 3% for phorids attacking leaf-cutting ants, Bragança & Medeiros, 2006). The other negative effects that these phorids exert over their hosts are a reduction in the foraging activity and load dropping (Tonhasca, 1996; Bragança *et al.*, 1998). Although the consequences of those negative effects for ant colony fitness have never been evaluated, we suspect that this apparently low negative impact, due probably in part to the low abundance of phorids in the field and the low frequency of nests with parasitoids (L.E. & P.J.F., in prep.), cannot exert enough pressure to exclude an ant species. The other possible mechanism is an arms-race type of coevolution, where a host species speciates as a consequence of the negative effect of the phorid, and then the parasitoid speciates in turn. However, as host ants have to defend themselves from several phorid species it is difficult to see how they could specialize or evolve a specific defence for each phorid species. This argument is the base of the asymmetry hypothesis, postulated for other parasitoids (Lapchin & Guillemaud, 2005).

Multivariate analyses helped us to understand why we did not find a strong relationship of phorid species with climatic variables in regression models: even considering a climatic gradient of 1800 km, most phorid species did not show a particular distribution related to the variation in climate considered, and were found at intermediate conditions, in the centre of the biplot. However, we could identify some species that were associated with particular climatic conditions. For example, *M. longipalpis* and *Apocephalus penicillatus* were found in humid and relatively cool environments, associated with the shadow of the trees of the forest (nest and hectare scales) although in hot localities (locality scale). *Eibesfeldtphora cumsaltensis* was found in drier and hotter forests, characteristic of the Dry Chaco. At the other extreme, *M. catharinensis* was found in grassland habitats characteristics of the Pampeana province, where it was exposed to greater changes in humidity. Folgarait *et al.* (2005), in a study of the geographical distribution of fire ant phorids with a similar extent to our transect (*c.* 2300 km), found that phorid species responded to climate such that it was possible to identify well-defined groups. In that work, however, the effect of host was not considered simultaneously in the CCA analyses. In the leaf-cutting ant–phorid system the effects of host-related variables were stronger overall than climate in accounting for the different response between phorid species, except at the locality scale.

Our results are encouraging from two perspectives. First, this system may be useful in future phylogenetic studies of coevolution, given the links between host-related variables and phorid richness in our data. Second, from an applied perspective, these parasitoids are potential candidates for the biological control of leaf-cutting ants, which are major pests in the Neotropics. Their dependence on hosts and relative independence from climate should favour the establishment of these parasitoids in very different environments. Although we presumed that phorids did not influence ant species richness, augmentative biocontrol programmes using phorids, in which very high numbers of parasitoids are released (as

Figure 2 Biplots from canonical correspondence analyses (CCA) for phorid species parasitoids of leaf-cutting ants using host and environmental variables in the explanatory matrices: (a, b) at the host's nest scale (a, CCA; b, partial CCA); (c, d) at the hectare scale (c, CCA; d, partial CCA); (e, f) at the locality scale with historical climatic variables (e, CCA; f, partial CCA). Variable abbreviations are defined in Table 1. Phorid species codes are: bra = *Myrmosicarius brandaoi*, cat = *M. catharinensis*, cri = *M. cristobalensis*, cru = *M. crudelis*, cum = *Eibesfeldtphora cumsaltensis*, gon = *M. gonzalezae*, lon = *M. longipalpis*, nec = *Apocephalus necdivergens*, nei = *A. neivai*, pen = *A. penicillatus*, set = *A. setitarsus*, tri = *E. trilobata*.

opposed to their low abundance in their natural environments), may be a promising alternative for the control leaf-cutting ant populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Phorid species and their leaf-cutting ant host species collected at each locality.

Appendix S2 Mean values and standard deviations of the most important variables registered at the nest scale when parasitoids were ovipositing.

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