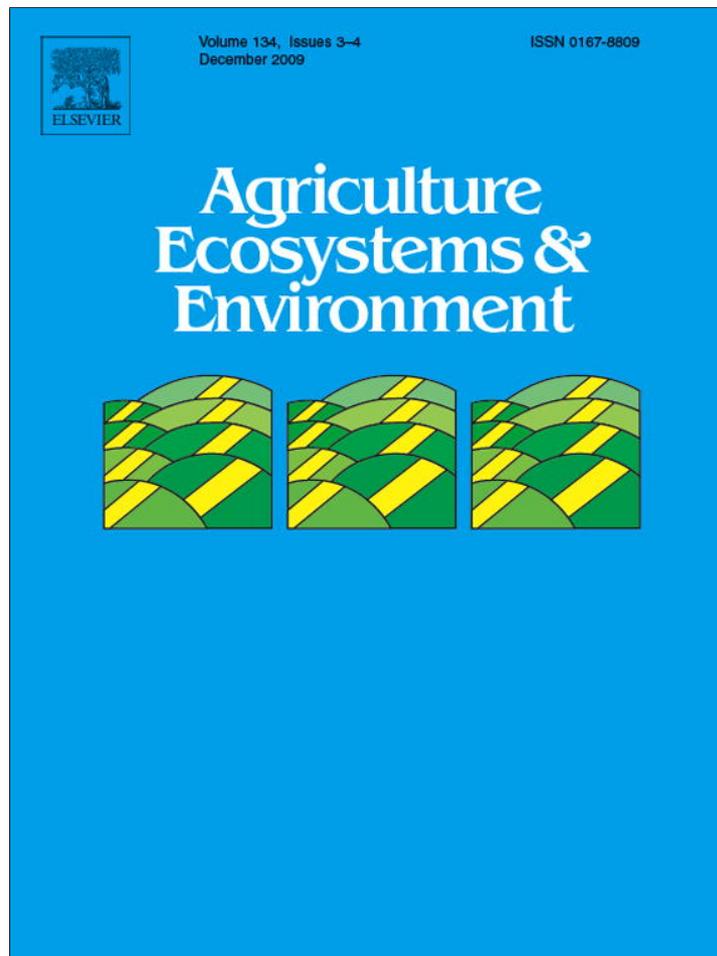


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Landscape and community drivers of herbivore parasitism in Northwest Argentina

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ABSTRACT

Small-scale variables likely influence parasitism more than variables operating at larger scales, because parasitoids respond directly to herbivores. To test this prediction, plants, herbivores, and parasitoids were collected and identified, and parasitism was estimated in 11 forest fragments and two continuous forests along a precipitation gradient in Northwest Argentina. Most herbivore and parasitoid morphospecies were site and diet specialists, collected from only one site and one host species, respectively. Parasitism ranged from 12.5% to 34.6% in the 11 forest fragments and two continuous forests. Forest size and the combination of forest size and % bean cover in the matrix explained 37.5% and 42.1% of the variation in parasitism, respectively. Parasitism was negatively related to forest size and positively related to % bean cover in the matrix. The proportion of generalist parasitoids significantly decreased with an increase in fragment size and this corresponded with a decrease in parasitism.

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1. Introduction

Most studies on parasitism have shown that landscape, community, and species characteristics are more important in determining parasitism rates than larger scale factors such as climate (Hawkins, 1994; Sumerford et al., 2000; Thies et al., 2005; but see Stireman et al., 2005). At the landscape scale parasitism increases with natural habitat area (Kruess and Tscharntke, 2000; Tscharntke et al., 2002) and matrix heterogeneity (Marino and Landis, 1996; Cappuccino et al., 1998; Altieri, 1999; Roland, 2000; Kruess, 2003; Schmidt et al., 2004), and decreases with natural habitat isolation (Kruess and Tscharntke, 1994, 2000). At smaller scales, the response of parasitism to community and species characteristics is highly variable. Simultaneously analyzing the effects of variables at large (e.g. climate), intermediate (e.g. landscape characteristics), and small (e.g. community characteristics) spatial scales is important for identifying the functional scale of parasitism and for improving our understanding of patterns and rates of parasitism in natural and agro-ecosystems.

Climate, landscape characteristics, and community characteristics affect plant–herbivore–parasitoid communities in a hierarchical manner. Climatic variables such as precipitation directly

affects plant communities (Delcourt and Delcourt, 1992; Holling, 1992), landscape attributes affect all three communities (Kruess, 2003), and community characteristics mostly affect herbivore and parasitoid communities (Stireman and Singer, 2003). Because parasitoid richness and abundance are mostly affected by community characteristics, an associated function such as parasitism will be more strongly affected by community characteristics than by landscape characteristics or precipitation. Specifically, our predictions are: (1) parasitism will not be related to precipitation, (2) parasitism will increase with forest fragment size and matrix structural complexity because both conditions enhance parasitoid diversity and abundance, and (3) parasitism will increase with herbivore and parasitoid richness and abundance. To test these predictions plants, herbivores, and parasitoids were collected and identified, and parasitism was estimated in 11 forest fragments and two reference forests along a precipitation gradient in Northwest Argentina.

2. Materials and methods

The study was conducted in the province of Salta, northwestern Argentina, between 22° and 23°S. The sites were located in a transition area between the Premontane Yungas, a humid subtropical montane forest, and the semi-arid Chaco, a dry thorn forest (Cabrera, 1976). During the last 20 years, large areas of forest in the transition Yungas–Chaco were replaced by soybean, white bean, sugar cane, and citrus plantations (Grau et al., 2005). This change in land cover has led to a heterogeneous landscape

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Table 1

Average annual precipitation, landscape characteristics, and herbivore and parasitoid characteristics for each site in Salta, Argentina. Precipitation (mm) is the mean annual precipitation from 1934 to 1990 (Bianchi, personnel communication). Distance (m): minimal distance between each site and the closest forest (>20 ha). Matrix is described in terms of % bean (soybean and white bean), citrus, and forest (secondary and primary forest) cover within an 8 km buffer around each fragment. Sites 5R and 11R are reference sites.

Site	Precipitation (mm)	Size (ha)	Distance (m)	Bean (%)	Citrus (%)	Forest (%)	Herbivore abundance	Herbivore richness	Parasitoid abundance	Parasitoid richness
1	610	26	750	68.5	2.8	18.4	94	26	17	10
2	610	188	1,027	70.9	3.6	17.1	122	24	12	10
3	626	22	1,026	66.4	2.3	21.1	120	31	15	8
4	640	44	2,021	67.5	1	25.5	93	26	15	10
5R	640	10,000	0	10.7	0	89.3	103	23	5	4
6	688	167	1,000	72.6	0	27.4	203	34	23	14
7	698	176	264	48.6	0	51.4	120	31	15	9
8	710	624	708	66.8	0.4	32.8	74	27	12	7
9	722	86	84	46.3	0	53.7	178	34	17	10
10	723	860	90	53.7	0	46.3	93	27	6	6
11R	788	4,359	365	28.1	2.1	61.6	212	46	26	15
12	886	119	607	45.6	11.1	41	113	38	16	11
13	929	180	50	41.9	6	51.5	135	21	24	14

composed of forest patches of different sizes and degrees of isolation, embedded in an agricultural matrix.

Eleven forest fragments and two sites of continuous forest (hereafter, reference sites) were selected using Landsat 5 TM images from 2001 and field observations. Precipitation in the sites ranged from 610 mm per year in the northeast to 929 mm in the southwest (Table 1). Sites ranged from 22 to more than 10,000 ha, and they were embedded in matrices of different composition. Matrix composition was described in terms of the % cover of bean crops (soybean and white bean) (low structural complexity), citrus plantations, and forest (high structural complexity) within 1-, 2-, 8-, and 16-km wide buffers around each site (ENVI 3.4, Research Systems, 2000). The buffers had the same shape as the sites perimeters.

2.1. Herbivore and parasitoid sampling

Herbivores were sampled three times per site ($n = 13$) at 11 d interval beginning with the rainy season (October to late November 2002). On each occasion, two persons walked for 4 h (total search time = 312 h) at least 200 m away from the forest edge in search of larval herbivores in the foliage up to 2 m. Up to ten individuals were collected per herbivore species and site. Lepidopterans, Dipterans, and Coleopterans were counted and assigned to morphospecies in the field. All collected individuals were subsequently reared to adults in Petri dishes lined with plaster to regulate humidity in the laboratory, larvae being fed their host plant until pupation. All adults obtained were preserved in 70% alcohol and identified to morphospecies following Borrer et al. (1989), Goulet and Huber (1993), Sbordoni and Forestiero (1998), Stehr et al. (1991). Host plants were identified to species following Digilio and Legname (1966) and Legname (1982) and with the help of local experts.

Parasitoid species richness was defined as the total number of parasitoid morphospecies per site. Parasitoid abundance was measured as total number of individuals reared from herbivores in the laboratory plus the number of individuals potentially emerging from the uncollected herbivores in the field, as determined by the proportion of herbivores parasitized in the laboratory. Parasitism was defined as the proportion of parasitized herbivores collected in a site, excluding herbivores that died from causes other than parasitism (e.g. fungi) (~35% mortality for other causes).

2.2. Data analyses

Best subset regression analyses (Statistix 7.0) were performed to examine the variables that best explained the

relationship between parasitism and climate, landscape, and community variables. The criteria for selecting the best subsets were the adjusted R^2 , and Mallows' Cp statistic, which should be less than or equal to the number of variables in the model (Azen et al., 2001). A correlation matrix among all the environmental variables was used to eliminate highly inter-correlated variables. After eliminating these variables, the independent variables included in the analysis were: average annual precipitation, forest size, distance from each site to the closest forest (>20 ha), % bean, citrus, and forest cover at 8 km around each site, plant richness, herbivore and parasitoid richness and abundance, and proportion of generalist parasitoids. Percent forest cover at 8 km around each site was correlated with % bean cover at 8 km around each site and with forest size, but all three variables were kept in the model because they have different biological effects on parasitoids.

To analyze the response of parasitism to matrix composition at different scales, simple linear regressions were calculated between % parasitism and % cover of citrus, bean and forest for four nested spatial scales: 1, 2, 8, and 16 km around each site. The coefficient of determination (R^2) of each regression was then plotted at the four scales to analyze the strength of the dependence on spatial scale. All data for both subset and simple linear regressions were rank-transformed to correct for non-normality (Conover and Iman, 1981).

To determine if the differences in the number of herbivores collected among sites (74–212) influenced the estimation of parasitism, a bootstrap analysis was run. In this analysis, herbivores were re-sampled using the minimum number of individuals as the sample size (i.e., $n = 52$ in site 8, excluding individuals dying for causes other than parasitism). This process was repeated 50 times. The mean and standard deviation of the 50 bootstrap estimates were compared with the actual measures of parasitism. All the observed values of parasitism fell within the range of mean values generated by the bootstrap analysis, indicating that there was no effect of sample size on parasitism.

3. Results

On total 1660 herbivores of 186 Lepidoptera, four Diptera, and one Coleoptera morphospecies were collected from 132 host plant species within the 13 sites. From these herbivores, 215 Hymenoptera, eight Diptera, and one Nematoda were reared and identified to 62 morphospecies.

One hundred and twenty seven herbivore morphospecies were collected from only one site (site specialists), 48 morphospecies were collected from two to four sites, and three

Table 2

Regression models showing the three subsets that best explained parasitism (%) with one and two independent variables. Independent variables are: (a) forest size (ha), (b) herbivore richness, and (c) forest cover (%), (d) bean cover (%), and (e) distance to closest forest (m). Adjusted R squares with * are significant according to the Mallows's C_p statistic.

Independent variables	Adjusted R square	R square	Residual SS
<i>a</i>	0.37*	0.43	104.192
<i>b</i>	0.33	0.39	111.761
<i>c</i>	0.25	0.31	124.835
<i>d + a</i>	0.42*	0.51	87.7157
<i>d + b</i>	0.39	0.49	92.3205
<i>a + e</i>	0.39	0.49	92.4779

morphospecies were collected from more than 10 sites (site generalists). No herbivore morphospecies was present in all sites. Similarly, most parasitoid species (31) were present in only one site (site specialists), 23 morphospecies were present in two or three sites, and three morphospecies were present in more than eight sites (site generalists). Only Bra1 was collected from 12 sites, and no morphospecies was present in all sites.

Most herbivores (122 morphospecies) were collected from only one plant species (diet specialists), 64 herbivores were collected from 2 to 23 plant species (diet generalists), and only one herbivore morphospecies was collected from 27 plant species. Similarly, most parasitoid morphospecies (24) were reared from only one herbivore morphospecies, 17 parasitoids were reared from 2 to 7 herbivore morphospecies, and two were reared from 11 and 10 herbivore morphospecies, respectively.

Parasitism ranged from 14.3% to 34.6% (median 23.0%) in the 11 forest fragments and reached 12.5% and 18.3% in the two reference sites, respectively. Forest size explained 37.5% of the variation in parasitism, and the combination of forest size and % bean cover explained 42.1% (Table 2). Parasitism was negatively related to forest size (Fig. 1a). In small fragments (22–200 ha) parasitism ranged from 19.5% to 34.6% and it was lowest (12.5%) in the largest site. In contrast, parasitism increased with % bean cover (Fig. 1b). Parasitism was lowest (12.5%) in sites surrounded by 10.7% bean cover and it increased to 21.3–28.1% in sites surrounded by more than 60% bean cover. Precipitation did not directly explain variation in parasitism.

The proportion of generalist parasitoids significantly decreased with increasing fragment size ($R^2 = 0.45$, $p = 0.011$, $n = 13$) (Fig. 2a). The proportion ranged from 0.60 to 0.95 in sites smaller than 200 ha, and declined to 0.46–0.86 in sites greater than 600 ha. In the largest site, 0.50 of the parasitoids were generalists. The relationship between the proportion of generalists and bean cover in the matrix was not significant ($R^2 = 0.17$, $p = 0.16$, $n = 13$) (Fig. 2b). When the two reference sites were removed, there was still a negative effect of fragment size on the proportion of generalist parasitoids ($R^2 = 0.40$, $p = 0.038$, $n = 11$), and the effect of bean cover remained non-significant ($R^2 = 0.07$, $p = 0.43$, $n = 11$).

The strength of the relationship between % parasitism and matrix composition was scale-dependent (Fig. 3). For bean and forest cover, the relationship between parasitism and % land cover was strongest at 1 km around each site ($R^2 = 0.50$ and $R^2 = 0.45$, respectively) and then it decreased. The relationship was positive in all cases, except for forest cover at all scales and bean cover at 16 km, and it was significant from 1 to 8 km around each site. The coefficient of determination (R^2) was higher for bean cover than for forest cover at all scales, except at 8 km, where both values were similar. For citrus cover, the relationship was strongest at 2 km around each site, but the relationship was not significant.

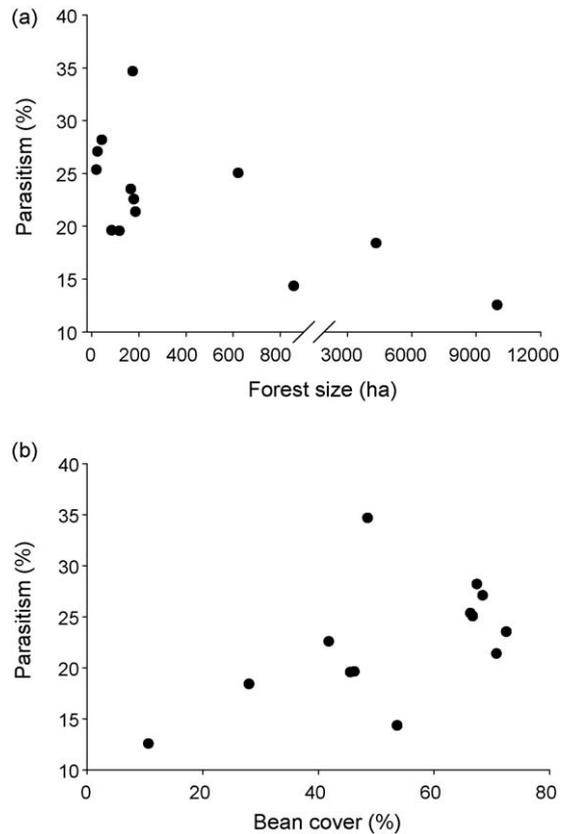


Fig. 1. Relationships between parasitism (%) and (a) forest size (ha), and (b) % bean cover within an 8-km buffer around each site in Salta, Argentina.

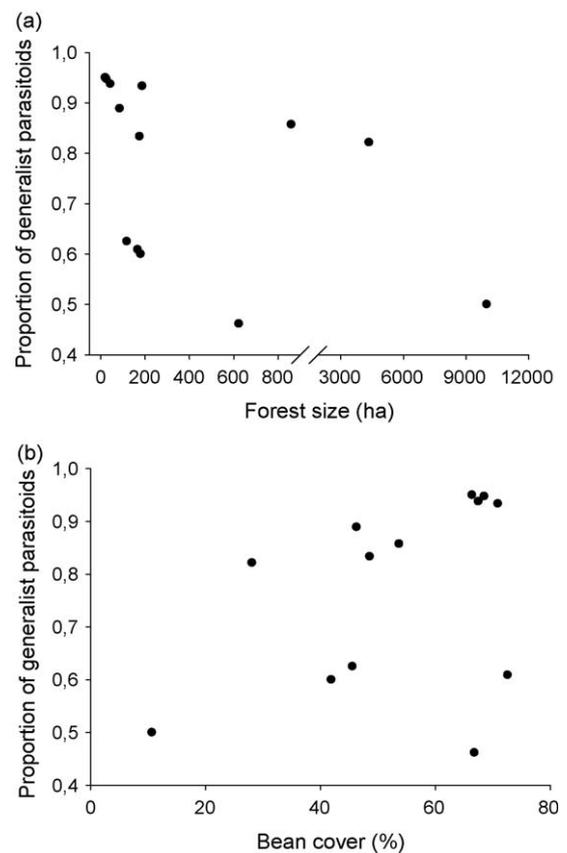


Fig. 2. Relationships between the proportion of generalist parasitoids and (a) forest size (ha), and (b) % bean cover within an 8-km buffer around each site.

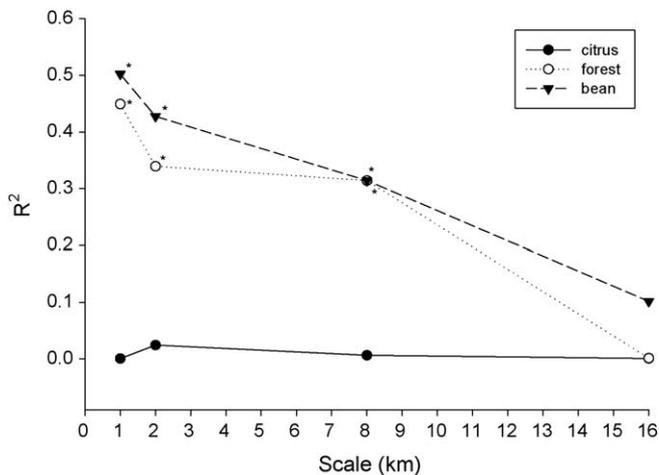


Fig. 3. Coefficients of determination (R^2) from simple linear regressions between % parasitism and % bean, forest, and citrus cover within buffers of 1, 2, 8, and 16 km around each site. The * indicate significant ($p < 0.05$) relationships.

4. Discussion

Contrary to our predictions, parasitism decreased with increasing forest size and matrix structural complexity. Parasitism was highest in small fragments surrounded by a matrix dominated by bean fields. In natural stands, higher parasitism rates in small and isolated fragments were attributed to alternative hosts or food sources in nearby habitats, larger size of host plant patches and lower parasitoid mortality within fragments (Cappuccino et al., 1998; Doak, 2000). In other studies lower parasitism in small and isolated sites were attributed to lower parasitoid diversity and abundance (trophic-level hypothesis of island biogeography), high extinction of parasitoids, lower fragment quality, and lower number of specialist parasitoids (Kruess and Tscharntke, 1994, 2000; Marino and Landis, 1996; Tscharntke et al., 2002).

A decrease in specialist parasitoid populations and an increase in generalist populations have resulted in higher parasitism in small fragments. In other area of the Chaco, Salvo et al. (2005) found similar results, where values of parasitism were higher in cultivated than in natural environments and this was attributed to higher host abundances which favored generalist parasitoids. Previous studies have suggested that specialists suffer greater population decrease in small fragments, probably because the fragments do not provide the minimum area required for them, which Kruess and Tscharntke (2000) found to be one order of magnitude greater than for herbivores. In addition, most specialists are probably unable to re-colonize isolated fragments due to their low dispersal abilities, in comparison with generalists, which usually have high dispersal abilities (Tscharntke et al., 2002, and references therein). Our analysis of the effect of bean cover on parasitoids supports this idea because the proportion of generalist parasitoids in the sites showed a close, positive relationship with bean cover at three spatial scales (1, 2, and 8 km), while the proportion of specialist parasitoids was less influenced by bean cover in the matrix and the relationship was negative (results not shown). These results suggest that generalists are able to disperse across the bean fields and re-colonize forest fragments or they can establish in the agricultural fields and colonize the fragments from there. In contrast, specialists are more prone to extinction in the fragments because there is no rescue effect from nearby populations (van Nouhuys and Tay, 2001) or there are no suitable hosts in the agricultural fields. Higher parasitism caused by generalists in small and isolated fragments may also result from a behavioral change. Parasitoids foraging behavior may be close to

the optimum when travel time is short (Cronin and Strong, 1999; Doak, 2000). While specialists are forced to travel for the suitable host, generalists can invest more time foraging, given the greater diversity of suitable hosts, with a consequent increase of parasitism in those fragments. These results add value to forest fragments embedded in agro-ecosystems given they act as reservoirs of generalist parasitoids that provide biological control services to surrounding crops (Landis et al., 2000).

The effect of matrix composition on parasitoid communities and patterns of parasitism was scale-dependent. Bean cover and forest cover were significantly related to % parasitism at 1–8 km around the sites. This result contrasts with other studies conducted in temperate environments, where significant effects of matrix on parasitism patterns were found up to 1.5 km around fragments of natural habitats (Kruess, 2003). This comparison becomes important when designing pest management strategies at the landscape scale (Altieri, 1999; Bianchi et al., 2006). Many studies conducted in temperate systems have concluded that fragmentation of natural habitats may favor herbivore outbreaks because herbivores are released from parasitism, as parasitoids go extinct in small and isolated fragments (Kruess and Tscharntke, 1994; Tscharntke and Brandl, 2004). Our results in a subtropical system suggest that in some circumstances forest fragmentation can increase parasitism.

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