



Effects of vegetation structure and landscape complexity on insect parasitism across an agricultural frontier in Argentina

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Received 21 September 2017; received in revised form 29 March 2018; accepted 7 April 2018
Available online 13 April 2018

Abstract

Insect parasitism patterns are influenced by vegetation structure and landscape complexity. Our objective was to examine the effects of vegetation structure and landscape complexity on parasitism based on direct measurements of structure and diversity indices as well as on metrics based on remote sensing using Quickbird images. We collected 2266 lepidopteran larvae and pupae, including different families and habits, to estimate parasitism, and recorded vegetation characteristics in five 100-m² transects and 18 1 ha-plots in the dry Chaco, Northwest Argentina. We calculated landscape metrics and semivariograms in the plots from the image. The plots represented four “complexity groups”: agricultural, riparian/hedgerow, bare ground, and forest plots. Mean parasitism in the study sites was 10.7% (min: 0%, max: 23%). Parasitism was highest in agricultural plots, lowest in forest plots, and intermediate in riparian/hedgerow and bare ground plots. The landscape model explained parasitism more than the vegetation model. The landscape final model included Normalized Difference Vegetation Index (NDVI) Range, a measure of landscape heterogeneity, and Mean Shape Index, a measure of patch shape irregularity, and their interaction. The vegetation model included basal area and the Coefficient of Variation of tree density among transects, a measure of tree spatial distribution within a plot. Our results agree with previous studies that found higher parasitism in agricultural vs. non-agricultural environments in the subtropics, while riparian/hedgerow plots were important for conserving parasitism, as reported for temperate environments. We showed that under-explored tools such as the semivariogram and satellite band combinations were useful for the assessment of parasitism and that studying vegetation and landscape complexity simultaneously can help us examine mechanisms in detail. The identified variables related to high parasitism should be used for image classifications with a functional approach.

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Keywords: Biocontrol; Chaco; NDVI; Parasitism; QuickBird; Semivariogram

Introduction

The current human- and climate-driven changes of landscapes are affecting biodiversity patterns and associated

ecological processes at all scales (MacDougall, McCann, Gellner, & Turkington 2013; Hautier et al. 2015). One key ecological process in natural and human-dominated ecosystems is insect parasitism (Godfray 1994; Hawkins 1994; Bianchi, Booij, & Tscharntke 2006). Insect parasitism by wasps (Hymenoptera) and flies (Diptera) is responsible for the control of herbivory in most terrestrial ecosystems. Both

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in human-dominated and in natural ecosystems levels of parasitism can occasionally be as high as 80% (e.g., Roland 2000; Bianchi, Goedhart, & Baveco 2008; Rusch, Valantin-Morison, Roger-Estrade, & Sarthou 2012) with an evident impact on ecological processes and on the economy of agricultural practices. It has been shown, though, that top-down control can be highly variable in space and time (Gripenberg & Roslin 2007), and that in general top-down control is stronger in human-dominated than in natural ecosystems (Chaplin-Kramer, O'Rourke, Blitzer, & Kremen 2011). Then, understanding which factors increase percent parasitism at landscape scales in both human-dominated and natural ecosystems has been a fundamental question (Marino & Landis 2000; Tschamtkke et al. 2007; Tschamtkke et al. 2012).

The multiple processes that drive parasitism operate at different spatial scales. Two key variables influencing parasitism are vegetation structure and landscape complexity (Roland, Taylor, & Cooke 1997; Kruess 2003; Thies, Steffan-Dewenter, & Tschamtkke 2003; Jakel & Roth 2004; Cronin & Reeve 2005; Bianchi et al. 2006; Chaplin-Kramer et al. 2011). For example, at the scale of an individual plant, high architectural heterogeneity can cause a decrease in parasitism rates of herbivores due to interference with the female parasitoid oviposition behavior (Gingras, Dutilleul, & Boivin 2002). At the scale of a plot, plant diversification within crops enhances parasitism by different mechanisms such as interference on herbivore movements, among others (Letourneau et al. 2011; Rusch, Bommarco, Jonsson, Smith, & Ekbom 2013). At the landscape scale parasitism increases with increasing matrix heterogeneity around the agricultural fields (i.e., landscape composition; Monmany & Aide 2009; Chaplin-Kramer et al. 2011). In relation to landscape configuration, parasitism increases with natural habitat area (Kruess & Tschamtkke 2000a,b; Tschamtkke, Steffan-Dewenter, Kruess, & Thies 2002), and decreases with increasing natural habitat isolation (Kruess & Tschamtkke 2000a,b; Schuepp, Herrmann, Herzog, & Schmidt-Entling 2011).

A growing number of studies take advantage of satellite image information to quantify the effects of landscape complexity on parasitism. Most studies calculating landscape metrics based on classified images only use landscape diversity indices (e.g., Shannon or Simpson) in relation to parasitism patterns and report a weak or absent relationship between those metrics and parasitism (Gardiner et al. 2009; Jonsson et al. 2012; Rusch et al. 2012). In addition, the majority of these studies focus on temperate agricultural fields or agro-ecosystems (Chaplin-Kramer et al. 2011) and they rely on coarse land cover classifications to derive measures of landscape complexity (Veres, Petit, Conord, & Lavigne 2011). As a result of these studies we know that percent cover of semi-natural environments is a strong landscape factor enhancing parasitism and that its effect is scale-dependent (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Veres et al. 2011). Many assumptions underlie this approach in which land cover types would influence parasitoids and parasitism

by modifying insect movement, resource availability, refugia from climate, and others (Boccaccio & Petacchi 2009; Klein, Steffan-Dewenter, & Tschamtkke 2006; Tschamtkke et al. 2007). But, the description of complexity needs to be refined in order to increase our understanding of the proposed mechanisms.

To link complexity with mechanisms we first need to interpret the relationship between landscape metrics as derived from satellite images and field measurements of vegetation structure. In addition, when describing the importance of landscape complexity for parasitism, we need to evaluate metrics related to insect movement, such as patch size, patch isolation, and patch shape simultaneously with metrics related to other mechanisms, such as patch diversity. Furthermore, including complex natural environments such as subtropical forests into the analyses would help refine hypotheses, given that landscape configuration of forests contrasts with that of agricultural fields and are reservoirs for many herbivore-parasitoid species (Bianchi et al. 2008; Mailafiya, Le Ru, Kairu, Calatayud, & Dupas 2010; Rand, van Veen, & Tschamtkke 2012; González, Salvo, Defagó, & Valladares 2016). In addition, previous studies in the subtropics have shown contrasting parasitism patterns differing from temperate regions (i.e., higher parasitism in agricultural than in natural environments; Monmany & Aide 2009; Salvo, Fenoglio, & Videla 2005), suggesting differences in operating mechanisms. One difference between regions may be that large and continuous areas of forest (and hence higher complexity) can still be found in the subtropics and parasitoids use forests as refugia while ovipositing in hosts located in agricultural areas. Last, subtropical forests are distributed in many developing countries, where landscape management and conservation is the most recommended strategy of biological control given its low cost and potential sustainability (Zumoffen, Salto, & Salvo 2012). In order to design relevant strategies we need to correctly interpret the relationship between complexity and parasitism.

Our objective in this study was to examine how parasitism was related to vegetation structure as measured in the field (plot scale) and to landscape complexity as derived from a high resolution QuickBird image (landscape scale). Our questions were: what aspects of vegetation structure and landscape complexity are best related to parasitism? Is vegetation structure more important than landscape complexity to explain parasitism? In relation to vegetation structure we expected that parasitism would be more related to variables indicating vertical heterogeneity, such as DBH (diameter-at-breast-height) diversity, because these would represent microhabitats for a diverse parasitoid community (Root 1973). In relation to landscape complexity metrics we expected that parasitism would be more related to satellite bands that indicate vegetation productivity, such as the Normalized Difference Vegetation Index (NDVI) band than to bands that indicate other structures, such as the panchromatic band (e.g. Shannon Diversity Index, SDI) because herbivore-parasitoid communities strongly depend on veg-

etation (Letourneau et al. 2011; Ebeling, Klein, Weisser, & Tschardtke 2012). In addition, metrics like patch size and shape were expected to significantly influence parasitism given their relationship with plant species diversity (Moser, Zechmeister, Plutzer, Sauberer, & Grabherr 2002). We collected field data and derived landscape complexity from a QuickBird image in 18 1-ha plots located across an agricultural-forest frontier in the seasonal dry Chaco in Northwest Argentina.

Materials and methods

Study site

This study was conducted in the dry Chaco ecoregion within the Tapia–Trancas watershed located in the province of Tucumán, NW Argentina (26°50'S, 65°20'W) (Monmany, Yu, Restrepo, & Zimmerman 2015). The dry Chaco shows a continental, warm and subtropical climate with mean annual temperature of 20°C (18–23°C) and annual rainfall of 450 mm falling between October and March (Bianchi & Yañez 1992). It is characterized by subtropical xerophytic vegetation that includes spiny, small trees and shrubs, some cacti, herbs, epiphytes, and vines (Cabrera 1976; Vervoort, Legname, & Grau 1981). Dominant tree species include *Schinopsis lorentzii* (Anacardiaceae) and *Aspidosperma quebracho-blanco* (Apocynaceae), whereas dominant shrubs include *Acacia aroma*, *Acacia praecox*, *Prosopis alba*, and *Cercidium praecox* (Fabaceae) (Digilio & Legname 1966). The Tapia–Trancas watershed is a complex mosaic of forest fragments embedded in a matrix of pastures, corn, sorghum, bean, and soybean fields (Aizen & Feinsinger 1994; Monmany et al. 2015).

Subtropical dry forests in general are the habitat of many unique and threatened species. The Chaco in particular has recently been shown to disappear faster than rainforests in Latin America (Aide et al. 2013); most of the native forest is being replaced by agriculture and cattle grazing. Agricultural frontiers within the dry Chaco arise as other ecosystem edges, where particularly high species diversity and complex ecological interactions are found (Fagan, Cantrell, & Cosner 1999). The Chaco ecoregion is one of the subtropical regions in the world where relatively detailed information on parasitoid-herbivore-plant communities in natural environments exists (Valladares, Salvo, & Godfray 2001; Monmany & Aide 2009; González, Salvo, & Valladares 2015). A rough comparison shows that parasitoid (Hymenoptera and Diptera) and herbivore (Lepidoptera) communities in the Chaco have intermediate values of species richness when compared with their temperate and tropical counterparts (DeVries 1994; Salvo & Valladares 1998; Kruess & Tschardtke 2000; Rott & Godfray 2000; Lewis et al. 2002; Monmany 2004; Morris, Lewis, & Godfray 2004; Valladares, Salvo, & Cagnolo 2006; Monmany & Aide 2009). To our knowledge, no biological control programs have been implemented in the area and

this is the first study examining hosts and parasitoids at the community level.

Sampling

Landscape complexity and vegetation structure

To describe landscape complexity we used the QuickBird image (2.6 m resolution for multispectral bands and 0.55 m resolution for the panchromatic band) collected in November 2007, centered on the study site and covering an area of 10 × 10 km. The image was pre-processed and landscape metrics calculated, as described in Monmany et al. (2015). Briefly, pre-processing included pan-sharpening and atmospheric correction of the image in ENVI 4.8 (Exelis Visual Information Solutions, Boulder, Colorado), after which we calculated two common vegetation indices, the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI), both derived from combining the red and infrared image bands. NDVI is used for assessing the primary productivity in terrestrial landscapes. EVI is similar to NDVI but it reduces the effects of radiometric contaminants from the atmosphere and within a canopy (Horning, Robinson, Sterling, Turner, & Spector 2010). EVI is more sensitive to canopy structure whereas NDVI is more sensitive to chlorophyll content so these two indices tend to complement each other. We similarly used the red, the infrared, and the NDVI bands to calculate the semivariogram, $\gamma(h)$, in each plot. The semivariogram is a geostatistical tool used to describe two-dimensional complexity from satellite images (Curran 1988; Costantini et al. 2012). Semivariograms calculated from satellite images have been used mainly to characterize canopy cover (e.g., Colombo, Chica-Olmo, Abarca, & Eva 2004; Johansen & Phinn 2006) but it is not clear how they complement traditional metrics. Because the semivariogram range indicates the distance at which the maximum variance is observed (sill), both parameters are useful to describe vegetation heterogeneity (Cohen, Spies, & Bradshaw 1990). The semivariogram parameters range and sill were determined for each plot in the *gstat* package (Pebesma 2004) in *R* (R Development Core Team 2017). To fit the best semivariogram model (spherical and exponential), weighted sum of squared differences was used and 150 m was the maximum distance for semivariance calculations. Last, using the Patch Analyst module (Rempel, Kaukinen, & Carr 2012) in ArcMap 10, we calculated seven landscape-level metrics on the panchromatic band, related to the proportion area-edge, the shape and aggregation of patches, and the diversity of patch types (see Appendix A: Table 1 in Supplementary material).

Vegetation and insect samples were taken in 2009 and 2010, and field corroboration of the satellite image was made to confirm that land cover had remained equal. In the field, we selected 22 1-ha plots from a large-scale regular grid based on accessibility and land cover representation to sample vegetation structure as described in Monmany et al. (2015). The minimum distance between plots was 800 m. The plots included agricultural fields for cow food (i.e., alfalfa,

corn, and fields resting and covered with wild herbs), riparian forests, and forests with different degrees of disturbance, including highly disturbed forests with bare ground. Within each plot we established ten 2×100 m-transects (each 10 m apart) along which vegetation characteristics were measured on trees larger than 5 cm DBH every 10 m. Between any two points separated by 10 m we established an additional measuring point determined randomly; thus the total number of sampled points per transect was 20 (starting point was 0 m). At each sampling point detailed information on vegetation structure was collected within a circle measuring 2 m in diameter, from which additional variables were calculated (see Appendix A: Table 1 in Supplementary material). A total of 2683 individuals from 50 woody plant species and 21 families were inventoried. To estimate foliage height diversity we recorded 25,665 points in total.

Herbivore and parasitoid sampling

Within 20 1-ha plots we established five 1×100 -m transects (each 20 m apart) along which all visually detected exophytic Lepidoptera larvae and pupae were collected on any plant species. The collections were made on all vegetation strata between 0.50 and 1.8 m. Herbivores were sampled once in each plot and the sampling of the plots was conducted in a random order to reduce temporal effects resulting from small-scale seasonal and phenological differences. All collected individuals were taken to the lab and reared to adults in individual plastic bags with a paper towel to regulate humidity. The bags were transparent and they received a natural light regime and ambient temperature. Larvae were fed their host plant until parasitoid emergence or completion of the herbivore pupal stage. All adults obtained and the remains of parasitized herbivores were preserved in 70% alcohol. Parasitism by wasps (Hymenoptera) and flies (Diptera) was considered and all types of strategies (i.e. endo- and ectoparasitism, koinobiont and idiobiont parasitoids) were included. Parasitism was defined as total number of parasitized herbivores/total number of herbivores collected in a plot.

Data analysis

In a previous study we analyzed landscape complexity as measured from the satellite image by means of a Two-way Cluster Analysis of the plots (Monmany et al. 2015). As a result of the clustering, the plots were grouped into four ‘complexity’ groups: (1) agricultural plots; (2) riparian/hedgerow plots; (3) bare ground plots; and (4) forest plots (Fig. 2 in Monmany et al. 2015).

In this study, to determine to what degree percent parasitism was related to landscape complexity as measured from the satellite image and vegetation structure as measured in the field we made a series of analyses. First, we used an analysis of variance (ANOVA) test to compare percent parasitism in the four landscape complexity groups identified by the Two-way Cluster Analysis in Monmany et al. (2015). Linear mean comparisons among the groups were posteriorly conducted

using the function *linear.comparison* in *R* (Bennett 2012) to identify the significantly different groups.

Second, to identify the landscape and vegetation variables that contributed most to changes in percent parasitism we made linear model selections where landscape and vegetation metrics were analyzed separately. Parasitism was analyzed as the response variable and landscape and vegetation metrics were explanatory variables. Before running the models, we removed highly inter-correlated variables ($r > 0.7$); the final explanatory variables for landscape were: NDVI semivariogram sill, NDVI range, mean EVI, and the panchromatic metrics Patch Richness (PR), Shannon Diversity Index (SDI), and Mean Shape Index (MSI) (see Appendix A: Table 1 in Supplementary material). The final explanatory variables for vegetation were: coefficient of variation of tree density among transects, number of trees higher than 10 m, basal area, and foliage height diversity. These explanatory variables represented landscape configuration and composition, vegetation structure, vegetation composition, and vegetation spatial arrangement. Global models were fit for each set of variables where variables, quadratic terms, and interactions were included. Interactions were included in pairs in random order using sampling without replacement (Crawley 2007). Next, the landscape and vegetation global models with the smallest *p*-values were selected for further analyses. Using these global models, backward stepwise deletions were made until only significant variables remained in the final models. Percent parasitism was arcsin-square-root-transformed and the landscape and vegetation variables were transformed calculating $\ln(x + 1)$ to improve normality.

Results

In the field we collected 2266 lepidopteran larvae and pupae belonging to different families and including diurnal and nocturnal species. In total 10.4% of the herbivores were parasitized, with a mean of 10.7% and a minimum and maximum of 0% and 23%, respectively. Two plots where pesticides had been recently applied (D. Colombres, personal communication) during herbivore collections were excluded from all analyses.

Percent parasitism differed significantly among the landscape complexity groups ($F = 4.717$, $df = 3$, $p = 0.045$; Fig. 1). Parasitism was highest in the riparian/hedgerow plots and in the agricultural plots, lowest in the forest plots, and intermediate in the bare ground plots. The highest variance was observed in the forest plots, where parasitism ranged from 0% to more than 15%, and the maximum value of parasitism was observed in the agricultural plots (23%). The linear comparisons showed that parasitism in forest was marginally different from the other three groups ($F = 4.118$, $t = 2.029$, $p = 0.059$, $\psi = 0.129$, $\text{adj.CI} = -0.050, 0.308$).

After fitting the global model for landscape variables (see Appendix A: Table 2 in Supplementary material), we ran backward stepwise deletions and the final model for

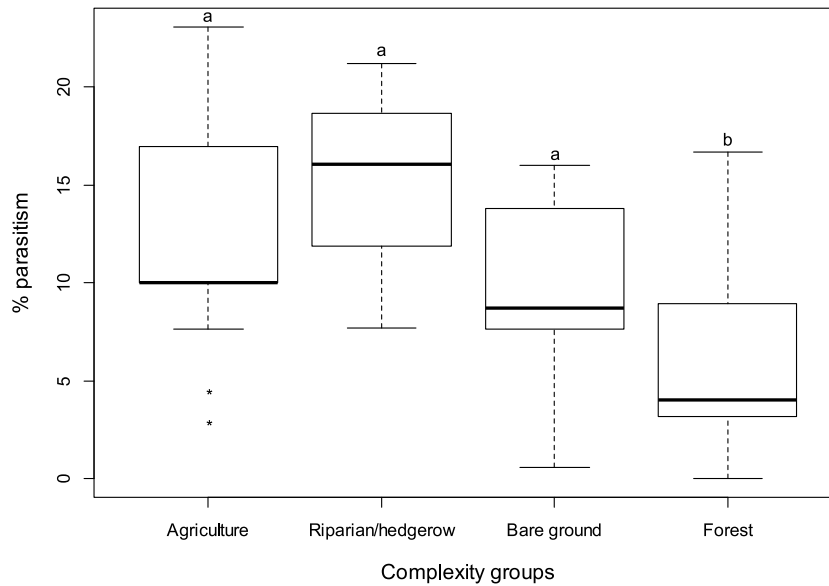


Fig. 1. Box-and-whisker plot of percent parasitism in the four landscape complexity groups. Each box shows the lower and upper quartiles, the black line within the box is the median, and the error bars are the minimum and maximum values, respectively. The two stars in the agricultural plots show the excluded values of parasitism in the two plots where pesticides had been applied.

Table 1. Coefficients resulting from backward stepwise deletions using the landscape and vegetation full models, respectively, where percent parasitism is the response variable. See Appendix A: Table 1 in Supplementary material for variable explanations.

	Estimate	Std. error	t Value	Pr(> t)
<i>Landscape</i>				
(Intercept)	−13.840	4.844	−2.857	0.0127
NDVI range	3.307	1.272	2.600	0.0210
MSI	16.414	5.792	2.834	0.0133
NDVI range × MSI	−3.822	1.521	−2.512	0.0249
<i>Vegetation</i>				
(Intercept)	0.36829	0.04919	7.486	<0.0001
Basal area	−0.14451	0.06190	−2.335	0.0339
CVdensity ²	0.16098	0.08392	1.918	0.0743

landscape was $\text{Parasitism} \sim \text{NDVI Range} + \text{MSI} + \text{NDVI Range} \times \text{MSI}$ ($\text{Adj. } R^2 = 0.5458$, $F = 7.809$, $df = 3, 14$, $p = 0.003$; Table 1). In addition, percent parasitism was fit to the global model for vegetation variables (see Appendix A: Table 2 in Supplementary material). The final model for vegetation after backward stepwise deletions was $\text{Parasitism} \sim \text{basal area} + \text{CVdensity}^2$ ($\text{Adj. } R^2 = 0.2306$, $F = 3.547$, $df = 2, 15$, $p = 0.05$; Table 1).

Percent parasitism was positively related to vegetation heterogeneity as represented by the NDVI Semivariogram Range; parasitism increased from 0% at a low value of Range to 23% at higher values of Range (Fig. 2A). Parasitism was less variable at high values of Range ($\ln(\text{NDVI Range} + 1) = 3.5$). The lowest values of NDVI Range were observed in forest plots, indicating low two-dimensional heterogeneity, and the highest values were observed in the

agricultural and riparian/hedgerow plots, indicating high two-dimensional heterogeneity in those plots. Parasitism was positively related to patch shape complexity as represented by Mean Shape Index (MSI). Increasing MSI represents increasing patch shape irregularity at the landscape level. Parasitism ranged from 0 to 8.95% at low values of MSI ($\ln(\text{MSI} + 1) = 0.82$) to 21% at higher values of MSI; the highest variability of parasitism was observed at low values of MSI (Fig. 2B). Low values of MSI were observed mainly in forest plots, indicating homogeneity in the shape of forest patches, and high values were observed in riparian and bare ground plots, indicating irregularity in the shape of these land cover patches. Parasitism was negatively related to the total tree basal area per plot (Fig. 2C). It decreased from 23% ($\text{Arcsin}(\text{SQRT}(\text{Parasitism})) = 0.501$) in plots with no trees (i.e. basal area = 0 m²/ha) to 4.02% in plots with 2.79 m²/ha ($\ln(\text{basal area} + 1) = 1.33$). The highest variability of parasitism was observed at intermediate values of basal area. Last, parasitism was positively related to the variation of tree density within plots, though the relationship was weak (Fig. 2D). Parasitism was highly variable ranging from 0% to 23% ($\text{Arcsin}(\text{SQRT}(\text{Parasitism})) = 0-0.501$) in plots with low values of CV ($\ln((\text{CV density})^2 + 1) = 0-0.05$) and slightly decreased to 21% in plots with high values of plant density CV. Low values of CV tree density corresponded to agricultural and bare ground plots.

Discussion

Percent parasitism was higher in the riparian/hedgerow and agricultural plots and lower in the forest plots across the agricultural-forest frontier in the dry Chaco. Metrics related to both vegetation structure and landscape complexity

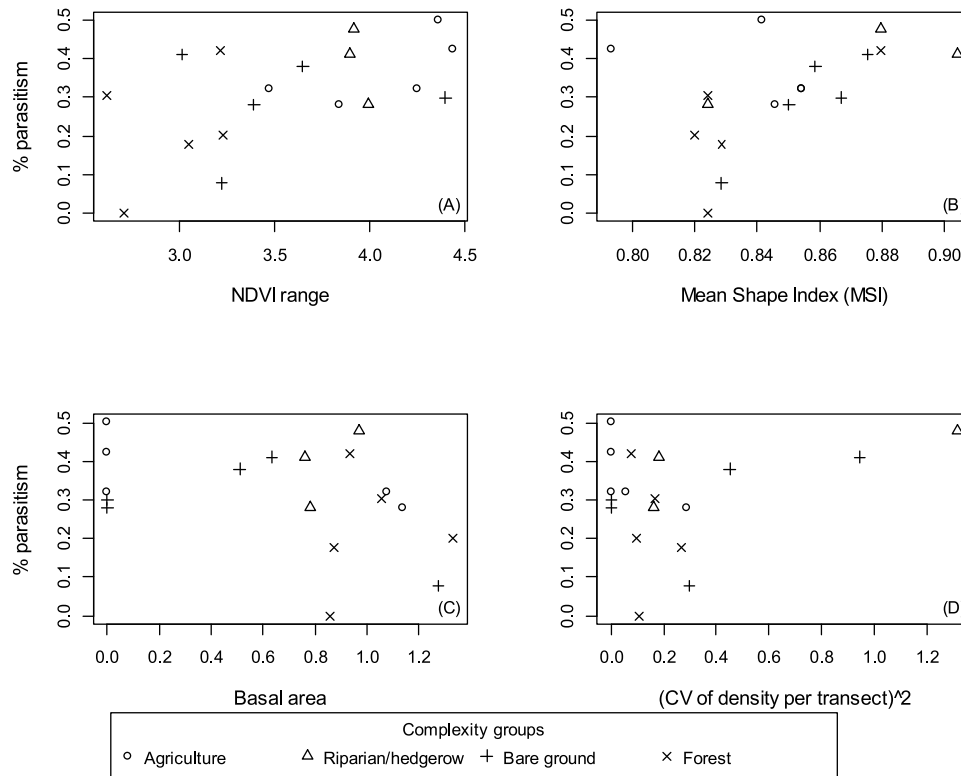


Fig. 2. Scatterplots of percent parasitism and (A) NDVI Range, (B) Mean Shape Index, (C) Basal area, and (D) (CV density among transects)², all selected by backward stepwise deletions. Percent parasitism was arcsin-square-root-transformed and the landscape and vegetation variables were transformed according to $\ln(x + 1)$. Symbols show the landscape complexity groups. Refer to Table 1 for statistical test results.

explained this pattern but the vegetation model had a lower fit than the landscape model. A few metrics were identified from a large set as key variables to determine parasitism patterns and should be included in future assessments: NDVI semivariogram Range, Mean Shape Index, the interaction between NDVI Range and Mean Shape Index and the field-collected variables basal area and CV of tree density among transects. NDVI range and MSI represent landscape two-dimensional heterogeneity, while the interaction between them represents the addition of different land covers that are at the same time more irregular in shape and more diverse in terms of plant species during the calculations of heterogeneity. Basal area is related to the total plant biomass and CV of tree density is related to the trees' spatial distribution within a plot. Both variables represent vegetation three-dimensional complexity at the scale of a plot.

Overall parasitism was low (20%) in comparison to other studies and this may be related to characteristics of our study site in particular or to climatic abnormalities that are being registered in the region, such as an increase in precipitation variability. During the sampling period lepidopteran populations showed a remarkable increase in comparison to previous years (pers. obs.) and parasitoid population may have been decoupled. Parasitism was high in the riparian/hedgerow plots and this result is in accordance with the growing body of evidence in temperate ecosystems showing percent cover of semi-natural environments as critical to maintain high para-

sitism rates that would benefit natural and human-dominated environments (Chaplin-Kramer et al. 2011; Veres et al. 2011; Zumoffen et al. 2012). Riparian vegetation has been previously reported as a refugium for some important parasitoids in commercial crops (e.g. Pfannenstiel & Unruh 2002); similarly, high parasitism in our study site may be a result of parasitoids finding alternate hosts and other resources in riparian plots, which were surrounded by agricultural plots. In fact, in a separate study conducted in the same plots we found that parasitoid abundance reached the highest values in riparian/hedgerow plots (manuscript in preparation). In addition, our results agree with previous studies that found higher parasitism in agricultural vs. non-agricultural environments (Salvo et al. 2005; Mailafiya et al. 2010; Monmany & Aide 2009; Gladbach et al. 2011). This result has been attributed to higher herbivore abundance, a dominance of generalist parasitoids, and a positive relationship between parasitism and temperature in agricultural fields, among other explanations. In a separate study we found that herbivore body length diversity was higher in the agricultural than in the other plots, and that parasitoid species composition was remarkably different in agricultural than in the other plots (manuscript in preparation). High herbivore size diversity would represent available resources for multiple parasitoid species in the agricultural plots and this could explain parasitoid species composition and higher parasitism in those sites.

Studies reporting small- and large-scale effects on parasitism have rarely examined both sources of variation simultaneously (but see [Kruess 2003](#); [Gibb et al. 2008](#)). Given that vegetation structure (small scale) represents three-dimensional complexity and landscape complexity (large scale) represents two-dimensional complexity, analyzing their combined effects on parasitism enables us to hypothesize mechanisms underlying parasitism. For instance, the three dimensional complexity represented by the field metrics basal area (negatively related to parasitism) and the CV of tree density (positively related) was determinant for parasitism and at the landscape scale, two dimensional complexity represented by NDVI Range, and Mean Shape Index (positively related to parasitism) was important. Two out of the five most important complexity metrics were measures of variability at different scales (i.e., CV of plant density and NDVI Range) and both were positively related to parasitism suggesting that our results support the “natural enemy” hypothesis ([Root 1973](#)). The mechanism proposed by this hypothesis is that a greater diversity of herbivore species and microhabitats within complex environments, represented in our sites by higher CV of plant density and higher NDVI Range, results in stable populations of parasitoids and high parasitism. Again, this mechanism is supported by our finding that herbivore body length diversity, a measure of herbivore diversity, was higher in sites showing high parasitism. CV of plant density and NDVI Range, though, were little inter-correlated (Pearson's $r = -0.13$), then the mechanisms shaping parasitism are likely operating in different ways at small and large scales.

Landscape metrics as calculated from the panchromatic band were not correlated in general to parasitism. The only significant panchromatic metric was Mean Shape Index. This agrees with previous studies reporting weak or no relationships between two-dimensional metrics and parasitism ([Chaplin-Kramer et al. 2011](#); [Jonsson et al. 2012](#); [Rusch et al. 2012](#)). It has been shown that different species of parasitoids are related in different degrees to landscape metrics and this may be related to both parasitoid body size and the scale of the analysis ([Perovic, Gurr, Raman, & Nicol 2010](#)). In addition, a differential effect of landscape complexity on parasitoids and hyperparasitoids have been demonstrated ([Rand et al. 2012](#)). In our study we considered all parasitic wasps (Hymenoptera) and flies (Diptera) including all parasitoid life strategies, thus the variation caused by species, body sizes and reproductive strategy can be a factor masking the relationship between parasitism and landscape metrics. Percent parasitism, however, was related to Mean Shape Index, suggesting that plant species diversity, a factor explaining MSI in other ecosystems ([Moser et al. 2002](#)), could be a sufficiently strong driving factor for some parasitoids in our study area. Plant species diversity in our study was highly correlated ($r > 0.7$) to four complexity variables and thus was not included in the models. But the final inclusion of MSI in the model shows that diversity in combination with other factors related to the proportion core/edge in a patch should be taken into account when assessing parasitism. The fact that NDVI Range, a

geostatistical tool, was an important explanatory variable for percent parasitism suggests on the one hand that this measure of landscape complexity explains parasitism better than other measures of NDVI variability, such as the standard deviation of NDVI and this could be related to the manner in which each of these metrics is calculated. On the other hand, it suggests that calculating landscape metrics using the red and infrared bands separately could result in interesting relationships that may lead to the identification of mechanisms. For example, based on our results, we would expect that parasitism will be related to the infrared metrics representing vegetation variability, such as Shannon Diversity. Other metrics calculated from the red and infrared bands such as Mean Shape Index, could be used to dissect the way in which two- and three-dimensional variables combine to shape parasitism.

Our study could be improved by incorporating factors that we did not take into account. First, matrix composition around the plots can be included in the description of two-dimensional complexity given the evidence identifying this variable as important for parasitism ([Kruess 2003](#); [Thies et al. 2003](#); [Schmidt, Thies, & Tschamtkke 2004](#); [Chaplin-Kramer et al. 2011](#)). Second, the effect of matrix should be explored at different scales to explore functional aspects of complexity ([Roland & Taylor 1997](#)). According to a previous study in another area of the Chaco, simple crops similar to alfalfa surrounded by more simple crops showed the highest percent parasitism and this effect varied across scales ([Monmany & Aide 2009](#)). In our study many agricultural plots were surrounded by the same cover type suggesting a similar pattern but we need to examine the effect of scale on parasitism. Third, it has been shown that the age of the crops (i.e. the time the same crop has been present in a region) is positively related to parasitism ([Zumoffen et al. 2012](#)). In our study area, the crops are relatively new in comparison to crops in Europe, for instance, and the agricultural frontier is actively expanding. Incorporating the age of the crops would add detail to the study when comparing regions.

Our study showed a novel way to examine the effects of two- and three-dimensional complexity on insect parasitism. To our knowledge this is the first study examining different satellite bands to describe the relationship between landscape complexity and parasitism. Parasitism was higher in riparian and agricultural plots than in the forest plots across an agricultural frontier in the threatened subtropical Chaco. Riparian/hedgerow plots have been identified as important habitats to maintain critical ecological processes such as parasitism. Further work should explore other aspects of complexity such as connectivity that would enhance parasitoid movement from the forests to the agricultural fields ([Klein et al. 2006](#); [Tschamtkke et al. 2007](#); [Boccaccio & Petacchi 2009](#)). In contrast to previous studies, we based the classification of habitats on a multivariate analysis using a number of landscape metrics instead of pre-assigning the land uses ([Monmany et al. 2015](#)). This leads us to the conclusion that pre-determined land-uses are not necessarily wrong but we argue in favor of our classification method for fur-

ther assessments of parasitism at a landscape scale because it decreases subjectivity. Our approach is a step toward the description of functional landscape complexity (Fahrig et al. 2011). Vegetation structure represented by basal area and CV of plant density and landscape complexity represented by NDVI Range and MSI should be used to determine categories of complexity that can be used to reclassify satellite images with a functional approach in the study of parasitism. In the face of current changes to biodiversity and ecological processes the conservation of natural and human-dominated ecosystems would benefit from these results (Bianchi et al. 2006).

Acknowledgements

E. Meléndez-Ackerman, A. Sabat, A. Salvo, and three anonymous reviewers made substantial contributions to the manuscript. A. Vásquez, J. Galindo, J. Mendivil, G. Peralta, E. Frana, E. Pelozo, M. Corvalán, A. de Cristóbal, V. Reche, B. Bugeau, D. Torres, C. Solís, L. Jofré, S. Bardavid, M. Mata, V. Casanova, I. García, C. Dansey, R. Medina, M. Sarmiento, A. and N. Galindo, M. and V. Monmany, and A. Garzia assisted in the field. D. Colombres, S. Cambera, B. Bocanera, H. Benejam, and Mr. Mirabella gave access to their properties. ProYungas Foundation and the Institute of Regional Ecology (National University of Tucumán, Argentina) gave logistic support in the field. The High Performance Computing Facility at UPR gave support for the landscape analysis (Puerto Rico INBRE grant P20RR-016470 from the National Center for Research Resources - National Institutes of Health-, and the Institute for Functional Nanomaterials award 0701525 from the EPSCoR program of the National Science Foundation). A.C.M.G. was supported by the Dean's Office of Graduate Studies and Research, the Biology Graduate Program, the Institute for Tropical Ecosystem Studies, NSF-EPSCoR, CREST-CATEC (UPR), Idea Wild, and the Organization of American States.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.baae.2018.04.002>.

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