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

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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-m^2 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.

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; Tscharntke et al. 2007; Tscharntke 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, & Tscharntke 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 & Tscharntke 2000a,b; Tscharntke, Steffan-Dewenter, Kruess, & Thies 2002), and decreases with increasing natural habitat isolation (Kruess & Tscharntke 2000a,b; Schueepp, 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, & Tscharntke 2006; Tscharntke 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, & Tscharntke 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-