



High agricultural intensity at the landscape scale benefits pests, but low intensity practices at the local scale can mitigate these effects

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ABSTRACT

Agricultural production has intensified over the last century both across increasingly homogenized landscapes and at the field level. This study analyzes the effects of land-use intensity at both landscape and local scales on the main insect pests, predators and yield of grain sorghum as a summer crop in Uruguay. It represents one of very few landscape studies focused on a reduced intensity production system other than organic agriculture and adds information from an under-studied subtropical region. Piecewise structural equation models were used to compare the direct and indirect effects of intensification at landscape scales and more sustainable practices at a local scale on densities of *Spodoptera frugiperda* (fall armyworm) and *Rhopalosiphum maidis* (corn leaf aphid), coccinellid abundance and yield over a two-year period in sorghum fields in western Uruguay. Greater landscape intensity resulted in increased *S. frugiperda* densities. Lower intensity crop-grazing rotation production systems reduced *R. maidis* densities compared to continuous cropping systems. Additionally, *S. frugiperda* and *R. maidis* interacted indirectly through apparent commensalism in continuous cropping systems, but not in crop-grazing rotational systems. Single cropping management resulted in lower *S. frugiperda* density, while insecticide use had no effect on pest or predator species. Our analysis affirms that agricultural intensification benefits herbivorous arthropod pests at the landscape scale, but that local management practices can mitigate some of these effects.

1. Introduction

Agricultural crops and livestock pastures cover approximately 38 % of the ice-free land surface globally (Smith et al., 2014), and agricultural production has continued to increase in intensity over the past 300 years (World Resources Institute, 2005). An important consequence of the intensification in agricultural ecosystems is the negative effect on biodiversity and ecosystem services (Flynn et al., 2009; Landis, 2017; Tschamntke et al., 2005). The abundance of vertebrates, invertebrates and plants is nearly 40 % lower in intensively managed agricultural landscapes than in sites with uncultivated vegetation (Newbold et al., 2015). Primary consumers, like most insect pests, however, often benefit from intensification (Rusch et al., 2016).

Agricultural intensification can occur at both the landscape scale and the local field-scale. Landscape intensity is characterized by fragmented natural habitats, larger crop fields with lower crop diversity and increasingly homogeneous land-use types (Margosian et al., 2009;

Ramankutty et al., 2018; Sirami et al., 2019; Tschamntke et al., 2005). Landscape homogeneity has been shown to increase habitat connectivity, leading to greater population densities of pest species (Balzan et al., 2016; Meehan et al., 2011; Rand et al., 2014) and altering food web structure (Tylianakis et al., 2007). It can also reduce the biological control services provided by natural enemies (Bianchi et al., 2006; Gardiner et al., 2009; Perović et al., 2010). Landscape intensification is often correlated with local intensification (Meehan et al., 2011; Norton et al., 2009).

Local intensity encompasses management practices, such as insecticide use and cropping frequency, as well as production systems such as organic versus conventional farming. Insecticide use can significantly depress generalist predator abundance and alter the composition of predator communities (Lee et al., 2001; Roubos et al., 2014). Cropping frequency (harvests per year) is also a form of local intensification. Double cropping requires greater inputs, increases disturbance and often results in degradation of soil health (Brennan and Acosta-Martinez,

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2017; Erb et al., 2013; Laney, 2002; Shriar, 2000). The most common metric of local intensification contrasts organic versus conventional production systems (Barbieri et al., 2017; Crowder et al., 2010; Rusch et al., 2014; Tuck et al., 2014; Winqvist et al., 2011). In many cases lower intensity management strategies at the local scale do increase soil health as well as the level of biodiversity supported by agricultural systems (Brennan and Acosta-Martinez, 2017; Larsen and Noack, 2017; Lichtenberg et al., 2017; Ponisio et al., 2016; Tschamtko et al., 2005), but see Kleijn et al. (2011).

There have been many studies tying the effects of landscape intensification and local intensification with negative effects on ecosystem services (Gagic et al., 2012; Gardiner et al., 2009; Liere et al., 2017; Power, 2010; Thies et al., 2011; Tschamtko et al., 2012) and a few tie those to crop yield (Liere et al., 2015; Perez-Alvarez et al., 2018). None, to our knowledge, have included crop yield and also evaluated the effects of contrasting production systems other than organic versus conventional. A production system more commonly used in South America is the rotation between agricultural crops and pasture for livestock grazing. This crop-grazing rotation involves winter and summer crops planted in sequence for 2–3 years followed by 2–4 years of grazing. The local intensity of a crop-grazing rotation is lower than for continuous crop systems, and has been shown to reduce soil erosion and increase soil community diversity (Molina and Perrachon, 2010). Though the effect on above-ground arthropods at a local scale is unknown, other studies have shown that sheep grazing in dryland grain production systems can reduce pest abundance and support higher parasitoid populations (Goosey et al., 2013, 2005).

In step with global trends of landscape homogenization (Margosian et al., 2009; Ramankutty et al., 2018), across Uruguay soybean production has been increasing for the past four decades resulting in decreased landscape crop diversity (Food and Agriculture Organization of the United Nations, 2018; Schnepf et al., 2001). Between 2002 and 2013 insecticide use in Uruguay jumped eight-fold (Food and Agriculture Organization of the United Nations, 2018), leaching into waterways (Ernst et al., 2018) and indicating an intensification of local agricultural land management. There have been efforts to support soil conservation and sustainable agriculture, however, with over 2.9 million ha managed under crop-grazing rotation production systems (Ferrari et al., 2013). The crop-grazing rotation system in Uruguay presents a valuable opportunity to examine the direct and indirect effects of intensification on pests and natural enemies in an agricultural crop in the southern hemisphere. The Paysandú region has a range of landscape homogeneities and intensities of local land use from which to study these effects at multiple scales. Most landscape studies have been carried out in the northern hemisphere (Chaplin-Kramer et al., 2011; Karp et al., 2018; Winqvist et al., 2011), so this study from Uruguay also adds an important contribution from an underrepresented region (New and Samways, 2014; Tuck et al., 2014). The goal was to evaluate the effects of agricultural intensification at local and landscape scales on pest densities, predator abundance and crop yield in the Paysandú region in western Uruguay.

The study system used was grain sorghum, a less intensively managed alternative summer crop to soybean, grown in both crop-grazing rotations and continuous crop systems. The fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), and aphids, including the corn leaf aphid, *Rhopalosiphum maidis* (Hemiptera: Aphididae), are the main pests in sorghum. As is the case for agricultural crops in other regions of South America Coccinellidae is the most abundant family of aphid predators (Fidelis et al., 2019; Ximenez-Embun et al., 2014) and *R. maidis* has been shown to elicit an aggregative response by coccinellids (Michels and Burd, 2007; Park and Obrycki, 2004). Observations from 59 sorghum fields collected over two years were used to examine the effects of three different aspects of agricultural intensification at the landscape and local scale using piecewise structural equation modeling. Landscape intensity was quantified as the proportion of the landscape under annual crop production within a 1 km radius of sorghum fields.

Greater landscape intensification was expected to positively correlate with local pest density (Rand et al., 2014) and to reduce the abundance of coccinellids (Chaplin-Kramer et al., 2011). Local intensification was represented by both production system (crop-grazing rotation versus continuous crop systems) and management (cropping frequency and insecticide use). We expected the lower intensity of crop-grazing rotation production systems to result in lower pest density (Goosey et al., 2005). Lower intensity management decisions were expected to have variable effects with single cropping leading to decreased pest density and predator abundance (Barros et al., 2010; Duyck et al., 2012; Ferguson et al., 1984; Groeneveld and Klein, 2015) and lack of insecticide use leading to increased predator abundance (Roubos et al., 2014).

2. Material and methods

2.1. Natural history and life cycles

Spodoptera frugiperda and *Rhopalosiphum maidis* are important pests of sorghum in Uruguay. *Spodoptera frugiperda* is a larval pest of many plants belonging to the family Poaceae, it has no diapausing stage and is unable to reproduce at mean temperatures below 10 °C (Luginbill, 1928). Consequently, populations do not survive year-round in Uruguay and the furthest south that year-round populations have been found is 27 °S (Murua and Virla, 2004), almost 10° north of the study region. *Spodoptera frugiperda* migrate each spring to regions in which they have seasonal populations (Mitchell et al., 1991). There are likely 3–4 generations in Uruguay given the latitude (Luginbill, 1928). *Rhopalosiphum maidis* is a globally ubiquitous aphid pest of over 30 genera of Poaceae, including sorghum and maize, often aggregating in the leaf whorl (Blackman, 2000; Gonzáles et al., 2001). Barley, a common winter crop in Uruguay, is also an important early season host and when no crops are available *R. maidis* survives on weedy monocots. In regions with mild winters *R. maidis* likely has 10–20 generations per year (Capinera, 2008). A key natural enemy group of *R. maidis* is Coccinellidae (Kring and Gilstrap, 1986), which has an abundant and diverse species assemblage in South America (Serra et al., 2013). Anthocoridae, Syrphidae and Chrysopidae can also be important predators of *R. maidis*.

2.2. Field sites and land-use intensity

To evaluate the effects of both local and landscape intensity on pest and natural enemy abundance in sorghum as a summer crop in the Paysandú region of Uruguay, a total of 59 sites were sampled over a period of two summer field seasons in 2016 (n = 34) and 2017 (n = 25) (see Supplementary Fig. 1 for a map of sample locations). None of the sorghum fields were irrigated and the majority were under no-till systems, consistent with national trends in which more than 80 % of cultivated land in Uruguay is no-till (Derpsch et al., 2010).

To address the effect of landscape intensity, the extent of the landscape planted with annual summer crops was quantified (Caballero-López et al., 2012; Gagic et al., 2017; Tuck et al., 2014). The proportion of land under annual crops was estimated using the Plans of Use provided to the authors as GIS shape files from the Ministry of Agriculture (Ministerio de Ganadería, Agricultura y Pesca or MGAP) for the corresponding planting season. Plans of Use data were available for only 41 of the 59 sites, however, and so for the other 18 sites the proportion of annual crops was estimated from Google Earth satellite images for 2015 and 2016 followed up by ground-truthing for each site (Midrega et al., 2014). The software program QGIS (QGIS Development Team, 2018) was used to delimit a 1 km radius around each site, a distance found to be most relevant in other landscape studies for both aphids and general predators (Caballero-López et al., 2012; Rusch et al., 2014; Thies et al., 2005; Winqvist et al., 2011). The proportion of land planted to annual crops was analyzed as a continuous variable (Zhao et al., 2014) ranging from less than 0.01 to 0.76 over the 59 sites with a normal distribution.

Local intensity was evaluated based on the agricultural production system and management. Local production system intensity was based on whether a field had a continuous crop or crop-grazing rotation history. Continuous crop fields had been under annual cultivation without periods of grazing for five or more years. Crop-grazing rotation fields had been grazed for at least three years and were subsequently transitioned to annual crops a maximum of one year before sampling with no more than one crop harvest prior to sorghum. Thirty-three sites were under continuous crop production and 26 sites were crop-grazing rotation production systems.

Local management intensity for each site was categorized by insecticide use and cropping frequency (single vs double in the year of sorghum planting). Winter crops planted prior to the summer sorghum in double cropping fields included oat, wheat and barley. If a field was grazed, fallow or planted to cover crops during the preceding winter it was categorized as single crop. Insecticides applied to the sorghum crop were either organophosphates or benzoylureas targeting *S. frugiperda* larval populations. Peak abundance of *S. frugiperda* occurred early in the growing season and all growers who applied insecticides did so only once before the sampling period used in this study.

2.3. Sampling of field sites

The summer sorghum crops at each site were sampled within a 10 × 10 m sampling plot located 8 m from the edge of the field (following Jonsson et al., 2012) every three weeks from December to April each year. To estimate densities of the two key sorghum pests at each site every 10th plant along two 10 m transects within the plot was visually inspected on each sampling date and counts were recorded of *R. maidis* (all instars) and *S. frugiperda* larvae per plant. The abundance and diversity of aphidophagous coccinellid predators at each site were monitored using three half-sized yellow sticky traps (Alpha Scents, Inc., West Linn, OR) placed on 2 m high posts attached just above plant height and arranged along the diagonal of the sampling plot. Sticky traps were used to sample the predators as they have been shown to both collect more species and more mobile life stages than destructive or field-count sampling methods (Schmidt et al., 2008). Counts of adult aphidophagous coccinellids, anthocorids, syrphids and chrysopids on yellow sticky traps from the same site and date were pooled by family and abundance was estimated as mean number per trap.

In addition to sampling the insect pests and predators at each field site, sorghum yield (kg/ha) for each site was provided by pest control advisors from a variety of organizations. Other factors known to be important for insects were also included as potential explanatory variables including field size, latitude, plant vigor, rainfall, temperature and a soil productivity index using information from the National Commission for the Agronomic Study of Land (CONEAT) (Ministerio de Ganadería Agricultura y Pesca, 2016). For plant vigor a mean chlorophyll content index (CCI) was measured on young leaves from three representative sorghum plants along the two transects at each site using a chlorophyll meter (Apogee CCM-200, Apogee Instruments, Logan, Utah). Measurements were taken from when the fifth leaf was visible at all sites to the soft dough stage (Vanderlip and Reeves, 1972), after which the chlorophyll content of leaves declines significantly as the plant transfers resources to the head of grain (Oyler et al., 2017). The CCI (a scale from 0 to 100 representing the transmission of light at 931/635 nm) has been shown to correlate well with plant nitrogen status (Richardson et al., 2002), although both water stress and aphid infestation are known to negatively affect CCI (Golawska et al., 2010; Schepers et al., 1996). Daily rainfall (mm) and maximum and minimum temperatures were obtained from three weather stations; all field sites were within 50 km of one of these weather stations. Data from the Glencoe Experimental Station and the Salto weather station was provided by the National Institute of Agro-fishery Research in Uruguay (INIA). Data from the Paysandú weather station was provided by the Mario A. Cassinoni Research Station (EEMAC) associated with the

University of the Republic (UdelaR). The standard deviation of total rainfall between sampling dates was used as a measure of seasonal rainfall variation. Accumulated rainfall was also evaluated. The number of days with a maximum temperature higher than 34 °C was used as a measure of extreme temperatures above which the juvenile development rates and survivorship of *R. maidis* and *S. frugiperda* decline (Early et al., 2018; Kuo et al., 2006).

2.4. Statistical analyses

The statistical environment of R was used for all data analyses (R Development Core Team, 2017) and the direct and indirect effects of landscape and local intensity on sorghum crop yield was investigated using structural equation models (SEMs) (Gagic et al., 2017; Jonsson et al., 2012). The R packages nlme (Pinheiro et al., 2018) and piecewiseSEM (Lefcheck, 2016) were used for SEM development and analysis. Piecewise SEMs (pSEMs) were used as they have relaxed sample size requirements and can manage nested and non-normally distributed data (Lefcheck, 2016). The pSEMs were generated from a set of component linear mixed effects models (LME) that were developed through standard model reduction using AIC and step-wise removal of non-significant variables to evaluate path directionality and strength of direct effects (Shipley, 2000). The assumption of normality was visually checked with Q-Q plots of component model residuals and Shapiro-Wilks tests (Thode, 2002). The component models were LMEs as the effects of SD rainfall and number of days above 34 °C required the inclusion of weather station as a random effect accounting for the lack of independence among sampling sites. Both the marginal and conditional R² values are reported for any component LME. Moran's I statistic was used to check for spatial autocorrelation in the residuals of each LME (Rusch et al., 2013). No spatial autocorrelation was found in any models. Cascading LMEs were pieced together using confirmatory path analysis to estimate the full pSEM model (Lefcheck, 2016), with indirect as well as direct effects. To determine standardized path coefficients raw coefficients were scaled using the standard deviation of x divided by the standard deviation of y (Lefcheck, 2016). Fischer's C statistic, based on p-values calculated from a test of directed separation, was used to evaluate full model fit (Shipley, 2009). A test of directed separation evaluates whether missing paths, that is, paths not defined in the component models, are significant (p < 0.05), but it controls for indirect effects already in the full model. A chi-squared test of Fischer's C with p > 0.05 indicates that the full model represents the data well and that there are no missing paths that could contribute additional explanatory power. If p < 0.05 the full model does not represent the data sufficiently and missing paths improve the fit. If significant missing paths were identified during analysis associated variables were considered for their ecological significance. If a case for ecological significance could be made, the alternate model was compared using AIC. If the alternate model had an AIC value more than two below the original model, the alternate model with its additional specified path was accepted.

2.5. Development of sorghum yield pSEM

Of the 59 sites sampled over the two-year period, only 49 had sufficient data available for all factors included in the sorghum yield pSEM. Three sample periods covering the period of peak abundance of the two key sorghum pests (weeks 4, 7 and 10) and the weeks of peak coccinellid abundance (weeks 7, 10 and 13) were used for analysis (see Supplementary Table 1 for all field sites and sample dates). A set of five hierarchical linear models were used to capture the hypothesized predictive relationships for sorghum yield (see Fig. 1). Linear models were developed for the density of the two key pests, coccinellid abundance, chlorophyll content and sorghum yield. Coccinellid abundance and pest densities were log transformed to reduce the influence of outliers and to normalize the data (Beduschi et al., 2015). To account for observed zeros in the data, prior to transformation a constant equal to the square of the

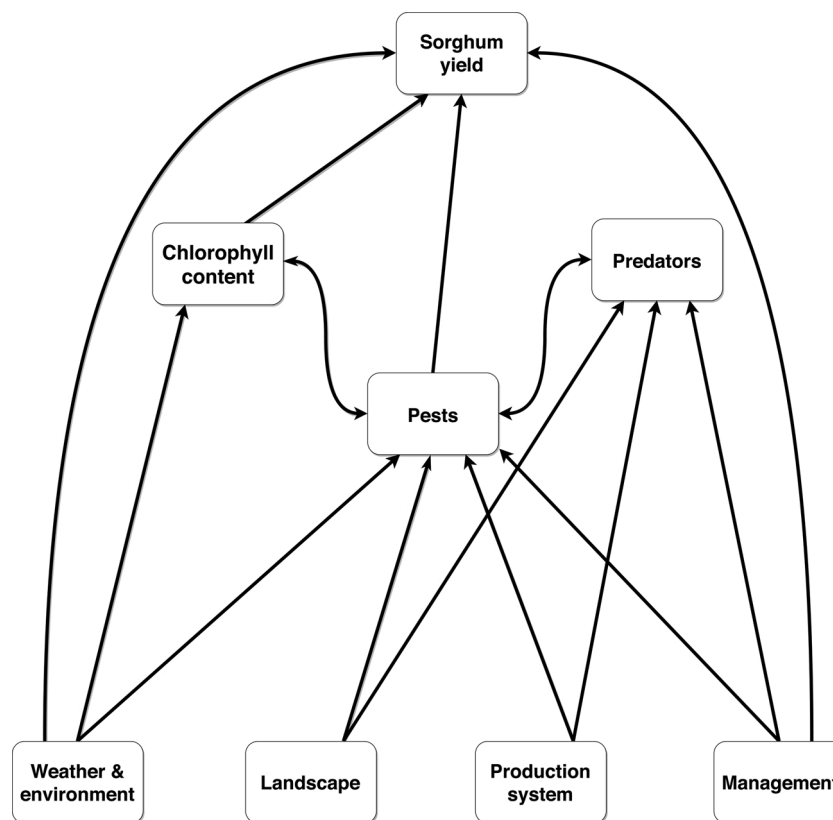


Fig. 1. The diagram shows the hypothesized effects that were tested in the preliminary component LME models for the sorghum yield piecewise structural equation model (pSEM). Factors are summarized by group and their hypothesized cascading influence on sorghum yield is shown. All tested factors listed by group can be found in Supplementary Table 3.

first quartile divided by the third quartile was added to the ranked observations (following Burton et al., 2016). The following factors were found to have significant effects in one or more of the hierarchical linear models used to develop the sorghum yield pSEM: proportion of land under annual crops within a 1 km radius (landscape intensity), crop-grazing rotational system (local production intensity), single cropping frequency (local management intensity), standard deviation of accumulated rainfall between sampling periods and number of days above 34 °C. The variation (standard deviation) in rainfall between regions and years provided greater explanatory power than year alone in all models. In all cases, the categorical variables were binary based on level of agricultural intensity.

2.6. Development of pest and predator linear models

To investigate some of the unexpected relationships revealed by the pSEM, the larger data set ($n = 59$) was examined using simpler linear models and a reduced set of variables. These models examined the effect of local production intensity on the relationship between *R. maidis* and *S. frugiperda* density and the correlation between *S. frugiperda* density and coccinellid abundance.

3. Results

3.1. Pest and predator abundance

Over the entire sampling period 292 *S. frugiperda* larva and 24,939 *R. maidis* were recorded from transects while 7,143 coccinellid beetles were caught on yellow sticky traps, of which 6,455 belong to aphidophagous species (see Supplementary Table 2 for details). Though 1,255 *Orius* sp. were caught on yellow sticky traps no linear model explained more than 6% of the variation so they were excluded from the

pSEM. Too few adult Chrysopidae and Syrphidae (131 and 139, respectively) were caught and so were also excluded from further analysis.

3.2. Sorghum yield pSEM

Landscape and/or local intensity factors had significant effects on four of the five component linear models used for the sorghum yield piecewise SEM, the exception being the model for chlorophyll content (Table 1). A directed separation test indicated a missing path (factors with $p < 0.05$ not included in an initial component linear model): a direct positive effect of the proportion of land under annual crops within 1 km on sorghum yield. Since an ecological justification for the inclusion of this factor could be made (see 4), it was included in the component linear model. For the final pSEM (Fig. 2, AIC = 94.8) a Fischer's C statistic of 32.8 ($df = 40$, $p = 0.8$) provided evidence of a good fit to the data. The proportion of land under annual crops within a 1 km radius around field sites, the metric used for landscape intensity, had a significant positive effect on *S. frugiperda* density, coccinellid abundance and sorghum yield (Fig. 2).

The pSEM analysis indicated that single cropping, a metric of lower local management intensity, resulted in lower *S. frugiperda* density (Fig. 2). Insecticide use aimed at *S. frugiperda* control, the other metric of local management intensity, had no effect on *S. frugiperda* density. There was a negative effect of crop-grazing rotation on aphid density compared to that in the continuous crop systems (Fig. 2). *Spodoptera frugiperda* density was positively associated with *R. maidis* density, though this effect depended on crop production system as demonstrated by the significant interaction (Table 1, Fig. 2).

Variation in rainfall (SD) had a strong negative effect on both chlorophyll content and sorghum yield. The number of extreme heat days (above 34 °C) had a positive effect on chlorophyll content, but a

Table 1

Direct effects of environmental and land-use intensity factors on the dependent variables of the five component models used for the piecewise SEM for sorghum yield (NA = not applicable, NS = not significant, CCI = Chlorophyll content index, * p = 0.06).

Component model	R ² _m	R ² _c	Intercept	Sf density	Rm density	CCI	Proportion annual crop	Rotation system	Interaction Sf density: System	Single crop	SD seasonal rainfall	Days > 34 °C
<i>S. frugiperda</i> density (ln)	0.40	0.62	-0.11	NA	NS	NS	2.64	NS	NA	-1.13	NS	-0.13
<i>R. maidis</i> density (ln)	0.44	0.45	5.53	1.06	NA	NA	NS	-1.96	-0.96	NS	NS	-0.14
Coccinellid abundance (ln)	0.25	0.25	2.31	-0.14	NS	NA	0.63	NS	NS	NS	-0.002*	NS
CCI	0.47	0.60	26.22	NS	-1.07	NA	NS	NS	NS	NS	-0.16	1.23
Yield (kg/ha)	0.35	0.58	3657.27	NS	NS	54.17	2157.87	NS	NS	NS	-10.84	NS

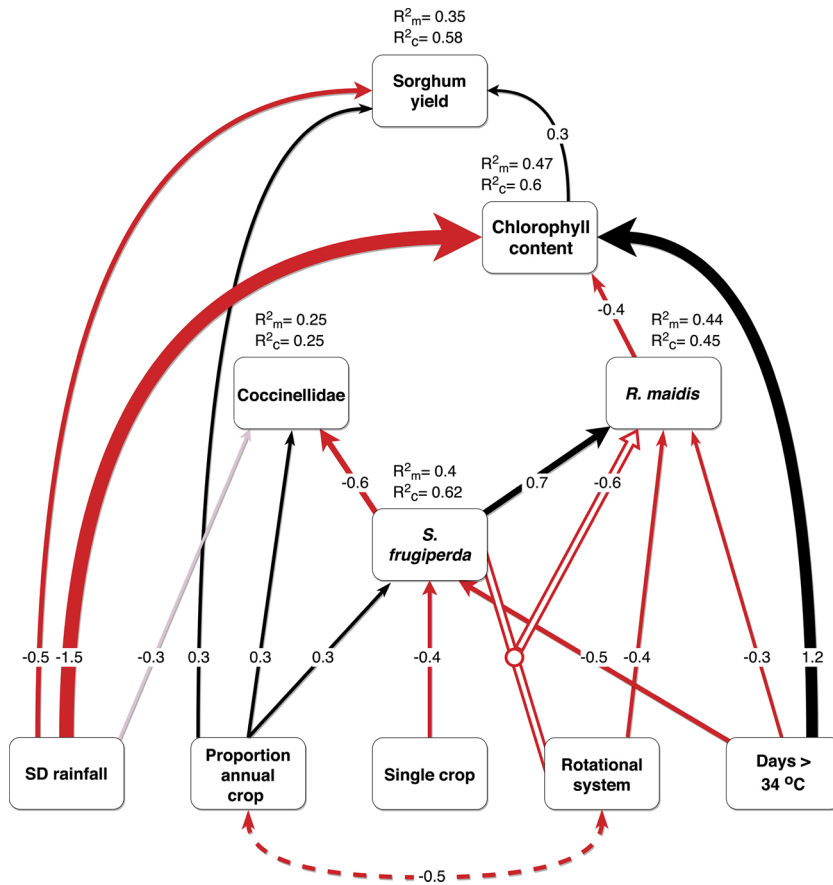


Fig. 2. Environmental and land-use intensity (landscape and local) effects for the sorghum yield structural equation model (pSEM). The diagram shows the direct and indirect effects of explanatory factors on yield in the final pSEM. Red arrows indicate a negative effect, black arrows a positive effect and the width of the arrow corresponds to the standardized path coefficient for each significant effect ($p \leq 0.05$). The grey arrow shows a marginally significant negative effect ($p = 0.06$) that improved the fit of the component model. Unfilled red arrows indicate a significant interaction between variables. The dashed arrow indicates two exogenous variables with significant correlated errors. Marginal and conditional R² values are given for all component LMEs.

negative effect on both *S. frugiperda* and *R. maidis* densities (Fig. 2).

3.3. Pest interaction linear models

The larger data set showed an even stronger pattern of the positive relationship between *R. maidis* and *S. frugiperda* densities in continuous cropping systems, but not in crop-grazing rotation production systems (Fig. 3A). The larger data set was also consistent with the pSEM in showing a negative correlation between aphidophagous coccinellid abundance and *S. frugiperda* density across production systems (Fig. 3B).

4. Discussion

This two-year study including nearly 60 field sites showed that higher landscape intensity benefitted the insect pests, but that lower intensity local production systems and management decisions decreased pest densities with cascading effects on sorghum yield in the Paysandú region of Uruguay. A higher proportion of annual crop acreage within a

1 km radius, representing greater landscape intensity, resulted in higher *S. frugiperda* density as found in other studies of pests with high dispersal ability in increasingly homogeneous landscapes (Andow, 1983; Tschamtko et al., 2005). Higher pest densities in a homogeneous crop landscape could also be facilitated by lower predator populations (Atuo and O’Connell, 2017). There was no link, however, between aphidophagous coccinellids and aphids in this study and coccinellids typically do not attack *S. frugiperda* under field conditions, though eggs can be a suitable alternative food source for captive rearing of *Eriopis connexa* (Silva et al., 2013). As we did not monitor natural enemies of *S. frugiperda* in this study we can only speculate that this may also have been a factor. Studies have found contrasting effects of landscape diversity on aphids (O’Rourke and Petersen, 2017; Roschewitz et al., 2005), but we found no effect of landscape intensity on *R. maidis* density in the pSEM. It is possible that 1 km was not the ideal spatial scale to examine landscape effects on *R. maidis* densities in this system (Thies et al., 2005) or that the sample size of the pSEM may have been inadequate to capture the nuance of a landscape intensity effect on patchy

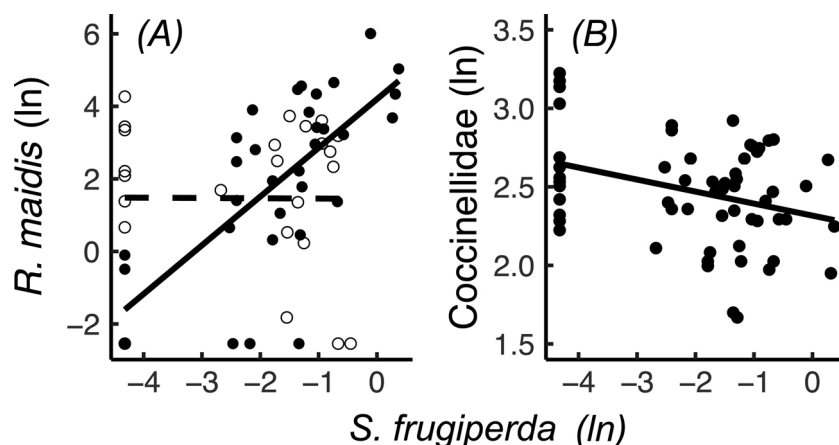


Fig. 3. The influence of *S. frugiperda* density in (A) on *R. maidis* density in continuous crop systems (filled circles and solid line, $y = 1.34x + 4.2$, $R^2 = 0.48$, $p < 0.001$, $n = 33$) and in crop-grazing rotational systems (open circles and dashed line, $y = -0.007x + 1.47$, $R^2 < 0.001$, $p = 0.98$, $n = 26$), and in (B) on coccinellid abundance for both production systems ($y = -0.08 + 2.32$, $R^2 = 0.11$, $p = 0.01$, $n = 59$).

and variable *R. maidis* densities. Other research has shown that parasitoids can benefit from diversified landscapes (Roschewitz et al., 2005), but our results show that in contrast coccinellids benefit from greater landscape homogeneity (Fig. 2). However, aphids also have other functional groups of predators including Carabidae and Staphylinidae, which, as ground dwellers may respond differently to landscape intensity. Greater landscape intensity also had a positive influence on sorghum yield. The direct effect of landscape annual agriculture on yield was not anticipated. The missing path analysis indicated that landscape intensity had a positive effect on yield. As this effect was likely due to a latent variable that was not directly measured, but can be inferred, like better soil quality in more intensively managed landscapes, it was included in the final model.

The lower local agricultural intensity of the crop-grazing rotation production system had a significant negative effect on *R. maidis* density that ultimately increased sorghum yield via a negative effect of *R. maidis* density on plant chlorophyll content (Fig. 2). *Spodoptera frugiperda* density had a significant positive effect on *R. maidis* density, but this effect was mitigated by a significant interaction between *S. frugiperda* and production system (Fig. 2). The larger data set supported the finding in the pSEM that *R. maidis* and *S. frugiperda* are significantly positively correlated, but only in continuous cropping systems (Fig. 3A). Insecticide use early in the season aimed at control of *S. frugiperda* had no effect on *S. frugiperda* density. Secondary pest outbreaks, facilitated by early-season use of insecticides, are a well-known phenomenon (Andow, 1983; Crowder and Jabbour, 2014; van den Bosch et al., 1973), but in our study this did not appear to be a factor. Other landscape research has shown that insecticide use disrupts natural enemy communities (Hill et al., 2017), but in our study we did not see any effect of insecticide use on aphidophagous coccinellid abundance.

Another metric for local agricultural intensity that had a significant effect in the pSEM was cropping frequency. Double cropping can result in greater disturbance and degradation of soil health (Brennan and Acosta-Martinez, 2017; Erb et al., 2013). The finding, however, that single cropping resulted in lower *S. frugiperda* densities was not unexpected. Since single cropping is often associated with earlier planting date (Can and Yoshida, 1999) it is likely that the sorghum plants in single cropped fields provided older less desirable plants for the return migration of *S. frugiperda* populations. Other research has also shown that *S. frugiperda* populations occur at higher densities and cause greater damage to late-planted summer crops (Ayala et al., 2014) underscoring the importance of local management decisions.

The negative effect of *R. maidis* density on chlorophyll content is consistent with previous research demonstrating a direct negative effect of aphid feeding on chlorophyll a, chlorophyll b and total chlorophyll

(Burd and Elliott, 1996). It is also worth noting that the variation in rainfall among sites is likely indicative of the effects of El Niño - Southern Oscillation (ENSO) weather patterns. During the first summer season (December 2015 - March 2016) the ENSO event was considered quite extreme (Hu and Fedorov, 2017) and the conditions in Paysandú, Uruguay were unusually dry and warm during the sampling period, though the spring and fall were extremely wet, consistent with past ENSO effects found in the region (Bidegain and Krecl, 1998). This resulted in greater variation in rainfall between years and sites in 2016 compared to 2017 though accumulated rainfall was not statistically different between years. There are implications for climate change in these data as well since both *R. maidis* and *S. frugiperda* densities were negatively affected by a greater number of very hot days. Both summer temperatures and variability in summer rainfall are projected to increase in climate change models for Uruguay (Cabre et al., 2016).

The most surprising finding from this research was a direct negative effect of *S. frugiperda* density on the abundance of aphidophagous coccinellids (Figs. 2, 3B) and the absence of a direct link between *R. maidis* density and coccinellid abundance in the pSEM (Table 1, Fig. 2). Coccinellid abundance was tested both downstream of aphids to allow for a response to prey density and also upstream of aphids to account for their potential role as biological control agents though neither of these relationships showed any significance. As these predators are not known to feed on lepidopteran larvae under field conditions, no linkage between *S. frugiperda* and coccinellids was initially considered. Recent studies have suggested, however, that cross-talk between the plant defense signaling pathways induced by leaf chewers and phloem feeders can not only lead to indirect interactions among insect herbivores that share the same plant, but also to indirect interactions with natural enemies (Rodríguez-Saona et al., 2010; Soler et al., 2012; Blubaugh et al., 2018). In a field study of dual-guild herbivory, lepidopteran caterpillars were found to interfere with the top-down suppression of aphid populations on brassica plants, with disruption of aphid-induced plant signaling considered the most likely explanation (Blubaugh et al., 2018). As it is known that coccinellid species can respond to aphid-induced plant volatiles (Xiu et al., 2019), and that plant volatiles induced by *S. frugiperda* herbivory can disrupt those induced by *R. maidis* (Rodríguez-Saona et al., 2010) this could help explain the direct negative effect of *S. frugiperda* density on aphidophagous coccinellid abundance. Thus the dual-herbivore facilitation that we observed in continuous cropping systems (Fig. 3A) can be considered a type of apparent commensalism in which *R. maidis* density benefitted from *S. frugiperda* suppression of coccinellid abundance, an indirect interaction between herbivore species that may have been mediated by the plant rather than a shared predator. It is increasingly accepted that indirect interactions affect the potential

for biological control (Culshaw-Maurer et al., 2020; Emery and Mills, 2020), but bottom-up indirect effects deserve more study.

In conclusion, this study parses the effects of local and landscape level intensification on insect abundance and biological control in an agricultural crop and provides further evidence that greater land-use intensity benefits agricultural pests at landscapes scales, but that local production systems and management decisions can mitigate these effects. It also demonstrates how intensification can have unexpected effects on indirect community interactions such as the dual herbivore facilitation resulting in apparent commensalism between *S. frugiperda* and *R. maidis* in more intensely managed continuous crop systems. This research provides an important foundation for further work in an understudied geographic region focused on the links for arthropod communities between landscape intensity and a crop-grazing lower intensity production system.

Author contributions

SE and NJM conceived the ideas and designed methodology. SE was responsible for field data collection and insect identification. HS and AR provided critical access to cooperative growers, local organizations as well as government data. HS and AR also provided local institutional support. SE, MJ and NJM analyzed the data; SE led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107199>.

References

Andow, D.A., 1983. The extent of monoculture and its effects on insect pest populations with particular reference to wheat and cotton. *Agric. Ecosyst. Environ.* 9, 25–35.

Atuo, F.A., O'Connell, T.J., 2017. The landscape of fear as an emergent property of heterogeneity: contrasting patterns of predation risk in grassland ecosystems. *Ecol. Evol.* 7, 4782–4793. <https://doi.org/10.1002/ece3.3021>.

Ayala, O., Navarro, F., Virla, E.G., 2014. Evaluation of the attack rates and level of damages by the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: noctuidae), affecting corn crops in the northeast of Argentina. *Rev. la Fac. Ciencias Agrar.* 45, 1–12.

Balzan, M.V., Bocci, G., Moonen, A.C., 2016. Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. *BioControl* 61, 141–154. <https://doi.org/10.1007/s10526-015-9711-2>.

Barbieri, P., Pellerin, S., Nesme, T., 2017. Comparing crop rotations between organic and conventional farming. *Sci. Rep.* 7, 1–10. <https://doi.org/10.1038/s41598-017-14271-6>.

Barros, E.M., Torres, J.B., Ruberson, J.R., Oliveira, M.D., 2010. Development of *Spodoptera frugiperda* on different hosts and damage to reproductive structures in cotton. *Entomol. Exp. Appl.* 137, 237–245. <https://doi.org/10.1111/j.1570-7458.2010.01058.x>.

Beduschi, T., Tschardtke, T., Scherber, C., 2015. Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes. *Landsc. Ecol.* 30, 1979–1990. <https://doi.org/10.1007/s10980-015-0224-2>.

Bianchi, F.J.Ja, Bojji, C.J.H., Tschardtke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Biol. Sci.* 273, 1715–1727. <https://doi.org/10.1098/rspb.2006.3530>.

Bidegain, M., Krecl, P., 1998. Comportamiento de la temperatura en el sudeste de sudamérica (Uruguay) asociado al fenómeno ENSO. Congreso Iberoamericano de Meteorología, Brazilia, Brazil.

Blackman, R., 2000. *Aphids on the World's Crops: an Identification and Information Guide*. Wiley, London, England.

Blubaugh, C.K., Asplund, J.S., Eigenbrode, S.D., Morra, M.J., Philips, C.R., Popova, I.E., Reganold, J.P., Snyder, W.E., 2018. Dual-guild herbivory disrupts predator-prey interactions in the field. *Ecology* 99, 1089–1098. <https://doi.org/10.1016/j.ecy.2192>.

Brennan, E.B., Acosta-Martinez, V., 2017. Cover cropping frequency is the main driver of soil microbial changes during six years of organic vegetable production. *Soil Biol. Biochem.* 109, 188–204. <https://doi.org/10.1016/j.soilbio.2017.01.014>.

Burd, J.D., Elliott, N., 1996. Changes in chlorophyll a fluorescence induction kinetics. *J. Econ. Entomol.* 89, 1332–1337.

Burton, J.I., Olson, D.H., Puettmann, K.J., 2016. Effects of riparian buffer width on wood loading in headwater streams after repeated forest thinning. *For. Ecol. Manage.* 372, 247–257. <https://doi.org/10.1016/j.foreco.2016.03.053>.

Caballero-López, B., Bommarco, R., Blanco-Moreno, J.M., Sans, F.X., Pujade-Villar, J., Rundlöf, M., Smith, H.G., 2012. Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biol. Control* 63, 222–229. <https://doi.org/10.1016/j.biocontrol.2012.03.012>.

Cabre, M.F., Solomon, S., Nunez, M., 2016. Regional climate change scenarios over South America for future climate (2080-2099) using the MM5 Model. Mean, interannual variability and uncertainties. *Atmosfera* 29, 35–60.

Can, N.D., Yoshida, T., 1999. Grain yield of sorghum cultivars in a double cropping system. *Plant Prod. Sci.* 2, 121–124. <https://doi.org/10.1626/pp.2.121>.

Capinera, J.L., 2008. Corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Hemiptera: Aphididae). In: Capinera, J.L. (Ed.), *Encyclopedia of Entomology*. Springer, Netherlands, London, England, pp. 1070–1072. https://doi.org/10.1007/978-1-4020-6359-6_440.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14, 922–932. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>.

Crowder, D.W., Jabbour, R., 2014. Relationships between biodiversity and biological control in agroecosystems: current status and future challenges. *Biol. Control* 75, 8–17. <https://doi.org/10.1016/j.biocontrol.2013.10.010>.

Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466, 109–112. <https://doi.org/10.1038/nature09183>.

Culshaw-Maurer, M., Sih, A., Rosenheim, J., 2020. Bugs scaring bugs: enemy-risk effects in biological control systems. *Ecol. Lett.* 1–33. <https://doi.org/10.1111/ele.13601>.

Derpsch, R., Friedrich, T., Kassam, A., Hongwen, L., 2010. Current status of adoption of no-till farming in the world and some of its main benefits. *Int. J. Agric. Biol. Eng.* 3, 1–25. <https://doi.org/10.3965/j.issn.1934-6344.2010.01.001-025>.

Duyck, P.F., Dortel, E., Vinatier, F., Gautjoux, E., Carval, D., Tixier, P., 2012. Effect of environment and fallow period on *Cosmopolites sordidus* population dynamics at the landscape scale. *Bull. Entomol. Res.* 102, 583–588. <https://doi.org/10.1017/S0007485312000089>.

Early, R., González-moreno, P., Murphy, S.T., Day, R., 2018. Forecasting the global extent of invasion of the cereal pest *Spodoptera frugiperda*, the fall armyworm. *NetBiota* 40, 25–50. <https://doi.org/10.3897/neobiota.40.28165>.

Emery, S.E., Mills, N.J., 2020. Effects of predation pressure and prey density on short-term indirect interactions between two prey species that share a common predator. *Ecol. Entomol.* 45, 821–830. <https://doi.org/10.1111/een.12855>.

Erb, K.-H., Habert, H., Jepsen, M.R., Kuemmerle, T., Lindner, M., Müller, D., Verburg, P.H., Reenberg, A., 2013. A conceptual framework for analysing and measuring land-use intensity. *Curr. Opin. Environ. Sustain.* 5, 464–470. <https://doi.org/10.1016/j.cosust.2013.07.010>.

Ernst, F., Alonso, B., Colazzo, M., Pareja, L., Cesio, V., Pereira, A., Márquez, A., Errico, E., Segura, A.M., Heinzen, H., Pérez-Parada, A., 2018. Occurrence of pesticide residues in fish from South American rainfed agroecosystems. *Sci. Total Environ.* 631–632, 169–179. <https://doi.org/10.1016/j.scitotenv.2018.02.320>.

Ferguson, H.J., McPherson, R.M., Allen, W.A., 1984. Effect of four soybean cropping systems on the abundance of foliage-inhabiting insect predators. *Environ. Entomol.* 13, 1105–1112.

Ferrari, J.M., Camilo, S., Hernandez, A., 2013. 2013 Anuario estadístico agropecuario. Ministerio de Ganadería Agricultura y Pesca, Montevideo, Uruguay.

Fidelis, E.G., Farias, E.S., Lopes, M.C., Sousa, F.F., Zanuncio, J.C., Picanço, M.C., 2019. Contributions of climate, plant phenology and natural enemies to the seasonal variation of aphids on cabbage. *J. Appl. Entomol.* 143, 365–370. <https://doi.org/10.1111/jen.12607>.

Flynn, D.F.B., Gogol-Prokurat, M., Nogueira, T., Molinari, N., Trautman Richers, B., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity

- under land use intensification across multiple taxa. *Ecology* 12, 22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x>.
- Food and Agriculture Organization of the United Nations, 2018. FAOSTAT database. Rome, Italy.
- Gagic, V., Hänke, S., Thies, C., Scherber, C., Tomanović, Z., Tscharntke, T., 2012. Agricultural intensification and cereal aphid – parasitoid – hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. *Oecologia* 170, 1099–1109. <https://doi.org/10.1007/s00442-012-2366-0>.
- Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B., Elek, Z., Garratt, M.P.D., de Groot, G.A., Hedlund, K., Kovács-Hostyánszki, A., Marini, L., Martin, E., Pevere, I., Potts, S.G., Redlich, S., Senapathi, D., Steffan-Dewenter, I., Świtek, S., Smith, H.G., Takács, V., Tryjanowski, P., van der Putten, W.H., van Gils, S., Bommarco, R., 2017. Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecol. Lett.* 20, 1427–1436. <https://doi.org/10.1111/ele.12850>.
- Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O’Neal, M., Chacon, J.M., Wayo, M.T., Schmidt, N.P., Mueller, E.E., Heimpel, G.E., 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19, 143–154. <https://doi.org/10.1890/07-1265.1>.
- Golawski, S., Krzyzanowski, R., Lukasił, I., 2010. Relationship between aphid infestation and chlorophyll content in Fabaceae species. *Acta Biol. Cracoviensia* 52, 82–86. <https://doi.org/10.2478/v10182-010-0022-8>.
- González, W.L., Gianoli, E., Niemeyer, H.M., 2001. Plant quality vs. Risk of parasitism: within-plant distribution and performance of the corn leaf aphid, *Rhopalosiphum maidis*. *Agric. For. Entomol.* 3, 29–33. <https://doi.org/10.1046/j.1461-9563.2001.00084.x>.
- Goosey, H.B., Hatfield, P.G., Lenssen, a.W., Blodgett, S.L., Kott, R.W., 2005. The potential role of sheep in dryland grain production systems. *Agric. Ecosyst. Environ.* 111, 349–353. <https://doi.org/10.1016/j.agee.2005.06.003>.
- Goosey, H.B., Hatfield, J.P., Rolston, M.G., Hatfield, P.G., Johnson, G.D., 2013. Hymenoptera parasitoid response to sheep grazing, tillage, and herbicides in wheat-fallow rotations. *J. Kansas Entomol. Soc.* 86, 22–35. <https://doi.org/10.2317/JKES110223.1>.
- Groeneveld, J.H., Klein, A.M., 2015. Pennycress-corn double-cropping increases ground beetle diversity. *Biomass Bioenergy* 77, 16–25. <https://doi.org/10.1016/j.biombioe.2015.03.018>.
- Hill, M.P., Macfadyen, S., Nash, M.A., 2017. Broad spectrum pesticide application alters natural enemy communities and may facilitate secondary pest outbreaks. *PeerJ* 5, e4179. <https://doi.org/10.7717/peerj.4179>.
- Hu, S., Fedorov, A.V., 2017. The extreme El Niño of 2015–2016 and the end of global warming hiatus. *Geophys. Res. Lett.* 44, 3816–3824. <https://doi.org/10.1002/2017GL072908>.
- Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. *J. Appl. Ecol.* 49, 706–714. <https://doi.org/10.1111/j.1365-2664.2012.02130.x>.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., et al., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proc. Natl. Acad. Sci.* 115, E7863–E7870. <https://doi.org/10.1073/pnas.1800042115>.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? *Trends Ecol. Evol.* 26, 474–481. <https://doi.org/10.1016/j.tree.2011.05.009>.
- Kring, T.J., Gilstrap, F.E., 1986. Beneficial role of corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Homoptera: aphididae), in maintaining *Hippodamia* spp. (Coleoptera: coccinellidae) in grain sorghum. *Crop Prot.* 5, 125–128. [https://doi.org/10.1016/0261-2194\(86\)90093-1](https://doi.org/10.1016/0261-2194(86)90093-1).
- Kuo, M.H., Chiu, M.C., Perng, J.J., 2006. Temperature effects on life history traits of the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: aphididae) on corn in Taiwan. *Appl. Entomol. Zool.* 41, 171–177. <https://doi.org/10.1303/aez.2006.171>.
- Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic Appl. Ecol.* 18, 1–12. <https://doi.org/10.1016/j.baae.2016.07.005>.
- Laney, R.M., 2002. Disaggregating induced intensification for land-change analysis: a case study from Madagascar. *Ann. Assoc. Am. Geogr.* 92, 702–726. <https://doi.org/10.1111/1467-8306.00312>.
- Larsen, A.E., Noack, F., 2017. Identifying the landscape drivers of agricultural insecticide use leveraging evidence from 100,000 fields. *Proc. Natl. Acad. Sci.* 114, 5473–5478. <https://doi.org/10.1073/pnas.1620674114>.
- Lee, J.C., Menalled, F.D., Landis, D.A., 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38, 472–483. <https://doi.org/10.1046/j.1365-2664.2001.00602.x>.
- Lefcheck, J.S., 2016. PIECEWISE SEM piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. <https://doi.org/10.1111/2041-210X.12512>.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalheiro, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martínez, E., Memmott, M.J., Morandini, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, J.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardinias, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T., Veselý, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Change Biol.* 23, 4946–4957. <https://doi.org/10.1111/gcb.13714>.
- Liere, H., Kim, T.N., Werling, B.P., Meehan, T.D., Landis, D.A., Gratton, C., 2015. Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield. *Ecol. Appl.* 25, 652–661. <https://doi.org/10.1890/14-0570.1>.
- Liere, H., Jha, S., Philpott, S.M., 2017. Intersection between biodiversity conservation, agroecology, and ecosystem services. *Agroecol. Sustain.* Food Syst. 41, 723–760. <https://doi.org/10.1080/21683565.2017.1330796>.
- Luginbill, P., 1928. The Fall Army Worm. United States Dep. Agric, Washington, DC. [https://doi.org/10.1016/0003-6870\(73\)90259-7](https://doi.org/10.1016/0003-6870(73)90259-7).
- Margosian, M.L., Garrett, K.A., Hutchinson, J.M.S., With, K.A., 2009. Connectivity of the american agricultural landscape: assessing the national risk of crop pest and disease spread. *Bioscience* 59, 141–151. <https://doi.org/10.1525/bio.2009.59.2.7>.
- Meehan, T.D., Werling, B.P., Landis, D.A., Gratton, C., 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci.* 108, 11500–11505. <https://doi.org/10.1073/pnas.1100751108>.
- Michels, G.J., Burd, J.D., 2007. IPM case studies: sorghum. In: Emden, H.F. van, Harrington, R. (Eds.), *Aphids as Crop Pests*. CAB International, Oxfordshire, UK, pp. 627–637. <https://doi.org/10.1079/9781780647098.0557>.
- Midega, C.A.O., Jonsson, M., Khan, Z.R., Ekbohm, B., 2014. Effects of landscape complexity and habitat management on stemborer colonization, parasitism and damage to maize. *Agric. Ecosyst. Environ.* 188, 289–293. <https://doi.org/10.1016/j.agee.2014.02.028>.
- Ministerio de Ganadería Agrícola y Pesca, 2016. Comision Nacional de Estudio Agronomico de la Tierra (CONEAT). MGAP, Montevideo, Uruguay.
- Mitchell, E.R., McNeil, J.N., Westbrook, J.K., Silvain, J.F., Lalanne-Cassou, B., Chalfant, R.B., Pair, S.D., Waddill, V.H., Sotomayor-Rios, A., Proshold, F.I., 1991. Seasonal population of fall armyworm, (Lepidoptera: noctuidae) in the caribbean basin and northward to Canada. *J. Entomol. Sci.* 26, 39–50. <https://doi.org/10.18474/0749-8004-26.1.39>.
- Molina, C., Perrachon, J., 2010. Sistemas agrícolas – ganaderos: una sistema Uruguayo. *Rev. Plan Agropecu.* 134, 63–67.
- Murua, M.G., Virla, E.G., 2004. Presencia invernal de *Spodoptera frugiperda* (Smith) (Lepidoptera: noctuidae) en el área maicera de la provincia de Tucumán. *Argentina. Rev. la Fac. Agron.* 105, 133–139.
- New, T.R., Samways, M.J., 2014. Insect conservation in the southern temperate zones: an overview. *Austral Entomol.* 53, 26–31. <https://doi.org/10.1111/aen.12071>.
- Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhussaini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., MacE, G. M., Scharlemann, J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. <https://doi.org/10.1038/nature14324>.
- Norton, L., Johnson, P., Joys, A., Stuart, R., Chamberlain, D., Feber, R., Firbank, L., Manley, W., Wolfe, M., Hart, B., Mathews, F., Macdonald, D., Fuller, R.J., 2009. Consequences of organic and non-organic farming practices for field, farm and landscape complexity. *Agric. Ecosyst. Environ.* 129, 221–227. <https://doi.org/10.1016/j.agee.2008.09.002>.
- O’Rourke, M.E., Petersen, M.J., 2017. Extending the ‘resource concentration hypothesis’ to the landscape-scale by considering dispersal mortality and fitness costs. *Agric. Ecosyst. Environ.* 249, 1–3. <https://doi.org/10.1016/j.agee.2017.07.022>.
- Oyier, M.O., Owuochie, J.O., Oyoo, M.E., Cheruiyot, E., Mulianga, B., Rono, J., 2017. Effect of harvesting stage on sweet sorghum (*Sorghum bicolor* L.) genotypes in western Kenya. *Sci. World J.*, 8249532.
- Park, Y.L., Obrycki, J.J., 2004. Spatio-temporal distribution of corn leaf aphids (Homoptera: aphididae) and lady beetles (Coleoptera: coccinellidae) in Iowa cornfields. *Biol. Control* 31, 210–217. <https://doi.org/10.1016/j.biocontrol.2004.06.008>.
- Perez-Alvarez, R., Nault, B.A., Poveda, K., 2018. Contrasting effects of landscape composition on crop yield mediated by specialist herbivores. *Ecol. Appl.* 28, 842–853. <https://doi.org/10.1002/eap.1965>.
- Perović, D.J., Gurr, G.M., Raman, A., Nicol, H.I., 2010. Effect of landscape composition and arrangement on biological control agents in a simplified agricultural system: a cost-distance approach. *Biol. Control* 52, 263–270. <https://doi.org/10.1016/j.biocontrol.2009.09.014>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2018. *Nlme: Linear and Nonlinear Mixed Effects Models. R Packag. Version 3.1-137*. <https://CRAN.R-project.org/package=Nlme>.
- Poniso, L.C., M’Gonigle, L.K., Kremen, C., 2016. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. *Glob. Change Biol.* 22, 704–715. <https://doi.org/10.1111/gcb.13117>.
- Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philos. Trans. R. Soc. B Biol. Sci.* 365, 2959–2971. <https://doi.org/10.1098/rstb.2010.0143>.
- QGIS Development Team, 2018. QGIS Geographic Information System. Open Source Geospatial Found. Proj. <http://qgis.org>.
- R Development Core Team, 2017. *R: a Language and Environment for Statistical Computing, Version 3.4.2*. Vienna, Austria.
- Ramankutty, N., Mehrabi, Z., Waha, K., Jarvis, L., Kremen, C., Herrero, M., Rieseberg, L. H., 2018. Trends in global agricultural land use: implications for environmental health and food security. *Annu. Rev. Plant Biol.* 69 <https://doi.org/10.1146/annurev-arplant-042817-040256>.
- Rand, T.A., Waters, D.K., Blodgett, S.L., Knodel, J.J., Harris, M.O., 2014. Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes. *Agric. Ecosyst. Environ.* 186, 135–143. <https://doi.org/10.1016/j.agee.2014.01.022>.

- Richardson, A.D., Duigan, S.P., Berlyn, G.P., 2002. An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytol.* 153, 185–194. <https://doi.org/10.1046/j.0028-646X.2001.00289.x>.
- Rodriguez-Saona, C.R., Musser, R.O., Vogel, H., Hum-Musser, S.M., Thaler, J.S., 2010. Molecular, biochemical, and organismal analyses of tomato plants simultaneously attacked by herbivores from two feeding guilds. *J. Chem. Ecol.* 36, 1043–1057. <https://doi.org/10.1007/s10886-010-9854-7>.
- Roschewitz, I., Hücker, M., Tschardtke, T., Thies, C., 2005. The influence of landscape context and farming practices on parasitism of cereal aphids. *Agric. Ecosyst. Environ.* 108, 218–227. <https://doi.org/10.1016/j.agee.2005.02.005>.
- Roubos, C.R., Rodriguez-Saona, C., Isaacs, R., 2014. Mitigating the effects of insecticides on arthropod biological control at field and landscape scales. *Biol. Control* 75, 28–38. <https://doi.org/10.1016/j.biocontrol.2014.01.006>.
- Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *J. Appl. Ecol.* 50, 345–354. <https://doi.org/10.1111/1365-2664.12055>.
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H.G., Ekbom, B., 2014. Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia* 175, 971–983. <https://doi.org/10.1007/s00442-014-2949-z>.
- Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tschardtke, T., Weisser, W.W., Winqvist, C., Woltz, M., Bommarco, R., 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. *Agric. Ecosyst. Environ.* 221, 198–204. <https://doi.org/10.1016/j.agee.2016.01.039>.
- Schepers, J.S., Blackmer, T.M., Wilhelm, W.W., Resende, M., 1996. Transmittance and reflectance measurements of corn leaves from plants with different nitrogen and water supply. *J. Plant Physiol.* 148, 523–529. [https://doi.org/10.1016/S0176-1617\(96\)80071-X](https://doi.org/10.1016/S0176-1617(96)80071-X).
- Schmidt, N.P., O'neal, M., Dixon, P.M., 2008. Aphidophagous predators in Iowa soybean: a community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 101, 341–350.
- Schnepf, R.D., Dohman, E., Markel, C.B., 2001. Agriculture in Brazil and Argentina: developments and Prospects for Major Field Crops, U.S. Department of Agriculture, Agriculture and Trade Report. Washington, DC. [https://doi.org/10.1016/S0378-4290\(01\)00197-6](https://doi.org/10.1016/S0378-4290(01)00197-6).
- Serra, W.S., González, G., Greco-Spingola, S., 2013. Lista sistemática y distribución geográfica de las especies de Coccinellidae (Insecta: coleoptera) presentes en Uruguay. *Boletín Soc. Entomológica Aragon.* 53, 229–242.
- Shipley, B., 2000. Cause and Correlation in Biology: a User's Guide to Path Analysis, Structural Equations and Causal Inference. Cambridge University Press, Cambridge, UK.
- Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90, 363–368.
- Shriar, A.J., 2000. Agricultural intensity and its measurement in frontier regions. *Agrofor. Syst.* 49, 301–318. <https://doi.org/10.1023/A:1006316131781>.
- Silva, R.B., Cruz, I., Zanuncio, J.C., Lourdes, M.De, Figueiredo, C., Zanuncio, T.V., Serrão, J.E., 2013. *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: noctuidae) eggs as alternative food for rearing of lady beetles *Eriopis connexa* (Germar) (Coleoptera: coccinellidae). *Biol. Control* 64, 101–105. <https://doi.org/10.1016/j.biocontrol.2012.09.013>.
- Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhassner, I., Lefebvre, G., Gaufré, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-García, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tschardtke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proc. Natl. Acad. Sci.* 116, 16442–16447. <https://doi.org/10.1073/pnas.1906419116>.
- Smith, P., Bustamante, M., Ahammad, Helal, Clark, H., Dong, H., Elsidig, E.A., Haberl, H., Harper, R., House, J., Jafari, M., Maser, O., Mbow, C., Ravingranath, N. H., Rice, C.W., Robledo Abad, C., Romanovskaya, A., Sperling, F., Tubiello, F.N., 2014. Agriculture, forestry and other Land use (AFOLU). In: Edenhofer, O., Pichs-Madruga, R., Sokona, Y., Ferahani, E., Kadner, S., Seyboth, K., Adler, A., Baum, I., Brunner, S., Eickemeier, P., Kriemann, B., Savolainen, J., Schlömer, S., von Stechow, C., Zwickel, T., Minx, J.C. (Eds.), *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 811–922.
- Soler, R., Badenes-Pérez, F.R., Broekgaarden, C., Zheng, S.J., David, A., Boland, W., Dicke, M., 2012. Plant-mediated facilitation between a leaf-feeding and a phloem-feeding insect in a brassicaceous plant: from insect performance to gene transcription. *Funct. Ecol.* 26, 156–166. <https://doi.org/10.1111/j.1365-2435.2011.01902.x>.
- Thies, C., Roschewitz, I., Tschardtke, T., 2005. The landscape context of cereal aphid – parasitoid interactions. *Proc. R. Soc. B* 272, 203–210. <https://doi.org/10.1098/rspb.2004.2902>.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W. W., Winqvist, C., Tschardtke, T., 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol. Appl.* 21, 2187–2196. <https://doi.org/10.1890/10.0929.1>.
- Thode, H.C., 2002. Testing for Normality. Marcel Dekker, Inc, New York, USA. <https://doi.org/10.1360/zd-2013-43-6-1064>.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity on ecosystem service management. *Ecol. Lett.* 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151, 53–59. <https://doi.org/10.1016/j.biocon.2012.01.068>.
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *J. Appl. Ecol.* 51, 746–755. <https://doi.org/10.1111/1365-2664.12219>.
- Tylianakis, J.M., Tschardtke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host – parasitoid food webs. *Nature* 445, 202–205. <https://doi.org/10.1038/nature05429>.
- van den Bosch, R., Messenger, P.S., Gutierrez, A.P., 1973. *An Introduction to Biological Control*. Springer, Boston, USA.
- Vanderlip, R.L., Reeves, H.E., 1972. Growth stages of sorghum [*Sorghum bicolor*, (L.) Moench]. *J. Agron. J.* 64, 13–16.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tschardtke, T., Weisser, W.W., Bommarco, R., 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *J. Appl. Ecol.* 48, 570–579. <https://doi.org/10.1111/j.1365-2664.2010.01950.x>.
- World Resources Institute, 2005. *Millennium Ecosystem Assessment, Ecosystems and Human Well-being*. Island Press, Washington, DC.
- Ximenez-Embun, M.G., Zaviezo, T., Grez, A., 2014. Seasonal, spatial and diel partitioning of *Acyrtosiphon pisum* (Hemiptera: aphididae) predators and predation in alfalfa fields. *Biol. Control* 69, 1–7. <https://doi.org/10.1016/j.biocontrol.2013.10.012>.
- Xiu, C., Zhang, W., Xu, B., Wyckhuys, K.A.G., Cai, X., Su, H., Lu, Y., 2019. Volatiles from aphid-infested plants attract adults of the multicolored Asian lady beetle *Harmonia axyridis*. *Biol. Control* 129, 1–11. <https://doi.org/10.1016/j.biocontrol.2018.11.008>.
- Zhao, Z., Hui, C., Hardev, S., Ouyang, F., Dong, Z., 2014. Responses of cereal aphids and their parasitic wasps to landscape complexity. *J. Econ. Entomol.* 107, 630–637.