



## Landscape complexity affects cover and species richness of weeds in Brazilian agricultural environments

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Received 1 October 2015; received in revised form 23 September 2016; accepted 3 October 2016  
Available online 11 October 2016

### Abstract

The influence of the landscape context on weed communities in farmland has been investigated mostly in temperate regions, while there is a paucity of information for the Neotropics. The aim of this study was to estimate the effects of landscape complexity on local weed communities in Paraná State, southern Brazil. We addressed three questions: (i) Do species richness and percent cover of weeds increase with increasing landscape complexity? (ii) Does landscape complexity similarly affect native and exotic species? and (iii) Do the effects of landscape attributes on local weed communities differ between spatial scales? To answer these questions, we assessed species richness and cover of weeds along the edges of 18 wheat fields. Altitude, field size and three landscape complexity metrics (percent cover of non-crop habitats; edge density and habitat diversity) were used as explanatory variables. Landscape metrics were calculated at four spatial scales: 0.5, 1, 1.5 and 2 km. We recorded 52 weed species (24 exotic, 25 native and 3 morphospecies) belonging to 45 genera and 18 families. Total richness and native richness increased with increasing SDI and ED at 0.5, 1.5 and 2.0 km radii, while exotic richness was related only to SDI at 0.5 km. Percent cover of weeds was positively correlated with ED at 0.5, 1.5 and 2.0 km radii; native cover and exotic cover did not respond to landscape complexity nor local factors. Our findings suggest that the increment of landscape complexity benefited particularly native species which seem to be less adapted to constant disturbances in the crop matrix than exotic species and probably depend on the presence of more stable habitats in the surrounding landscape. Therefore, agri-environment schemes designed to preserve biodiversity in farmland must promote landscape complexity through the diversification of crops and conservation of non-crop habitats at multiple spatial scales.

### Zusammenfassung

Der Einfluss des Landschaftskontextes auf die Unkrautgemeinschaften im Ackerland wurde meist in gemäßigten Breiten untersucht, während für die Neotropis nur wenige Informationen verfügbar sind. Das Ziel dieser Untersuchung war, die Auswirkungen der Landschaftskomplexität auf lokale Unkrautgemeinschaften im Bundesstaat Paraná (Süd-Brasilien) zu bestimmen. Wir fragten: (1) Steigen Artenreichtum und Bedeckungsgrad der Unkräuter mit zunehmender Landschaftskomplexität? (2) Beeinflusst die Landschaftskomplexität einheimische und exotische Arten in gleicher Weise? (3) Verändern sich

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die die Effekte der Landschaftsmerkmale auf die lokalen Unkrautgemeinschaften mit der räumlichen Skala? Wir bestimmten Artenreichtum und Bedeckungsgrad der Unkräuter entlang der Ränder von 18 Weizenfeldern. Höhe, Feldgröße und drei Maße der Landschaftskomplexität (Flächenanteil von naturnahen Habitaten, Dichte der Feldrandstrukturen und Habitatdiversität) dienten als unabhängige Variablen. Die Landschaftsparameter wurden für vier räumliche Skalen berechnet: Radien von 0.5, 1.0, 1.5 und 2.0 km. Wir stellten 52 Unkrautarten aus 45 Gattungen und 18 Familien fest (24 exotische und 25 einheimische Arten sowie drei Morphospezies). Der Gesamtartenreichtum und der Artenreichtum der Einheimischen stiegen mit zunehmender Habitatdiversität und Feldranddichte für die 0.5-, 1.5- und 2.0-km-Radien, während der Artenreichtum der Exoten nur mit der Habitatdiversität bei 0.5 km zunahm. Der Bedeckungsgrad der Unkräuter war für die 0.5-, 1.5- und 2.0-km-Radien positiv mit der Feldranddichte korreliert, während die Bedeckungsgrade der einheimischen und exotischen Arten weder auf die Landschaftskomplexität noch auf lokale Faktoren reagierten. Unsere Ergebnisse legen nahe, dass zunehmende Landschaftskomplexität insbesondere einheimische Arten begünstigte, die weniger an ständige Störungen in der Feldfruchtmatrix angepasst sind als exotische Arten. Deshalb müssen Agrar-Umwelt-Programme zum Erhalt der Biodiversität die Landschaftsheterogenität durch eine Diversifizierung der angebauten Feldfrüchte und den Erhalt naturnaher Habitats auf unterschiedlichen räumlichen Skalen fördern.

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**Keywords:** Arable fields; Biodiversity; Edge density; Landscape heterogeneity; Ruderal plants

## Introduction

Agricultural intensification negatively affects biodiversity and related ecosystem services at local and landscape levels (Flohre et al. 2011; Meehan, Werling, Landis, & Gratton 2011; Tschardtke, Klein, Kruess, Steffan-Dewenter, & Thies 2005; Weibull, Östman, & Granqvist 2003). The local management of agricultural fields that includes the overuse of agrochemicals and intensive tillage operations as well as the massive conversion of natural and semi-natural habitats into arable fields (landscape simplification) has resulted in biodiversity losses, which also includes the decline of crop-associated species such as weeds (Gabriel, Thies, & Tschardtke 2005; Meyer, Jauker, & Steffan-Dewenter 2009; Roschewitz, Gabriel, Tschardtke, & Thies 2005).

Weeds provide benefits and disservices in agroecosystems (Petit et al. 2016); on the one hand, these plants negatively affect crop productivity due to competition for light, water and nutrients (Oerke 2006). On the other hand, weeds can also support high biological diversity and enhance soil health (Kumalasari & Bergmeier 2014). Moreover, weeds provide resources for birds (Marshall et al. 2003) and beneficial insects such as pollinators (Gibson, Nelson, Hopkins, Hamlett, & Memmott 2006; Requier et al. 2015) and natural enemies (Landis, Wratten, & Gurr 2000; Meyer et al. 2009; Stephan, Albertsson, Wang, & Porcel 2016).

The overuse of herbicides and tillage operations stimulates the periodic colonization of arable fields by weeds through seed rain from natural and semi-natural habitats (e.g., field edges, road verges, fallows, hedgerows, forest fragments, grasslands) in the surrounding landscape (Fried, Petit, Dessaint, & Reboud 2009; Gaba, Chauvel, Dessaint, Bretagnolle, & Petit 2010; Gabriel et al. 2005). Therefore, complex landscapes with high habitat diversity and relatively high percentage of non-crop habitats provide great opportu-

nity for the spillover of organisms between distinct habitat types (Tschardtke et al. 2012). Indeed, studies conducted in temperate regions have indicated that complex landscapes support higher weed species richness than do simplified landscapes dominated by arable fields (Gaba et al. 2010; Gabriel et al. 2005; Kovács-Hostyánszki, Batáry, Báldi, & Harnos 2011; Poggio, Chaneton, & Ghersa 2010; Roschewitz et al. 2005). Additionally, these studies found that weeds exhibit significant associations with landscape variables within 0.2, 0.5, 1 and 2 km radii, suggesting that these spatial scales are the most relevant for weed flora in agricultural landscapes.

Native and exotic species exhibit similar life-history characteristics (Leishman, Thomson, & Cooke 2010) and maybe respond in the same way to environmental conditions and landscape elements. In fact, studies have indicated that both native and exotic plants presented similar responses to landscape heterogeneity (Deutschewitz, Lausch, Kühn, & Klotz 2003; Levine 2000; Sax 2002). However, recent studies suggest that exotic species are better adapted than native species to constant human-induced disturbances (Catford et al. 2012; Chen et al. 2017; Pyšek, Richardson, & Williamson 2004). Thus, the risk of biological invasion increases with increasing anthropogenic disturbances at local and landscape levels (Malavasi, Carboni, Cutini, Carranza, & Acosta 2014; Polce, Kunin, Biesmeijer, Dauber, & Phillips 2011). Conversely, high levels of landscape complexity increase the availability of less perturbed habitats for native species, which under low levels of anthropogenic disturbances can impede invasions by exotic species (Chen et al. 2017; Cornell & Karlson 1997).

So far, the influence of the landscape context on local weed species richness has been investigated mostly in temperate regions, while there is a paucity of information for the Neotropics. The aim of this study was to estimate the effects of landscape complexity on local weed communities

in the edges of wheat fields in Paraná State, southern Brazil. Here, high landscape complexity means that the landscape presents high diversity of crop and non-crop habitat types and high proportions of non-crop habitats. Thus, we calculated three landscape complexity metrics at different spatial extents: percent cover of non-crop habitats (NCCover), edge density (ED) and landscape Shannon diversity index (SDI), hereafter habitat diversity. Additionally, we used field size and altitude as local explanatory variables.

We aim to answer three questions: (i) Do species richness and cover (%) of weeds increase with increasing landscape complexity? (ii) Do landscape complexity variables similarly affect native and exotic species? and (iii) Do the effects of landscape attributes on local weed communities differ between spatial scales? We expect that overall species richness and cover of weeds will increase with increasing landscape complexity (Fig. 1A). We also expect that the positive effects of landscape complexity variables and spatial scales will be stronger on native species (Fig. 1C and B, respectively) which seem to be less adapted to constant disturbances in the crop matrix and probably depend on the presence of more stable habitats in the surrounding landscape.

To our knowledge, this is the first study which investigates the relationship between the local weed communities and the surrounding landscape composition in a Neotropical region. The positive effect of landscape complexity on the spillover of weeds is probably more pronounced in the Neotropics, when compared to temperate regions. Such a remarkable effect could occur as a response to the warm climate, which allows farmers grow more crops per year, resulting in high levels of agricultural intensification on local and landscape levels. We argue that landscape complexity is probably crucial for the maintenance of native weed diversity in crop-dominated regions and possibly reduces the risk of biological invasion.

## Material and methods

### Study sites

We conducted the study in 54 edges distributed among 18 conventionally managed wheat fields (three edges per field) that encompass a gradient of landscape complexity in the Paraná State, southern Brazil (Fig. 2). Nine sites were sampled in 2012 and nine in 2013. All fields were sown by the direct planting system (no-till farming), were located in non-overlapping landscapes, and the distance between the sites varied from 4.4 to 45.9 km. Field size ranged from 10.2 to 77.8 ha and altitude varied from 380 to 690 m above sea level.

We selected the sampling sites by varying the structure of surrounding landscape (previously accessed by using land use maps), as well as the consent of farmers who authorized the data collection on their lands. The soils in all sites have the same parent material (basalt) and consist of reddish clay (Rhodic Ferralsol; FAO 1994). The study region encompasses fragments of tropical forest, wetlands, pastures, abandoned

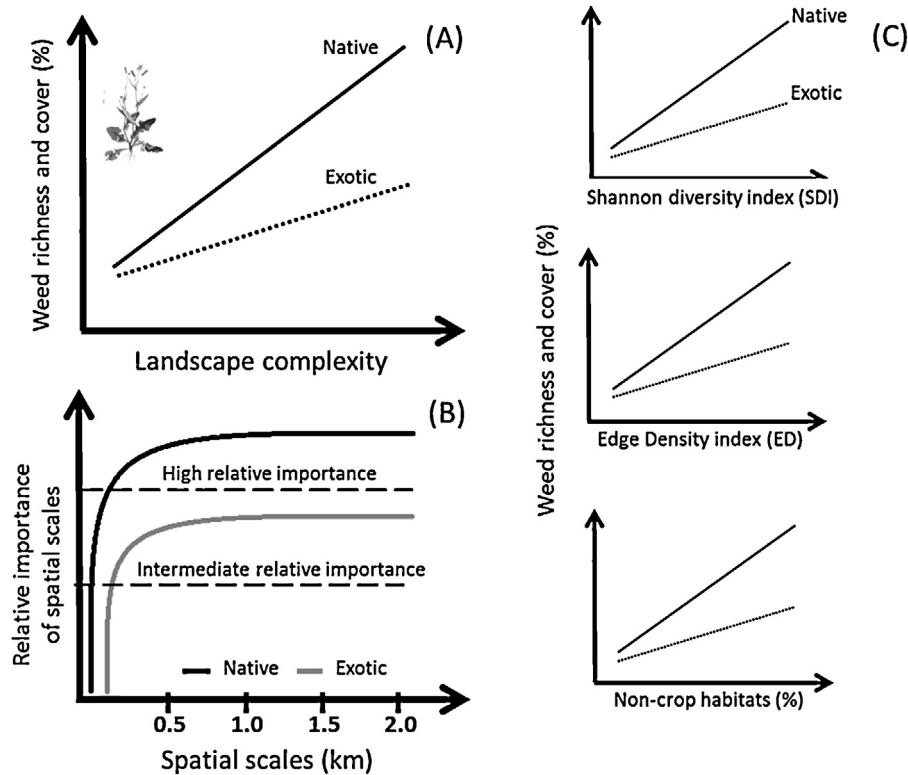
pastures, and perennial monocultures such as coffee, citrus and eucalyptus plantations. All habitats listed above are immersed in a matrix of cereal fields, where the following crop-rotation is adopted: soybean is cultivated in the summer, wheat in the winter, and corn in both seasons. Tropical forest and abandoned pastures are the dominant non-crop habitats in the study region. Forest habitat is represented by the Seasonal Semideciduous Forest (SF), a type of Atlantic Forest that suffered intensive habitat loss and currently covers only 7% of its original extent (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota 2009). Abandoned pastures are composed by exotic grasses (*Brachiaria* sp.) and scattered bushes, and present a high diversity and density of weeds, which also occur in forest edges, crop edges, pastures, road verges, wetlands and hedgerows.

### Weed surveys

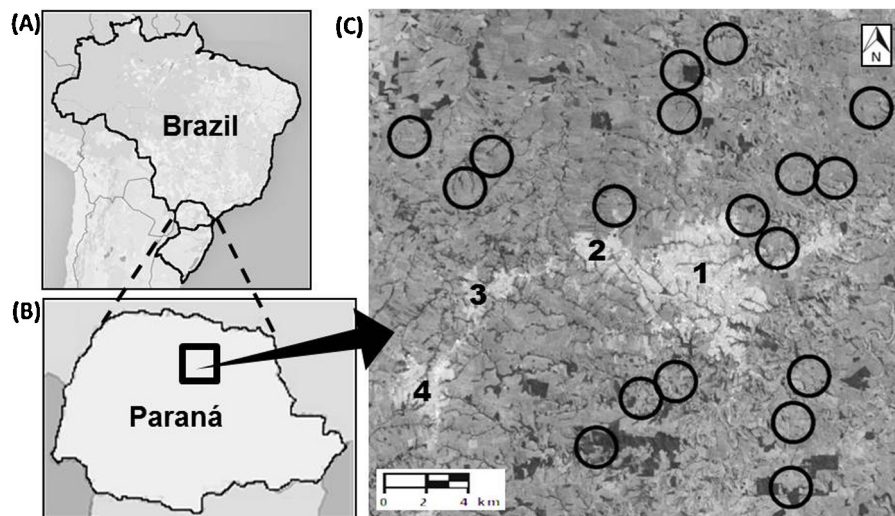
We sampled weeds (herbs and grasses) in 15 plots (1 m × 5 m) at each of the 18 study sites, totalizing 54 edges. The plots were established in three distinct edges per site, with five sampling points per edge, spaced 5 m apart. The edges were randomly selected. We used identification keys available in Kissmann and Groth (1999a, 1999b, 1999c) to identify all herbs and grasses within the plots to the finest possible taxonomic level. Additionally, we classified each weed species according to its origin: native or exotic to South America. This classification was done using data available in the Invasive Species Compendium (<http://www.cabi.org/isc/>), as well as literature information. We estimated species richness and percent cover of native and exotic species, as well as of total species richness (native + exotic). Species richness and percent cover were estimated per site; therefore, we pooled the weed data from the three edges of each site. Species richness is the cumulative number of all species recorded in the three edges, and percent cover is the mean cover of the same three edges, which we estimated visually. To minimize the effects of herbicide and fertilizer inputs, we set up the 15 sampling plots outside of the wheat fields, along the wheat edges; the plots were narrow, uncultivated strips of 1–5 m in width. Plots were fixed at 1 m from the first wheat row, as well as from other adjacent cereal fields. All the sampling plots presented weeds, bare soil and scattered bushes, but trees were absent. Additionally, all sites were sampled once during the stages of wheat grain formation, when herbicide applications are rare. Indeed, herbicides are used routinely in the first 24 days after seedling emergence, during the critical period of weed competition in wheat crops (Agostinetto, Rigoli, Schaedler, Tironi, & Santos 2008).

### Landscape variables

Studies conducted in temperate regions have indicated that local weed communities exhibit significant associations with landscape composition within a 2-km range (Gabriel et al. 2005; Kovács-Hostyánszki et al. 2011; Roschewitz et al.



**Fig. 1.** (A) Expected relationship between weeds and landscape complexity within Brazilian agricultural environments. (B) Expected relative importance of spatial scales to explain the relationship between weeds and landscape complexity. Dashed lines represent the threshold of intermediate and high relative importance of spatial scales. (C) Expected relationship between weeds (native and exotic) and landscape complexity metrics (habitat diversity, edge density and percent cover of non-crop habitats). Dotted and continuous lines in (A) and (C) refer to native and exotic weeds, respectively.



**Fig. 2.** (A) Location of Paraná state in Brazil, (B) location of study region in northern Paraná State and (C) location of the 18 landscape sectors in the metropolitan region of Londrina city.

Source: “Metropolitan region of Londrina city” 23°55′46″S and 51°19′11″W. Google Earth. September 04, 2013. The numbers 1, 2, 3 and 4 represent the urban area of the cities of Londrina (1), Cambé (2), Rolândia (3) and Arapongas (4). Black circles represent the landscape sectors of 2 km radius.

2005). Considering these dimensions as a reference, we calculated the landscape metrics at four spatial scales, with radii ranging from 0.5 to 2 km (at 0.5-km intervals) using the field

edges as centroid. We used Landsat/TM 5 satellite images, as well as ground verification to generate a land cover and land use map at 1/50,000 spatial scale. The satellite images have a

**Table 1.** Variation of landscape metrics (min–max) for the percent cover of non-crop habitats (NCCover), landscape Shannon diversity index (SDI) and edge density index (ED) at four spatial scales.

Landscape metrics	Spatial scales (km)			
	0.5	1.0	1.5	2.0
(NCCover)	0.3–71.9	4.4–73.5	7.4–81.3	7.4–74.4
SDI	1.28–3.00	1.16–3.40	1.44–3.03	1.56–3.06
ED	299–536	182–422	178–409	178–387

spatial resolution of 30 m, are projected in UTM SAD 1969, and were acquired between 2010 and 2012. We mapped a total of 12 land cover and land use classes: wheat, corn, citrus, coffee, abandoned pasture, forest, wetland, water, built-up area, sugarcane, eucalyptus and greenery. Then, we calculated three landscape complexity metrics: (1) percent cover of non-crop habitats (NCCover), edge density (ED) and landscape Shannon diversity index (SDI). For the four spatial scales described above, we calculated those three metrics for each landscape. The three variables related to landscape complexity varied considerably among sites and spatial scales (Table 1). The percent cover of non-crop habitats (NCCover) comprised the total area covered by forest fragments, abandoned pastures and wetlands. SDI values range from 0 to infinity (Nagendra 2002) and increase with an increasing number of habitat types in the landscape. ED quantifies the amount of edges in the landscape and consists of the sum of the lengths (m) of all edges, divided by the total landscape area ( $m^2$ ), multiplied by 10,000 to convert to hectares (McGarigal 2015). We calculated SDI and ED using all the land use classes mapped in the landscapes. All the landscape metrics were calculated using the software ArcGIS 10.1 (ESRI 2005) with the *Patch Analyst* extension for SDI and ED (Rempel, Kaukinen, & Carr 2012). Additionally, we estimated field size (ha) and altitude (m.a.s.l) and used them as explanatory variables. Prior to analyses, altitude and ED were log-transformed.

## Statistical analysis

We used Generalized Linear Mixed models (GLMMs; Zuur, Ieno, Walker, Saveliev, & Smith 2009) to estimate the relative contribution of explanatory variables (NCCover), SDI, ED, field size and altitude on species richness and cover (%) of native weeds, exotic weeds and total richness. We modeled weed species richness and percent cover using Poisson and Gaussian error structure, respectively. For each dependent variable, we analyzed five competing models plus a null model, which represented the absence of effect similarly to Martensen, Ribeiro, Banks-Leite, Prado, and Metzger (2012). We used mixed models with GLMM. Since our data were collected in two years the variable ‘year’ was included in the models as a random effect.

We identified the best models according to the Akaike Information Criterion (AIC, Burnham & Anderson 1998) with the three following parameters: (1) Akaike Information Criterion with the small sample correction (AICc); (2) AICc weight (wAICc); and (3) AICc delta value ( $\Delta AICc$ ). AICc ranks the models from best to worst (Hurvich & Tsai 1989); wAICc represents the weight of evidence in favor of a given model being the best of the set (Burnham & Anderson 2002); and  $\Delta AICc$  is the difference between the AICc of a model and the best model with lowest AICc value (Martensen, Pimentel, & Metzger 2008). The models that presented p-values  $< 0.05$ , wAICc  $\geq 0.10$  and  $\Delta AICc \leq 2.0$  were considered as equally plausible to explain the patterns of the response variables. We conducted the AICc analysis at each of our four spatial scales (0.5–2 km). All analyses were performed in R version 3.0.2, using the “lme4” package (Bates, Maechler, Bolker, & Walker 2014), with glmer function for weed species richness and the “nlme” package (Pinheiro, Bates, DebRoy, & Sarkar 2015) with lme function for weed cover (%).

## Results

We recorded 52 weed species (25 natives and 24 exotic species) belonging to 45 genera and 18 families (see Appendix A). Three species were identified to the genus level and were not classified as native nor exotic. Species richness and percent cover varied considerably among the 18 sites: total weed richness (min = 2 to max = 26 species), native weed richness (min = 0 to max = 14), exotic weed richness (min = 2 to max = 11 species), total weed cover (min = 1.7 to max = 73.2%), native weed cover (min = 1.1 to max = 41.9%) and exotic weed cover (min = 1.5 to max = 53%). The following species were the most common ones: the exotic *Commelina benghalensis* L., which occurred in 14 sites; the native species *Emilia sonchifolia* (L.) DC and *Bidens pilosa* L., both of which occurred in 12 sites; and the exotic *Sonchus oleraceus* L., occurring in 11 sites.

Total richness was positively associated with SDI and ED at 0.5, 1.5 and 2 km radii. Total weed cover (%) presented significant association only with ED also at 0.5, 1.5 and 2 km radii. Native richness increased with increasing SDI and ED independently of the used spatial scale, while exotic richness was exclusively and positively explained by SDI only at 0.5 km radius (see Table 2 and Fig. 2). The percent cover of non-crop habitats, field size and altitude had no effect on the species richness and cover of weeds. Native weed cover and exotic weed cover were not explained by any of the explanatory variables.

## Discussion

As expected, our results suggest that the local species richness and cover of weeds increased with increasing landscape complexity at multiple spatial scales. These findings

**Table 2.** Plausible models to explain the weed richness and cover in 18 agricultural landscapes in Paraná State, southern Brazil. AICc = Akaike Information Criterion with the small sample correction;  $\Delta$ AICc = delta value of AICc; and wAICc = weight of evidence of the models. Asterisks indicate the level of significance of the models (model fit). Landscape metrics: Shannon diversity index (SDI) and edge density index (ED).

Dependent variable	Model	Spatial scales (km)	$\Delta$ AICc	wAICc
Total weed richness	~SDI***	0.5	0.0	0.991
	~ED**	2.0	0.0	0.744
	~ED**	1.5	0.0	0.634
	~SDI*	1.5	2.0	0.209
Total weed cover (%)	~ED*	1.5	0.0	0.849
	~ED*	2.0	0.0	0.767
	~ED*	0.5	0.0	0.724
Native weed richness	~SDI***	0.5	0.0	0.968
	~ED**	2.0	0.0	0.669
	~ED*	1.5	0.0	0.592
	~SDI*	1.5	2.0	0.191
Exotic weed richness	~SDI*	0.5	0.0	0.485

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

\*\*\*  $p < 0.001$ .

are consistent with the results of studies conducted in European agricultural landscapes. Gabriel et al. (2005) found that local weed species richness in wheat fields was strongly influenced by habitat diversity and edge density at 2.0 km radius. Similarly, Roschewitz et al. (2005) also observed that local weed species diversity was higher in wheat fields localized in complex landscapes than fields in simplified landscapes.

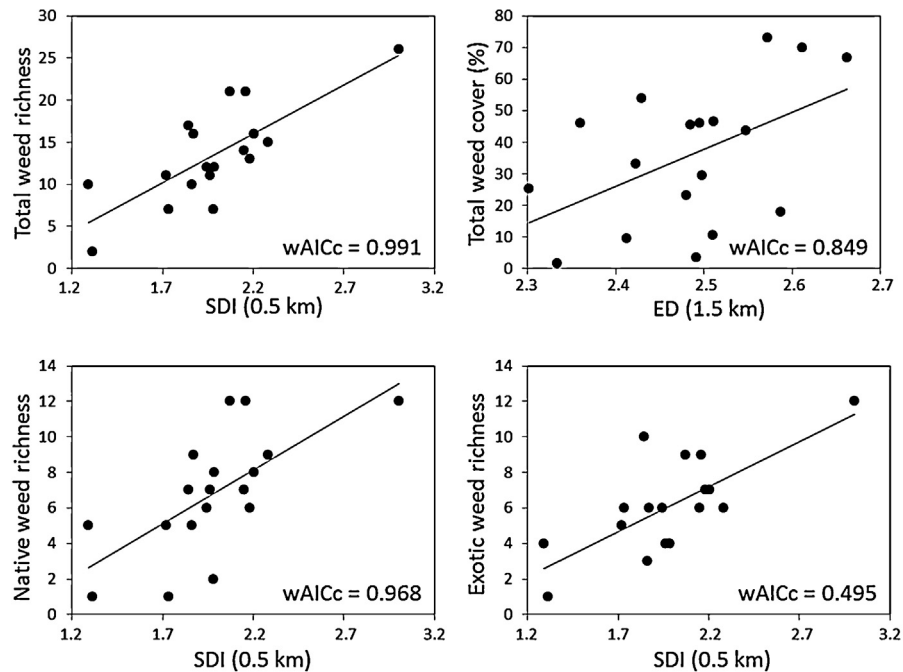
A high diversity of crop and non-crop habitats in the surrounding matrix may maintain a large weed species pool (Gabriel et al. 2005; Ma 2008; Valone & Hoffman 2002; Zobel 1997) and may enhance colonization probabilities due to a spillover of species through seed rain from a variety of adjacent habitat types (Dunning et al. 1992; Roschewitz et al. 2005). Furthermore, ED probably intensifies the effects of SDI on the spillover of weeds for two reasons. First, edges are submitted to less intensive herbicide and fertilizer applications (Roschewitz et al. 2005; Wagner & Edwards 2001) and support higher weed species richness and cover compared to the center of the crop (Gabriel et al. 2005; Hald 1999; Wilson & Aebischer 1995). Second, edges support a variety of ruderal habitats such as hedgerows, road merges and forest edges. These habitats are relatively stable, free of agrochemicals and can provide spatio-temporal refuges for crop-associated biodiversity (Altieri 1999; Tschamtkke et al. 2007, 2012) including weeds (Fried et al. 2009; Gaba et al. 2010; Gabriel et al. 2005).

### Combined effects of edge density and habitat diversity

The synergic effect of habitat diversity and edge density on the spillover of weeds can be particularly important in the study region where both agricultural matrix (cereal fields) and the dominant non-crop habitat type (tropical forest) seem to

be unsustainable environments for the long-term persistence of weeds. Cereal fields are highly managed; the warm climate allows two or more crops per year resulting in constant disturbances throughout the year. On the other hand, tropical forest is relatively stable; however, the low light conditions in the understory prevent the occurrence of crop-associated weeds, restricting them to forest edges. Indeed, shaded environments disrupt weed seed germination and retard weed growth (Schonbeck 2013). In this context, the absence of effect of non-crop habitats on weeds was probably influenced by the dominance of tropical forest.

Our results also supported the hypothesis that the positive effects of landscape variables and spatial scales will be stronger on native species than on exotic species. The increment of landscape complexity benefited both native and exotic species, but only native species presented multi-scale responses. Indeed, native richness was explained by the synergic effect of habitat diversity and edge density at 0.5, 1.5 and 2 km radii, while exotic richness exhibited positive association only with habitat diversity at 0.5 km radius. These findings can be associated with the fact that native species present low tolerance to constant human-induced disturbances (Fleming, Diffendorfer, & Zedler 2009; Shea, Roxburgh, & Rauschert 2004). Thus, native weeds seem to depend on the presence of more stable habitats (e.g., crop edges, natural and semi-natural habitats) in the surrounding landscape to maintain high species richness in crop dominated regions. In contrast, exotic species have novel evolutionary histories (e.g., enemy release, high physiological plasticity, high propagule pressure) that confer competitive advantages in the colonization of highly perturbed environments (Catford et al. 2012; Moles, Gruber, & Bonser 2008). Therefore, high habitat diversity and high edge density in the surrounding landscape seem to be crucial to increase



**Fig. 3.** The best supported models and spatial scales of the relationship between weeds and the landscape metrics SDI and ED in Paraná State, southern Brazil. SDI = Shannon's diversity index, ED = edge density index and wAICc = weight of evidence of the model.

the availability of more stable habitats for native species. Additionally, under low levels of anthropogenic disturbances native diversity can increase community resistance against invasions by exotic species (Chen et al. 2017; Cornell & Karlson 1997) (Fig. 3).

Native cover and exotic cover did not respond to landscape complexity nor local factors (altitude and field size). This absence of effects may be related to the contribution of native and exotic invasive species that presented high percent cover in both simple and complex landscapes. Another possible explanation could be associated with local management, especially herbicide and fertilizer applications that significantly affect local weed cover (Gabriel et al. 2005; Kovács-Hostyánszki et al. 2011; Sutcliffe & Kay 2000) and could counterbalance the effects of our explanatory variables. However, we minimized the effects of agrochemicals by sampling weeds in uncultivated strips in the edges of wheat fields. Additionally, weed surveys were conducted during the period of wheat grain formation in which fertilizers and herbicides are not used. Thus, weed cover may be also determined by other local factors such as soil properties, field management history and competition for light and water.

Finally, field size did not affect weeds maybe due to the low variation of field size among the sampled sites with 72% of them smaller than 35 ha. The absence of effect of altitude on weeds can be associated with physical characteristics of the study region that are relatively homogeneous. Therefore, the variations in altitude did not involve drastic changes in environmental conditions. Indeed, all sites are located in flat mechanized reliefs, present the same soil type (Rhodic Ferralsol) and the same predominant habitat types. Moreover,

most weeds present high tolerance to natural environmental changes (Clements et al. 2004) and probably are less sensitive to local climatic changes related to variations in altitude. This can be especially true for cosmopolitan weeds such as *B. pilosa* and *S. oleracius* that are adapted to both hot climate in the Neotropics and freezing winters in temperate regions.

### Importance of weeds for biodiversity maintenance

Despite the status of crop pests, weeds are important components of biodiversity in agroecosystems and should be considered in initiatives related to biodiversity conservation in crop-dominated regions. Studies conducted in Brazil showed that weed species that are commonly found in the study region present positive association with beneficial insects and mites, which control pests in crops. For instance, Silveira, Bueno, Pierre, and Mendes (2003) found that the weeds *B. pilosa*, *Amaranthus* sp. and *Alternanthera* sp. provide alternative food (floral resources) and shelter for two predatory insects *Orius thyestes* (Herring) and *Orius per punctatus* (Reuter) (Hemiptera, Anthocoridae). Gravena (1992) observed that high densities of the herb *Ageratum conyzoides* in citrus plantations increased populations of predatory mites resulting in the effective biological control of citrus pest mites.

Here, for the first time we report the effects of landscape complexity on weeds in agricultural landscapes within a Neotropical region. Our findings indicate that the increment landscape complexity had a positive impact mainly on native species. Despite the absence of effect of non-crop habi-

tats on weeds, we highlight that these habitats are extremely important for biodiversity conservation in agricultural landscapes (Altieri 1999; Fahrig et al. 2011; Tschamtkte et al. 2007, 2012). Non-crop habitats are important elements of habitat diversity and directly contribute to the increment of landscape complexity. The presence of natural and semi-natural habitats such as abandoned pastures, forest fragments, wetlands, hedgerows and road merges increases the availability of stable environments for biodiversity, especially in periods of disturbance in cereal matrix such as harvest and pesticide applications (Tschamtkte et al. 2012). Therefore, agri-environment schemes designed to preserve biodiversity in farmland should promote landscape complexity through the diversification of crops as well as conservation and restoration of natural and semi-natural habitats at multiple spatial scales.

## Acknowledgments

We are grateful to the owners of private lands where the sampled wheat fields are located. Hugo R. Medeiros and Adriano H. Thibes received a research grant from CAPES (Coordination for the Improvement of Higher Education Personnel). CNPq (Brazilian Government Research Council) provided a research grant for Milton Cezar Ribeiro (312045/2013-1), who also thanks FAPESP (process 2013/50421-2) for their financial support. We thank M. King, a native English speaker from Canada, for proofreading the manuscript, and the three anonymous reviewers who helped us to substantially improve the manuscript.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.10.001>.

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