Effect of landscape composition and arrangement on biological control agents in a simplified agricultural system: A cost–distance approach

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ARTICLE INFO

ABSTRACT

Landscape simplification has been clearly demonstrated to have negative impacts on the in-crop density and biological-control activity of natural enemies in agricultural landscapes. The role of spatial arrangement of the landscape, however, has not been investigated in agroecosystems. We applied cost–distance modeling to investigate the relationship between the in-crop density of natural enemies and the structural connectivity of non-crop land uses surrounding crops within Australian cotton landscapes. We further compared the explanatory power of this approach with the more commonly used spatially specific proportional-area approach, which considers landscape composition in terms of the proportional area of a given land use within a given radius. Cost–distance metrics offered a more significant explanation of in-crop density for the predatory beetle *Dicranolaius bellulus* (Coleoptera: Melyridae) than did the proportional-area approach. The in-crop density for this species was positively and significantly correlated with the connectivity of wooded land uses within a 3000 m radius. However, for natural enemy taxa that responded to landscape characteristics at smaller spatial scales (within a 750 m radius), namely *Oxyopes* spp. (Araneae: Oxyopidae) and *Trichogramma* spp., (Hymenoptera: Trichogrammatidae), the proportional-area approach gave a more significant explanation of in-crop density. Herbivore taxa responded weakly to proportional area at all scales and showed no correlation to cost–distance metrics. Findings indicate potential for simplified agricultural landscapes to be 'selectively' manipulated to enhance colonization of the crop by natural enemies, but not herbivores, by improving connectivity between crops and non-crop resources, through the presence of woody vegetation.

1. Introduction

1.1. Conservation biological control at the landscape scale

To thrive in agricultural landscapes, natural enemies rely on non-crop habitats to provide resources and favorable conditions which may be absent in crop fields. These include refugia from disturbances, alternate sources of food (prey or host organisms and nectar sources) and alternative habitats (Landis et al., 2000). Due to landscape simplification, these resources are usually either scarce or sparsely distributed in agroecosystems (Tscharntke et al., 2005). Habitat management (Landis et al., 2000) aims to manipulate agricultural areas to improve the efficiency of biological control by selectively providing resources that benefit natural enemies but not pest arthropods (Gurr et al., 2004). These efforts

have generally been focused at the field scale, either within fields (Hossain et al., 2002; Mensah, 1999) or in the surrounding field margins (Lavandero et al., 2005). However, because many arthropods utilize resources at the landscape scale (Tscharntke et al., 2005), the potential exists for habitat management at the landscape scale as well (Landis et al., 2000). For habitat management to be successful it should be based on a sound understanding of the underlying ecological processes (Gurr et al., 1998); in this instance, the way arthropods utilize resources at the landscape scale.

A growing body of evidence suggests that the activity of natural enemies within crops suffers as a consequence of landscape simplification and loss of non-crop habitats at a landscape scale. For example, compared with agricultural landscapes with high levels of non-crop land use, simplified landscapes exhibit reduced natural-enemy activity within crops (Schmidt et al., 2008; Schmidt and Tscharntke, 2005; Thies et al., 2003; Thies and Tscharntke, 1999). Landscape-scale studies in agroecosystems have generally focused on the relationship between the landscape and natural enemies, in terms of landscape composition, using a *spatially spe-*

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cific proportional-area approach; in which the proportional area of a land use (e.g., proportional area of non-crop land), within a specific radius, is related to the density or activity of arthropods within crops. Such studies have demonstrated a clear link between non-crop land uses and the activity of natural enemies within crops (Bianchi et al., 2005; Prasifka et al., 2004; Schmidt et al., 2008). Moreover, by varying the radius within which the land-use areas are calculated, this approach has demonstrated that different arthropod taxa respond to landscape composition at different spatial scales (Bianchi et al., 2005; Elliott et al., 2002; Roschewitz et al., 2005; Schmidt et al., 2008). For example, Roschewitz et al. (2005) found that the while parasitic wasps (Hymenoptera: Ichneumonoidea, Chalcidoidea) responded most strongly to landscape composition within 1000–2000 m radius of winter wheat crops, the host insects *Sitobion avenae* Fabricius, *Metopolophium dirhodum* Walker, and *Rhopalosiphum padi* L. (Hemiptera: Aphididae), showed correlations at all spatial scales analyzed up to a radius of 3000 m.

Despite the popularity of the spatially specific proportional-area approach, a limitation exists.

The constraint of the spatially specific proportional-area approach is that it considers only area, ignoring the spatial arrangement of land uses. For example, in (Fig. 1) each of the three landscapes has the same proportional area of non-crop land use, however the spatial arrangement of these three landscapes are noticeably different and are likely to have very different consequences for dispersing arthropods.

Without understanding how the landscape arrangement affects natural enemy movement between crop and non-crop habitats at the landscape level it is difficult to design landscapes for optimal biological control.

1.2. The case for connectivity in agroecosystems

Dispersal between habitat patches has long been recognized as pivotal for conservation of species in natural ecosystems, particularly in the context of metapopulation theory (e.g., Hanski, 1999). The role of landscape connectivity in facilitating dispersal between habitat patches has consequently emerged as a key area of research in conservation ecology (Hanski, 1999; Letourneau, 1998; Tischendorf and Fahrig, 2000). The lessons learned, and the methods used, in conservation ecology in natural ecosystems may be adapted for conservation biological control in agroecosystems, because both disciplines share the aim of encouraging the persistence of target taxa in specific landscapes (Letourneau, 1998). Despite the growing awareness of the land uses that are associated with increased activity of natural enemies within crops, and the spatial scale at which these associations are strongest, the role of connectivity between favorable resources in the wider landscape has not yet been investigated in the context of conservation biological control.
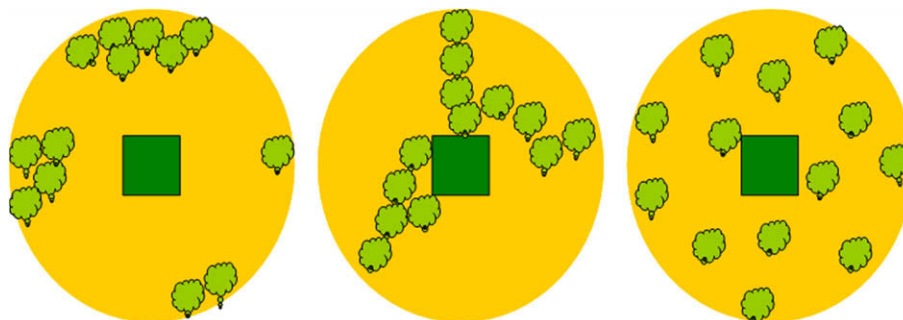
1.3. Functional connectivity and cost–distance analysis

The degree to which a landscape is *functionally connected* for a given species is a combination of two factors: (i) the landscape-specific structural connectivity of habitat patches and, (ii) the species-specific dispersal ability, which includes the dispersal capacity, but also the response to non-habitat land uses (i.e., the hostility of the matrix) which mitigates the ability of the species to move between habitat patches (Tischendorf and Fahrig, 2000). Therefore to assess functional connectivity for a given species a model must consider not only structural connectivity, but also the species-specific dispersal activity and the effects of the matrix on that dispersal (Chardon et al., 2003; Tischendorf and Fahrig, 2000). This can be addressed with a cost–distance approach (Chardon et al., 2003; Verbeylen et al., 2003) in which different land-use types can be assigned different costs to represent the degree of favorability for each taxon of interest. A standard component of GIS software, the 'cost–distance' tool models the dispersal of an individual throughout the landscape by identifying paths which maximize the use of favorable land uses. In this way, cost–distance analysis can elucidate the way animals utilize the landscape during dispersal, by identifying favorable land uses (habitat patches and corridors); unfavorable land uses (hostile matrix) and the degree to which the latter disrupts functional connectivity for a given species. Cost–distance analysis has been employed in conservation ecology and has been found to accurately predict the behavior of dispersing animals, for example, in predicting presence or absence of speckled wood butterflies *Pararge aegeria* L. (Lepidoptera: Satyridae) in isolated habitats (Chardon et al., 2003); the land uses favored by dispersing hedgehogs *Erinaceus europaeus* (Driezen et al., 2007); and the degree of gene flow between European roe deer *Capreolus capreolus* in fragmented landscapes (Coulon et al., 2004).

1.4. Cotton farms in Australia

Although Australian cotton farms are characteristically large cleared areas, due to water needs, they often occur close to rivers and riparian remnant vegetation (Lovett et al., 2003). Reversing a history of large-scale landscape simplification, the Australian cotton industry is now encouraging the conservation and rehabilitation of natural areas and of native vegetation on cotton farms to address the concerns of groundwater levels, soil erosion, carbon sequestration, and loss of biodiversity (Reid et al., 2003). Such natural areas and native vegetation act as providers of multiple ecosystems services (*sensu* Gurr et al., 2003); additionally encouraging biological control, by providing the non-crop resources required by natural enemies. Native vegetation on cotton farms, such as remnant woodlands, and shelterbelts, has been demonstrated to harbor natural enemies throughout the year (Rencken, 2007) and to act as a source for immigration into cotton crops (Schellhorn and Silberbauer, 2003; Silberbauer and Gregg,

Fig. 1. Three hypothetical landscapes with a crop field at the center (box) and the same proportional area of non-crop habitat surrounding the crop field.

2003; Yee, 1998; D.J. Perovic et al., unpublished data). Natural areas have also been shown, throughout the world, to be strongly correlated with activity of natural enemies within crops (Bianchi et al., 2005; Elliott et al., 2002; Marino and Landis, 1996; Prasifka et al., 2004). Identifying the extent to which these habitats are favorable, and the spatial arrangements that maximize their effects, would facilitate landscape-scale habitat management in cotton agroecosystems.

Accordingly, the first aim of this study was to analyze the relationship between the area of specific non-crop land uses and the density of natural enemies within cotton fields, and to identify the spatial scale at which these relationships occur. More specifically we aimed to test the hypothesis (A) that *the area of non-crop land surrounding cotton fields is positively related to natural enemy density within the crop*. We used the 'spatially specific proportional-area approach' to examine the relationships. The second aim of this study was to analyze the relationship between the density of biological control agents within cotton crops and the arrangement of the landscape surrounding cotton crops, given that dispersing arthropods move through the landscape to colonize nearby crops. More specifically, we aimed to test the hypothesis (B) that *the structural connectivity of non-crop land uses surrounding cotton crops has a stronger effect on natural enemy density within crops than does the proportional non-crop area alone*. We designed a cost–distance approach to identify (i) land uses which act as habitat patches for arthropod natural enemies, and the level of contrast between preferred (habitat) and non-preferred (matrix) land uses, and (ii) the spatial scale at which each taxon perceives and moves through the landscape. Cost–distance can potentially identify favorable land uses surrounding the crop, as does the spatially specific non-crop area approach, but it can further incorporate a measure of the spatial arrangement of these land uses and therefore has the potential to make more powerful habitat manipulation and landscape management recommendations.

2. Materials and methods

2.1. Study area and site selection

The study area (approximately 900 km²) was between the towns of Narromine, Trangie, and Gin Gin in the Macquarie Valley, central-western New South Wales, Australia (148°E, 31°S). The area characteristically includes both cropping and grazing land. Irrigated cotton is the most important summer crop and is grown mainly along the Macquarie River. About 90% of the cotton grown in this area is the transgenic variety, Bollgard® II.

Following Thies et al. (2003), 15 cotton fields were selected for sampling, each separated by at least 3 km. The landscape surrounding these fields ranged from extremely simplified, with 100% irrigated cropping land (measured at a 1.5 km radius scale) to relatively complex, with only 25% irrigated crop land.

2.2. Arthropod sampling

In each selected cotton field, arthropods were sampled in a 5 × 5 m² quadrat at 70 m from the field edge. Sampling consisted of two passes with a mechanical vacuum sampler; each cotton plant within 1 m of a row was sampled by moving the nozzle of the sampler vertically over the plant at a rate of 20 cm/s. Vacuum-collected samples were frozen on site, transported in portable freezer to the laboratory, and identified to species level wherever possible (Araneae were determined only to genus, due to the difficulty of identifying juveniles). Sampling was done prior to cotton bolling on 18 November 2006, 2 December 2006, 18 December 2006, and 11 January 2007.

### 2.3. Spatially specific proportional-area analysis

Land uses around each sampling field were determined using aerial photographs (New South Wales Department of Lands 2006) and field inspections. Land use was categorized as cropland (non-cotton), grassland, wooded areas [scattered farm trees, shelterbelts, native woodland (remnant and revegetated) and riparian vegetation], or water bodies. The area covered by each of these land uses was calculated using ArcGIS™ 9.1 (ESRI, 2005) software and expressed as the proportion of the total landscape area at three spatial scales defined by respective radii of 750, 1500, and 3000 m around each sampling quadrat within fields (Fig. 2a).
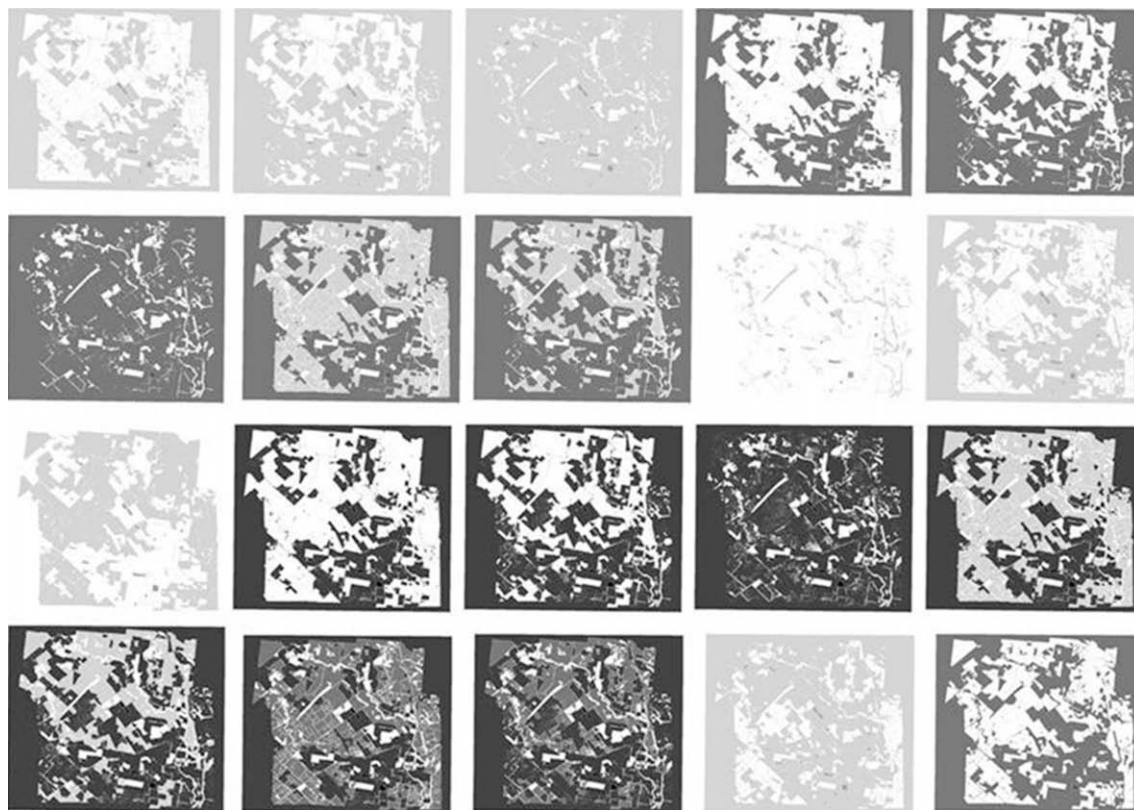
2.4. Cost–distance analysis

Functional connectivity of the landscape surrounding sampling fields was measured using cost–distance metrics developed using the ArcGIS™ 9.1 (ESRI, 2005) 'cost–distance' tool; which models the dispersal of a species between a designated *source* and *destination* on a surface, or map grid, known as a 'cost–raster' (Fig. 2b). Each cell of the cost–raster is assigned a 'cost' based on the land use that occupies that cell. The cost given to a land use represents the degree to which the land use favors dispersal for a particular arthropod taxon. The lowest cost (1) is assigned to those land uses that represent highly preferred habitat patches for a particular taxon; less favorable habitats are assigned higher costs (e.g., 2) and highly unfavorable land uses, or inhospitable matrix, are assigned much higher costs (e.g., 50). Based on the costs in the cost–raster, the 'cost–distance' tool generates a *cost–distance raster*, another map grid (Fig. 2c), in which the value of each cell represents the lowest cumulative cost to reach that cell along a path between the source and destination.

To determine the level of favorability among the different land uses, we followed a method similar to that of Chardon et al. (2003), Verbeylen et al. (2003), and Driezen et al. (2007) by testing arthropod data against different sets of costs (cost–ratios) from multiple cost–rasters in which the relative costs of each land use varied. We generated 20 sets of cost–ratios for the landscape surrounding each sampling point (Fig. 3 and Table 1). As all study taxa were common cotton entomo-fauna, cotton fields were assigned the most favorable cost, 1, for all rasters. Water bodies, such as irrigation reservoirs and lakes, were always given a higher cost relative to other land uses. Costs assigned to each of the remaining land uses (wooded areas, grassland, leys, and cropland) were based on trends which emerged from our 'spatially specific proportional-area analysis' (see Section 2), and from other studies (e.g., Bianchi et al., 2005; Elliott et al., 2002; Prasifka et al., 2004; Thies and Tscharntke, 1999), which suggest that unmanaged land is favorable for natural enemies: cost–ratios r1–r15 assigned wooded areas with the most favorable cost, 1 (Table 1). An inverse response by a taxon to a cost–ratio would indicate that the assumption that cotton fields and wooded areas are favorable for dispersal of that taxa is incorrect; cost–ratios r16–r20 were designed to further validate this assumption and separate cotton fields and wooded areas, by assigning wooded areas with less favorable costs: 2 or 10 (Table 1).

Cost–distance rasters were generated for each of the 20 sets of cost–ratios. The perimeter (the buffer) defined by respective radii of 750, 1500, and 3000 m surrounding each sampling field, represented the source; and the sampling quadrat within each cotton field represented the destination between which distance was modeled for cost–distance rasters (Fig. 2b and c). In this manner, we generated cost–distance rasters for each site at three spatial scales (750, 1500, and 3000 m radii). We used two metrics to represent landscape connectivity: (i) *cost–area*, (ii) *cost–path*. The *cost–area* metric was generated for each spatial scale by adding
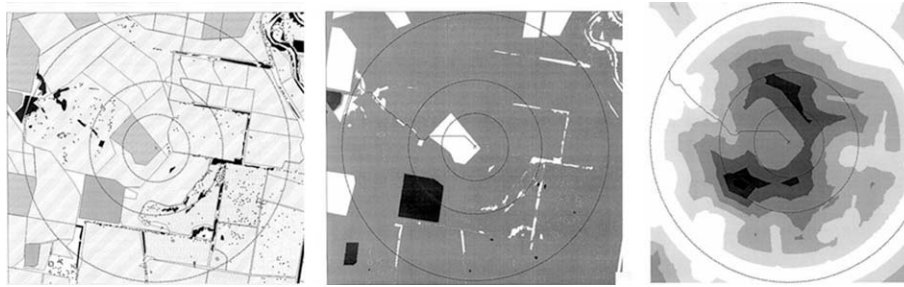
Fig. 2. (a, left) Map of land uses surrounding site 14. Circular buffers surrounding sampling site represent the spatial scales, respective radii of 120 (not shown), 750, 1500, and 3000 m, within which land-use areas were calculated. (b, middle) Cost–raster (r11) surrounding sampling site (site 14). Costs represent the level of favorability of land use for dispersing arthropods. Lighter shades represent higher levels of favorability. Dispersal through landscape was modeled between "sources," buffers at respective radii of 120 (not shown in figure), 750, 1500, and 3000 m, and "destination," sampling site. Least cost–path between sites and 3000 m shown. (c, right) Cost–distance raster (for r11) surrounding sampling site (site 14). The cumulative cost–distance values between the "source," 3000 m buffer, and the "destination," sampling site. Darker shades represent higher cumulative cost–distance values. Least cost–path for this scale also shown.

Fig. 3. Cost–rasters used for cost–distance analysis. White, habitat patches; shaded areas, matrix. Darker shades represent higher costs. See Table 1 for costs.

Table 1
Sets of cost–ratios used in cost–distance analysis. Land-use types and costs shown.

Land-use type	r1	r2	r3	r4	r5	r6	r7	r8	r9	r10	r11	r12	r13	r14	r15	r16	r17	r18	r19	r20
Scattered farm trees, shelterbelts	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	10
Native woodlands, riparian vegetation	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	10
Horticultural trees	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	10
Cotton Fields	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Grasses	1	1	2	1	1	10	2	2	1	1	50	2	2	10	10	1	1	2	2	1
Leys	1	2	2	1	10	10	2	10	1	50	50	2	50	10	50	1	1	2	1	1
Crop	2	2	2	10	10	10	10	10	50	50	50	50	50	50	50	1	2	1	2	10
Water	4	4	4	20	20	20	20	20	100	100	100	100	100	100	100	4	4	4	4	20

the value of each cell in the cost–distance raster. This metric represents the overall level of structural connectivity between cotton fields and other favorable land uses (habitat patches) throughout the landscape over each spatial scale. The *cost–path* metric was generated using the 'cost–path' tool in ArcGIS™ 9.1 (ERSI, 2005), which identifies the path from the destination to the source with the lowest cumulative cost based on the cost–distance raster (Fig. 2c). This metric represents a single path of least-resistance

(the most effective corridor) for movement of a taxon into crops from the perimeter (buffer) of each spatial scale.

2.5. Data analysis

2.5.1. Spatially specific non-crop analysis

Arthropod taxa with an overall average density greater than one individual m^{-2}, were analyzed for correlations with land-use variables. The land uses most strongly correlated with in-crop density of each arthropod taxon were identified using a generalized linear mixed model (GLMM) with Poisson distribution and a logarithmic link function in Genstat 9 (Genstat for Windows, 2006); 'dispersion' was estimated, rather than being fixed at '1' (to identify cases of overdispersion). The weekly mean per site for each taxon was used as the response variable.

Our regression analysis was limited by the strong correlations that existed among the major land-use types. By not including the significantly correlating variables ($p < 0.05$) in the same regression, we avoided over-fitting models and the spurious inclusion of land-use variables into the final regression model. We omitted cropland from the regression analysis as it correlated significantly with most of the other land-uses variables at all spatial scales. Similarly, data for 'other taxa' were not included in the regression analyses to avoid over-fitting models. Correlation analysis identified that the density of *Oxyopes* spp. and Cicadellidae were strongly correlated.

2.5.2. Cost–distance analysis

The cost–ratios that most strongly correlated with in-crop density of each arthropod taxon were determined using a GLMM as described for the spatially specific proportional-area approach above. The cost–ratio that gave the lowest residual mean deviance was considered to most closely match with the actual level of preference of each taxon for each land use (i.e., low costs for favorable habitats and high costs for unfavorable habitats). A negative sign indicated that in-crop density for a species increased as the costs of reaching the crop decreased.

Cost–distance metrics were added to the proportional area metrics to identify whether they significantly improved the model after the inclusion of proportional area metrics.

3. Results

3.1. Natural enemies

A total of 682 predators were obtained in the vacuum–collected samples. The most abundant were *Oxyopes* spp. (Araneae: Oxyopidae) ($n = 363$) and *Dicranolaius bellulus* (Guérin-Méneville) (Coleoptera: Melyridae) ($n = 73$). *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) ($n = 25$) were the most abundant parasitoids.

3.2. Herbivores

A total of 1272 individuals were captured. Thysanoptera were most common (711 adults and 143 juveniles). Approximately 30% of the thrips were Aelothripidae, which are facultative predators feeding on smaller arthropods (e.g., mites) but may also feed on plant parts in the absence of prey (Mould and Heming, 1991). Pest thrips identified were *Frankliniella schultzei* (Trybom), *Frankliniella. fusca* (Hinds), *Thrips tabaci* Lindeman, and *Thrips imaginis* Bagnall (Thysanoptera: Thripidae).

Cicadellidae were the most common Hemiptera with 178 adults and 390 nymphs. *Orosius orientalis* (Matsumura) and *Austroasca viridigrisea* (Paoli) (Hemiptera: Cicadellidae) were most abundant.

3.3. Spatially specific non-crop area analysis

3.3.1. Natural enemies

The density of *Oxyopes* spp. within cotton fields was positively correlated to the proportional area covered by trees within 120 m radius; this gave the only significant regression model for this taxon (Table 2).

Density of *D. bellulus* correlated positively, but not significantly, to the proportional area covered by trees at the 1500 m scale.

Density of *Trichogramma* spp. was positively, and strongly significantly, correlated with the proportional area of cotton crops at the 750 m scale (Table 2).

3.3.2. Herbivores

The density of *A. viridigrisea* within cotton fields was positively correlated with the proportional area of grasses at the 3000 m scale (Table 2). Regression models for Thripidae and for *O. orientalis* were not significant at any spatial scale.

3.4. Cost–distance

3.4.1. Natural enemies

Dicranolaius bellulus and *Trichogramma* demonstrated significant correlations to the cost–path metric for cost–ratios that assigned cropland as unfavorable and wooded areas as favorable. The most significant correlation to cost–path for the in-crop density of *Trichogramma* was at the 750 m scale to ratios *r6–r8*, which assigned wooded areas and cotton fields to be highly favorable land uses (Table 2). For the density of *D. bellulus* in crops, the most significant response was at the 1500 m scale to *r12*, but all ratios which assigned cropland as highly unfavorable, and grassland as either favorable or mildly unfavorable were significantly correlated to in-crop density for this species (Table 2).

The cost–area metric also demonstrated highly significant correlations for the in-crop density of *D. bellulus*. Ratios which assigned cropland as highly unfavorable and grassland as either favorable or mildly unfavorable were most significantly correlated to in-crop density for this species. Additionally *D. bellulus* was the only species for which the addition of cost–distance metrics significantly improved regression models after the inclusion of the proportional-area data (without over-fitting or overdispersion) (Table 2).

3.4.2. Herbivores

Cost–distance metrics were not significant for any of the tested herbivore taxa (Table 2).

4. Discussion

4.1. The relationship between non-crop area and the density of arthropods in cotton fields

Findings from the proportional-area analysis agree with previous studies showing that the relationship between the in-crop density of arthropods and the land uses that surround the crop field is taxon specific, both in terms of the most influential land uses (Bianchi et al., 2005; Elliott et al., 2002) and the spatial scale at which land uses have the strongest influence (Bianchi et al., 2005; Roschewitz et al., 2005; Schmidt et al., 2008). For *Oxyopes* spp., and *Trichogramma* spp., the most significant relationship with the surrounding landscape was at the smaller scales (120 and 750 m, respectively); for *D. bellulus*, and *A. viridigrisea* the strongest response was at the larger scales (1500 and 3000 m, respectively). Additionally, the land uses to which each taxon responded most strongly also varied: *Trichogramma* spp. had a highly significant re-

Table 2
Summary of step-wise GLMM regression analysis of relationship between arthropod taxa and landscape metrics for significant regression models only: showing landscape metric, spatial scale at which landscape metric was measured, terms which entered regression and Wald statistic, degrees of freedom and significance from adding term to regression model in forward step-wise fashion.

Taxon	Spatial scale	Metric	Model	Stepwise regression	Wald statistic	df	p-Value
D. bellulus	3000	Cost–path	r12[a]	+r12	18.69	1, 16	<0.001
	1500	Cost–area	Trees + r14 + trees.r14	+trees	13.34	1, 16	0.002
				+r14	15.93	1, 16	0.001
				+trees.r14	16.50	1, 16	<0.001
Trichogramma	750	Proportional area	Cotton	+cotton	13.91	1, 18	0.002
	750	Cost–path	r6[b]	+r6	13.85	1, 18	0.002
Oxyopes	120	Proportional area	Trees	+trees	5.61	1, 16	0.031
A. viridigrisea	3000	Proportional area	Grasses	+grasses	7.30	1, 18	0.015

[a] Cost–path for *r1*, *r4*, *r9*, and *r12* were identical; therefore all paths were equally significant.
[b] Cost–path for *r6–r8* were identical; therefore all paths were equally significant.

sponse to cotton area, whereas *D. bellulus* and *Oxyopes* responded most strongly to trees and *A. viridigrisea* responded most strongly to grassland area. Therefore, *hypothesis A* (*the area of non-crop land surrounding cotton fields is positively related to natural enemy density within the crop*) is supported for two of the three natural enemy species examined, as the area of non-crop land use (wooded areas) was positively related to the density of both *Oxyopes* spp. and *D. bellulus* within cotton crops. The herbivore, *A. viridigrisea* was also positively related to the area of non-crop land use (grassland). This fact illustrates a complexity which is often present in conservation biological control studies: that potential pest species may benefit from conditions that favor natural enemies. The minor cotton pest, *A. viridigrisea* and the generalist predator *D. bellulus* were both favored by grassland. Fortunately, the type of non-crop vegetation that was found to be most favorable for *D. bellulus* and for *Oxyopes* spp. (i.e., woody vegetation) did not favor *A. viridigrisea*. This is a preliminary indication that cotton landscapes could be manipulated in a fashion that selectively favors these predators over the herbivore; an extension of the much smaller scale, selectivity described by Baggen and Gurr (1998).

The land use to which *Oxyopes* spp. and *D. bellulus* responded most favorably, wooded areas, is consistent with other work. For example both have been demonstrated to move into cotton fields from neighboring shelterbelts (D.J. Perovic et al., unpublished data).

4.2. The relationship between landscape arrangement and the density of arthropods within cotton

The findings from our cost–distance analysis indicate that wooded land in the landscape surrounding cotton fields is a land use that favors natural enemies, and that highly managed land uses, such as cropland (non-cotton), are unfavorable. The level of preference towards grassland, however, varied between taxa and functional guilds. For example, *A. viridigrisea* preferred grasslands. *D. bellulus* preferred grasslands over cropland, but preferred wooded areas most. *Trichogramma* spp. most preferred cotton fields.

The land uses and the spatial scale to which taxa responded most significantly (when significant responses were evident) were similar for the proportional area and cost–distance analyses. For example, the conclusion that *D. bellulus* responded favorably to wooded areas and unfavorably to cropland at the larger scales is supported in both analyses. Potentially, the cost–distance technique can determine, not only the most favorable land uses, but also the importance of structural connectivity of these land uses for each taxon, and the level to which less favorable land uses disrupt structural connectivity of favorable habitats. The omnivorous *D. bellulus* has been observed, in previous studies (Schellhorn and

Silberbauer, 2003; Silberbauer and Gregg, 2003; Yee, 1998) to forage in a variety of vegetation types, including annual crops, native vegetation and grasses, before and after visiting cotton crops. The response to cost–distance metrics observed in the present study suggests that *D. bellulus* prefers wooded areas over grassland whereas non-cotton cropland is highly unfavorable. It is possible that such a negative response to non-cotton cropland was due to most cropland being fallow (i.e., bare ground). However, many studies suggest a negative effect of cropland on natural enemies even when not left fallow (Roschewitz et al., 2005; Schmidt et al., 2008; Thies et al., 2003; Thies and Tscharntke, 1999). The disturbance regime typical of cropland provides one explanation for the negative response by *D. bellulus*; as undisturbed areas are vital for the immature life stages of this species (Deutscher and Wilson, 2006; Lawrence and Britton, 1991).

Dicranolaius bellulus was the only taxon for which the addition of cost–distance metrics significantly improved the regression after the inclusion of the proportional-area data in the model. Therefore, *hypothesis B* (*the arrangement of non-crop land uses surrounding cotton crops has a stronger effect on natural enemy density within crops than does non-crop area alone*) only holds for *D. bellulus*, but not the other taxa tested. *Why is it then that cost–distance metrics have not proved more significant for taxa other than D. bellulus?* The spatial scale at which arthropods respond to the landscape composition and structure reflects the dispersal ability of the taxon (Steffan-Dewenter et al., 2001; Tscharntke et al., 2005). Species with limited dispersal abilities, for example, *Trichogramma* (e.g., Kölliker-Ott et al., 2004; McDougall and Mills, 1997; Wright et al., 2001), are most strongly affected by local, small scale, conditions, and are therefore expected to respond to landscape arrangement most strongly at smaller scales; conversely species such as *D. bellulus*, with greater dispersal ability which are more actively vagile, are affected by conditions from the broader landscape and are therefore expected to respond to the landscape at the larger spatial scale. Thus the connectivity of favorable habitats affects *Trichogramma* and *Oxyopes*, less strongly, as they will tend to remain in the local area; but for *D. bellulus*, having to actively traverse across greater distances of the landscape, connectivity of favorable habitats is more acutely influential on the ability to reach and colonize crops. Second, the in-crop density of a species is affected by, not only immigration into a patch, but also natality. Landscape features will only give significant correlations if immigration is the stronger determinant of in-crop density. The taxa for which adults and juveniles were found together in the cotton fields (a sign that population growth is occurring within the crop), namely *Oxyopes* spp., *A. viridigrisea*, *O. orientalis*, and the Thripidae, showed the weakest response to landscape metrics. (*Note.* Juveniles and adults were only pooled in the analysis only for *Oxyopes* spp.)

4.3. The utility of the cost–distance approaches for habitat manipulation recommendations

In the present study, we have tested, for the first time, the utility of the cost–distance approach in conservation biological control. Cost–distance is applied slightly differently here than the more familiar application in conservation ecology (such as in Coulon et al., 2004), where the movement between two known habitat patches is measured (often for the sake of identifying corridors). In the present study, the destination of movement is a known habitat (the cotton crop) but the source is a set distance away from the destination, rather than a specific habitat patch within the landscape. This application was chosen to conform to the spatially specific proportional-area approach, so that the two approaches could be compared directly. However, having placed the crop 'patch' in the center of the landscape as the *destination* for dispersing individuals, we have put the emphasis on crop recolonization. What the cost–distance metrics represent here, then, is how landscape arrangement facilitates or hinders the ability of a taxon to disperse through the landscape and colonize a cotton crop from a distance of 750, 1500, or 3000 m away. Cost–distance identifies both suitable habitats in the landscape, and the arrangement of these habitats, relative to each other and to the crop, to enhance the colonization of the crop patch from surrounding non-crop sources. Rather than simply identifying potential habitats in the surrounding landscape as the spatially specific proportional-area approach does, the cost–distance approach yields more specific recommendations for habitat manipulation and landscape management.

4.4. Conclusions and implications for management

The negative effects of landscape simplification on biological control are well documented (see Bianchi et al., 2006; Gurr et al., 2003; Tscharntke et al., 2007, 2005). Further, 'unmanaged' and 'undisturbed' land uses are often identified as being positively correlated with in-crop density and activity of natural enemies (Bianchi et al., 2005; Elliott et al., 2002; Marino and Landis, 1996). Patterns of disturbance such as harvest, fallowing, and pesticide application can reduce natural-enemy population build-up and persistence in agricultural landscapes (Landis et al., 2000). Thus, undisturbed areas, such as remnant vegetation and shelterbelts, may act as vital 'habitat islands' in agricultural landscapes (see minimum dynamic area concept: Letourneau, 1998). Metapopulation theory (Hanski, 1999) highlights the importance of connectivity between habitat patches to allow populations to persist within a landscape. Conservation biological control aims for not just the general conservation of natural enemies within a landscape, but also to maximize recolonization of crop 'patches.' Therefore cost–distance analysis could be very valuable for conservation biological control and habitat manipulation studies to identify how this recolonization can be facilitated. For mobile predators, that show contrasting responses to land use, such as *D. bellulus*, our cost–distance analysis suggests that connectivity between cotton fields and wooded habitats is an important component for landscape-scale habitat manipulation. Although cropland strongly disrupts habitat connectivity and the ability of taxa to reach and colonize cotton fields, the long continuous linear nature of semi-natural wooded areas such as shelterbelts, which are often the only vestige of non-crop land proximal to crops, offers the potential to improve the connectivity of agricultural landscapes. These elements have been shown to act as a donor habitat for *Oxyopes* spp. and *D. bellulus* (and the predator *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae)) into cotton crops in previous work (D.J. Perovic et al., unpublished data), further demonstrating their potential to enhance crop colonization by natural enemies. Conservation biological control in cotton therefore stands to gain much from the addition of such wooded elements, in the often otherwise barren landscape, as these generalist predators have been identified as the key predators in this system (Stanley, 1997; Deutscher and Wilson, 2006). *Oxyopes* spp. in particular are considered to be a key predator for the management of the emergence pest *Creontiades dilutus* (Stål) in Bt cotton (Deutscher and Wilson, 2006; Farrell et al., 2008).

Habitat manipulation using shelterbelts could have a multifunctional ecosystems service effect; these land uses have also been shown to be sources for vertebrate natural enemies (Gámez-Virués et al., 2007; Munro et al., 2007), as well as reducing wind erosion and the risk of salinity, and providing protection for crops and livestock (Brouwer, 1998; Carberry, 1997). These management strategies are expected to enhance biological control within cotton fields, as they favor important generalist predators, but they are not expected to benefit the pest entomo-fauna that we studied, as these taxa did not respond strongly to the proportional area or structural connectivity of wooded land uses.

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