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Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop

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Abstract Agricultural intensification may lead to higher pest pressure through the loss of natural plant assemblages, and associated reduction in natural enemy diversity, while providing increased crop area. We investigate the influence of field margin vegetation and landscape complexity on natural enemy diversity and crop damage caused by two Lepidoptera tomato pests (*Tuta absoluta* and Noctuidae). At the local scale, fields were bordered with herbaceous field margins of varying vegetation diversity. At the landscape scale, these fields were set in landscapes with increasing landscape complexity. Margin vegetation diversity was higher in landscapes with lower arable land cover, and was associated with increased floral resources and enemy diversity, with the latter being negatively related to *T. absoluta*-caused fruit injury. Total crop damage increased with arable land cover. These results imply that the suitability of farming practices for the conservation of natural enemies and pest control services is influenced by the landscape context.

Keywords Conservation biological control · Landscape ecology · Multiple pest management · Noctuidae · *Solanum lycopersicum* · *Tuta absoluta*

Introduction

Natural pest control is an important ecosystem service, carried out by predators and parasitoids, supporting agricultural production (Elmqvist et al. 2010) and which provision is influenced by the availability of non-cropped habitat at local and landscape scales (Tscharntke et al. 2005). However, changes associated with recent agricultural intensification, including the loss of natural habitat to monocultures, the reduction of landscape heterogeneity and increased insecticide inputs, have become a main driver of biodiversity and ecosystem service loss, which may lead to higher pest pressure (Meehan et al. 2011; Jonsson et al. 2012). The link between agricultural intensification and pest abundance is partly explained by the loss of natural plant assemblages from local and landscape scale habitats, which reduces the diversity of natural enemies and results in a lower pest control (Jonsson et al. 2012; Grez et al. 2014). Moreover, simpler

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landscapes with increased crop area are expected to be more attractive to pests (Poveda et al. 2012; Meehan et al. 2011), as suggested by the resource concentration hypothesis (Root 1973). On the other hand, the higher availability of perennial habitats in complex landscapes may induce negative interactions between natural enemies, resulting in higher pest abundance (Thies et al. 2005; Martin et al. 2013).

There is a growing body of evidence that more complex landscapes, defined as landscapes with a high non-crop area cover and habitat diversity (Thies et al. 2005), support more diverse natural enemy communities (Chaplin-Kramer et al. 2011). Similarly, semi-natural habitat type (Sarthou et al. 2014), vegetation diversity (Letourneau et al. 2011) and the provision of alternative resources such as nectar, pollen and alternate hosts or prey (Carrié et al. 2012; Balzan et al. 2014) at the local scale were shown to increase natural enemy diversity. An increase in plant and insect biodiversity through local habitat provisioning in simple landscapes can be expected to provide the greatest effects on ecological processes in adjacent field crops in comparison to habitat allocation in complex landscapes, where biodiversity is overall higher (Tscharntke et al. 2005). However, the relative contribution of local and landscape complexity is often less clear (Chaplin-Kramer and Kremen 2012; Veres et al. 2013). For example, plant species and functional diversity at the field scale are affected by landscape complexity (Carlesi et al. 2013; Gabriel et al. 2005) and increased vegetation diversity is positively related to natural enemy diversity (Letourneau et al. 2011). Thus landscape complexity can also be expected to affect natural pest control services through this indirect pathway. An additional difficulty in understanding the relationship between natural pest control services and complexity at both scales is the presence of operating direct and indirect effects, which may counteract one another (Poveda et al. 2012; Chaplin-Kramer and Kremen 2012). For example, increased availability of flowering resources, associated with the presence of vegetation diversity at the local scale, provides non-pest resources to natural enemies (Wäckers and van Rijn 2012) and can disrupt the pest's ability to locate and access the host plant (Finch and Collier 2000). However the availability of nectar resources from non-crop plants may also increase the fitness of several Lepidoptera pests, and therefore may increase yield loss (Balzan and Wäckers 2013). These results suggest that understanding the relative importance of different mechanisms in regulating natural pest control remains critical for developing a spatial strategy that ensures the provision of natural pest control services.

The objective of this research was to examine the direct and indirect pathways, acting at local and landscape scales, through which natural enemy diversity and crop damage suppression in conventional tomato cultivation are regulated. During this study we measured landscape complexity, field margin vegetation and insect biodiversity and crop damage caused by Lepidoptera pests in conventional tomato (*Solanum lycopersicum* L.) fields in the region of Tuscany (Italy), where this is one of the main annual crops. Cumulative crop damage estimates were used as they are probably the most practical assessment of impact on crop productivity and correlate with herbivore suppression from natural enemy populations (Augustin et al. 2004). It is hypothesised that increased vegetation diversity and availability of floral resources are associated with enhanced natural enemy diversity (H1), and that the latter is negatively related to pest pressure (H2). We also hypothesise that landscape complexity is associated with (H3) increased enemy diversity and (H4) lower pest pressure. Information generated from this research will provide insight into the importance of natural plant assemblages from local and landscape scales for regulating Lepidoptera-caused crop damage, which has implications for the management of tomato crop.

Materials and Methods

Study site and experimental design

The study was carried out in 2010 and 2011 in the province of Grosseto (42°46′N, 11°06′E), Tuscany, Italy (supplementary data Fig. S1), where processing tomato is an important horticultural crop. The study area is characterised by a Mediterranean climate, with relatively elevated temperature and dry spells recorded during the summer period. Semi-natural habitats consist of woodlots, hedgerows, abandoned agricultural land and riparian habitats. Twenty fields in landscapes with a gradient of landscape complexity (ranging from 39.90 to 84.81 % of arable land cover) and with dates for planting of tomato plants ranging from April to June were selected. The ten fields surveyed during 2011 were selected from the same five farms that provided the ten fields surveyed during 2010. Field selection was restricted to the same farms in order to reduce variability in crop management. Pest management strategies in conventional fields within the study area are mainly based on periodic application of pesticides, namely deltamethrin, lambda-cyhalothrin, Indoxacarb and spinosad (Balzan and Moonen 2012). Tomatoes were planted in rows with intra-row crop distances between 0.4 and 0.5 m, and inter-row distance ranged from 1.40 to 1.70 m. During statistical analysis, crop management was incorporated within the analysis by including farm as a cluster in the models to account for differences in crop management and possible spatial aggregation Data Analysis. Combining data from all fields in both years increased statistical power and allowed us to assess patterns in the data that are independent of year-to-year variation. To determine if our sites were spatially independent Mantel tests (999 iterations) were used to assess spatial auto-correlation of field vegetation diversity and crop damage data (Goslee and Urban 2007). Mantel tests show no spatial auto-correlation for crop damage ($r = 0.02$, $p = 0.33$) and vegetation diversity ($r = 0.07$, $p = 0.23$). Crop damage and field margin surveys of vegetation and arthropod diversity were timed to the phenology of the crop, and were carried out 7–14 days before the harvest date.

Vegetation surveys of herbaceous field margins

A vegetation survey of field margins within tomato fields was carried out. Since farmers within the study area remove vegetation from uncropped habitats through mechanical and chemical measures before planting the tomatoes (Balzan and Moonen 2012), field margins had a width that varied between 1 to 1.5 m and mainly consisted of herbaceous annual plants. Within each field, vegetation surveys in eight geo-referenced 3 × 0.5 m continuous belt transects (two transects per field margin and at a distance of around 10 m from a middle point in the field margin) were carried out. A 0.5 × 0.5 m quadrat was used to measure the vegetation cover throughout the belt transect. All flowering dicotyledonous species within the belt transects were identified and the number of flowering units present within each plot was scored. One flower 'unit' was counted as a single flower (e.g. *Convolvulus arvensis* L.) or, in the case of multi-flowered stems, as an umbel (e.g. *Daucus carota* L.), head (e.g. *Trifolium pratense* L.), racemes (e.g. *Medicago sativa* L.), spike (e.g. *Plantago lanceolata* L.) or capitulum (e.g. *Picris echioides* L.).

Arthropod sampling

Arthropod surveys were carried out along the same belt transects used for the vegetation surveys, in order to provide an indication of the influence of plant diversity on natural enemies abundance. Surveys involved fifteen standard sweeps to monitor flower visitors along the transects, each having an area of 3 × 2 m. The vegetation and arthropod surveys were also timed to the phenology of the crop and were carried out at the same time of the crop damage surveys.

According to previous reports that emphasise the importance of assigning arthropods to different functional groups (Tscharntke et al. 2007), all collected arthropods were identified to the order, family and/or species level in order to categorise them into functional groups: predators, parasitoids, chewing and sucking herbivores, and pollinators. Organisms that could not clearly be assigned to a trophic group were not included in the analyses. The abundance of Hymenoptera parasitoids was recorded by summing the abundance of Ichneumonoidea, Chalcidoidea, Chrysidoidea and Proctotrupoidea parasitoids. The abundance of predators was calculated by measuring the abundance of zoophagous Miridae and Nabidae (Hemiptera), Coccinellidae (Coleoptera), Chrysopidae (Neuroptera), Formicidae (Hymenoptera), Thomisidae, Araneidae, Liocranidae, Theridiidae, Salticidae, Philodromidae, Gnaphosidae, Tetragnathidae (Araneae), Opiliones and Pseudoscorpionida. The natural enemy taxonomic group richness was calculated by counting the number of the aformentioned predatory and Parasitica groups. The availability of alternate prey was calculated by measuring the density of sap-sucking Hemiptera, since this group made up most of all herbivores recorded within the field margins and these are likely to be beneficial for several generalist predators important for pest control in the tomato crop.

Monitoring crop damage from Lepidoptera pests

Lepidoptera pests of tomato within the study area include Noctuidae pests, such as *Helicoverpa* *armigera* Hübner (Noctuidae), and recently the invasive alien species *Tuta absoluta* Meyrick (Gelechiidae) (Balzan and Moonen 2012). Fruit damage caused by these pests was measured in three replicate quadrats consisting of two plants adjacent to a field margin and located in a central part of the field and adjacent to the field margin (with a distance of about 1 m from the margin) where vegetation transects were carried out. A standardised timed (5 min) survey for apparent fruit damage in the upper and middle part of the tomato crop canopy was carried out. Fruits showing symptoms of noctuid and *T. absoluta* characteristic damage were classified accordingly and the number of surface burrows and galleries recorded. The cumulative number of burrows/galleries per quadrat for each pest was used to quantify fruit injury, while crop damage is defined as the total number of fruits with Lepidoptera-caused galleries per quadrat.

Landscape analysis

A land use vector map was created for buffers of 1-km radius around the centroids of the sampled fields using aerial photos provided by the WMS service of the Tuscany Region (GEOscopio-WMS). Landscape patches, defined as relatively homogeneous areas that differ from their surroundings, were assigned to a particular land use type. Fourteen land uses were recorded from the study area (supplementary data Table S1) and included field crop (annual cropping systems and orchards) and non-crop habitat types (herbaceous field margins, hedges, woodland, old field abandonment, riparian vegetation, and surface water bodies). The digitalization of landscape patches was done with QGIS, and vector data were later imported into GRASS GIS and converted to raster maps. The r.le program (Baker and Cai 1992) was then used to calculate the Shannon-habitat type diversity and the land cover area within the surrounding landscapes. Based on observations from other studies, indicating an important role of habitat diversity at this scale on biological control services (Grez et al. 2014) and on Lepidoptera communities (Scalercio et al. 2012; Ricci et al. 2008), a buffer with a radius of 250 m was chosen to evaluate the effect of complexity within the immediate landscape on variables measured within a focal field. Similarly, a buffer of 1000 m was used to evaluate the effects of landscape complexity at larger scales on crop damage suppression (Letourneau and Goldstein 2001; Veres et al. 2013; Grez et al. 2014). Arable land cover was used as a proxy of landscape complexity (Thies et al. 2005) as it correlated with the diversity of habitat types calculated following Shannon's index within landscape buffers of 1 km radius ($R = -0.986$, $p < 0.0001$, $n = 20$).

Data analysis

The plant species richness and Shannon diversity index (H) were calculated for each field margin. The influence of the categorical variable field on the plant species richness in field margins was measured using a generalised linear mixed model (GLMM) with a negative binomial distribution and with farm identity as a random variable. The significance of field identity was then measured by dropping this parameter from the model and comparing the two models.

The influence of farm identity, landscape complexity and year on field margin plant species richness was investigated by fitting a generalised linear model (GLM) containing all explanatory variables and their interactions (Zuur et al. 2009), and using a quasi-poisson distribution to account for overdispersion. The significance of each independent variable was assessed by elimination from the full model and an analysis of variance with a F-test was then performed to compare the models. The influence of local and landscape scale habitat variables on natural enemies was investigated using a GLMM with a negative binomial error distribution, since data was over dispersed (Fournier et al. 2012; Skaug et al. 2013). The structure of the models' random effects was selected by performing several models with a different structure of the variables year, field and farm identity (Zuur et al. 2009). The latter two variables were set as nested random effects to group fields from the same farm, that is with similar management together, and in order to remedy for pseudoreplication arising from overlapping landscape sectors around focal fields that belong to the same farm (Millar and Anderson 2004). The model with the lowest Akaike Information Criterion (AIC) was selected. The significance of the fixed variables was tested through elimination of the least significant effects or interaction, using likelihood ratio tests in which deviance with and without the term in the models were compared using a χ^2 test. This was repeated with landscape data at the two selected spatial scales. The influence of flower abundance of the most abundant flowering species on natural enemy abundance and richness, and the relation between habitat complexity at local and landscape scales on crop damage were similarly assessed through a GLMM with a negative binomial error distribution.

Path analysis was used to investigate whether field margin plant species richness and arable land cover affected crop damage parameters and whether this was through a direct or indirect effect (Rosseel 2012). Since the dataset failed to meet the assumption of multivariate normality (Shapiro–Wilk multivariate normality test, $W = 0.70$, $p < 0.001$), the Satorra–Bentler adjustment for non-normality was used. The Satorra–Bentler scaled χ^2 is a correction of the model χ^2 statistic (Satorra and Bentler 2001). Moreover, since the data collected from fields is nested within farms, all data was aggregated at the farm level by consistently estimating parameters over the farm cluster using a pseudo-maximum likelihood strategy (Oberski 2014). A theoretical model (supplementary data Fig. S2), including the relations between the measured variables was used as a starting point. The most parsimonious path analysis model was then selected through backwards selection involving the elimination of the least significant effect. Path analysis diagrams showing the relationships between the variables were then produced for the most parsimonious model. The path coefficients in the diagrams can be described as the fraction of the standard deviation of the endogenous variable for which the designated variable is directly responsible (Wright 1934). All analyses were performed using The R Project for Statistical Computing (R Core Team 2013).

Results

In total 142 plant species were recorded from the surveyed field margins (supplementary data table S2). Plant species richness varied significantly among different fields ($df = 19$, $\chi^2 = 56.89$, $p < 0.001$), ranging from monospecific strips to a maximum of 17 species per belt transect, but was not significantly different between farms (Table 1). Fields surrounded by a higher arable land cover in both landscape buffers had a lower plant species diversity ($r = 250$ m and 1000 m). Results indicate a significant effect of the interaction between arable land cover and the categorical variable farm in landscape buffers with a radius of 250 m, indicating that the effect of arable land cover also depends on the farm identity. A significant effect of the interaction between arable land cover and the categorical variable year was recorded for landscapes with a radius of 1000 m, indicating that the effect of arable land cover on field margin plant species richness depends on the year of the study.

With a relative abundance of 54.86 %, sap-sucking herbivores were the most abundant arthropod functional group collected from field margins. Predators and parasitoids made up 22.41 and 5.07 % respectively, while pollinators accounted for 3.89 % of arthropods collected. Higher field margin plant species richness was associated with increased natural enemy group abundance and richness (Table 2), supporting our hypothesis H1 (Fig. 1) but this depends on the time of harvest and landscape complexity. Increased natural enemy abundance and diversity were recorded in field margins with increased plant diversity and harvested later in the season. Increased vegetation diversity in field margins surrounded by landscapes with higher habitat diversity and harvested later in the season was also associated with a higher diversity of natural enemies (Table 2). We also measured the influence of flower abundance, for the most common flowering species, on the abundance of the natural enemy functional groups. The flower abundances of *D. carota* and *P. echioides* were positively related to the abundance of predators, while *Coleostephus myconis* (L.) Cass. was associated with increased parasitoid abundance (Table 3). The flower abundances of *D. carota, C. myconis* and *Pulicaria dysenterica* (L.) Bernh. were also associated with increased natural enemy group richness.

Results show that field margin vegetation diversity and habitat-type diversity within the surrounding landscape influence tomato crop damage caused by Lepidoptera pests (Table 4). The minimum adequate GLMM, obtained from supplementary data table S3, indicates lower magnitude of total crop damage for fields characterised with higher field margin plant species richness and with a late harvest date. This effect was dependent on the effect of year, and indicates a stronger suppressive effect during 2011. The effect of landscape habitat type diversity on total crop damage was also significantly influenced by the effects of harvest time and year. Landscapes with higher habitat diversity and harvested later were

Table 1 GLM results for measuring the influence of percentage arable land cover, farm and year, and each interaction term, at different spatial scales on field margin plant species richness

Independent variable	r = 250 m				r = 1000 m			
	df	F	p	Effect	Residual df	F	p	Effect
Year (YR)	1, 13	6.07	0.03	+	1, 13	6.68	0.02	+
Farm (F)	4, 13	1.00	0.44		4, 13	2.77	0.07	
Arable land cover (A)	1, 13	6.44	0.02	−	1, 13	8.30	0.01	−
A × F	2, 8	6.16	0.02		2, 8	0.70	0.52	
A × YR	1, 7	0.39	0.55		1, 7	10.61	0.01	−
YR × F	3, 10	0.78	0.53		3, 10	1.09	0.40	
A × F × YR	2, 5	2.10	0.22		2, 5	0.19	0.84	

Significance values correspond to deletion tests. Effect: direction of significant effects and interactions

associated with lower Lepidoptera-caused damage, but the effect was significantly different between years.

Noctuidae-caused fruit injury was lower in fields surrounded by more complex landscapes but no significant effect was recorded for *T. absoluta*-caused injury (Table 4). Fruits harvested later had a higher fruit injury, suggesting an important temporal effect for both pests. Field margin vegetation diversity (H) was associated with a higher initial noctuid-caused fruit injury during 2011 but we have observed a significant negative interaction with time. This suggests that fields harvested later during the season and characterised with increased margin vegetation diversity have less fruit injury caused by noctuid pests. Similarly, fields with higher vegetation diversity in field margins and harvested early had a higher *T. absoluta*-caused injury, while those with increased margin vegetation diversity and late harvest were associated with lower *T. absoluta*-caused injury.

The path analysis indicates that arable cover is positively related to total crop damage (Fig. 2) and *T. absoluta* and Noctuidae-caused fruit injury (Fig. 3), suggesting increased crop damage in simple landscapes. The magnitude of crop damage increased with harvest time and was higher during 2010, which was soon after the first records of the invasive *T. absoluta*. Lower field margin vegetation diversity at the field scale was associated with reduced flower richness, which was shown to be positively related to natural enemy richness in field margins. Increased natural enemy richness was in turn negatively related to *T. absoluta*-caused crop injury (Fig. 3a), but we did not find a significant influence on total crop damage (Fig. 2) and Noctuidae-caused fruit injury (Fig. 3b). Results obtained here support previous observation from GLMM analysis that *T. absoluta*-caused injury is higher in crop adjacent to diverse field margins. The structure of the abundance models indicates that natural enemy abundance is higher in field margins with increased vegetation cover and alternative prey abundance (Fig. 2b, supplementary data Fig. S3). Increased natural enemy abundance was associated with lower *T. absoluta*-caused fruit injury but no significant reduction in Noctuidae-caused fruit injury and total crop damage was recorded.

Discussion

Results from this study indicate that natural enemy diversity in field margins is positively related to vegetation diversity. More diverse field margins had higher flower richness, with the latter being associated with increased natural enemy diversity. The establishment of field margins with increased availability of floral resources is likely to provide benefits to several entomophagous species (Wäckers and van Rijn 2012). However, results presented here also indicate a sampling effect as more diverse margins are likely to host flowering species that augment enemy diversity, and flower abundance of *D. carota* and of several Asteraceae species were associated with higher enemy richness. Apiaceae species, including *D. carota*, have

Table 2 The influence of Shannon-habitat type diversity (H_{land}) measured at different landscape scales (r = 250 m and 1000 m) around the focal field, Shannon vegetation diversity (H_{veg}) and time of sampling (T) on the abundance of flower visiting arthropod functional groups and taxonomic group richness of natural enemy (NE) groups in field margins, measured using GLMM with a negative binomial distribution

Independent variables	df	250 m									1000 m								
		NE taxonomic group richness			Predators abundance			Parasitoids abundance			NE taxonomic group richness			Predators abundance			Parasitoids abundance		
		χ^2	p	Effect	χ^2	p	Effect	χ^2	p	Effect	χ^2	p	Effect	χ^2	p	Effect	χ^2	p	Effect
H_{veg}	1	13.45	0.0002	+	11.19	0.001	+	6.42	0.01	+	13.99	0.0002	+	11.28	0.001	+	6.42	0.01	+
H_{land}	1	1.89	0.17		0.19	0.66		0.36	0.55		0.20	0.65		2.14	0.14		0.04	0.83	
T	1	3.21	0.07	+	0.36	0.55		7.03	0.008	+	2.00	0.16		0.45	0.50		6.86	0.009	+
$H_{veg} \times H_{land}$	1	1.92	0.17		0.20	0.65		0.04	0.85		0.16	0.69		0.004	0.95		0.001	0.97	
$H_{land} \times T$	1	0.24	0.63		1.09	0.30		1.03	0.31		0.30	0.59		0.56	0.45		2.47	0.12	
$H_{veg} \times T$	1	6.37	0.01	+	3.15	0.08	+	3.03	0.08	+	5.87	0.02	+	3.60	0.06	+	3.01	0.08	+
$H_{veg} \times H_{land} \times T$	1	7.56	0.006	+	3.94	0.047	+	1.43	0.23		13.34	0.0003	+	7.24	0.007	+	0.46	0.50	

The difference deviance of the two compared models following backward elimination and significance using a χ^2 test are shown. Effect: direction of significant effects and interactions

accessible floral nectaries and are very efficient at attracting a large number of flower visitors (Memmott 1999), while composites have narrow disc flowers in Asteraceae allowing nectar to pool and increasing nectar accessibility (Fiedler and Landis 2007).

Local scale interactions relating to vegetation and natural enemy diversity appear to be modulated by landscape processes. Results obtained from the GLM indicate that increased arable land cover was negatively associated to field margin plant diversity (Table 1), while the latter was associated with increased natural enemy diversity (Table 2). Our results also indicate that the effect of field margin vegetation diversity on natural enemies also depends on landscape habitat diversity, and higher vegetation diversity in margins located in more diverse landscapes were associated with greater natural enemy diversity. Overall, these results suggest that lower field margin plant diversity in fields within simple landscapes is associated with reduced natural enemy diversity. These results complement previous observations that landscape complexity increases local natural enemy diversity (Chaplin-Kramer et al. 2011), but demonstrate that this effect may be caused by an indirect pathway acting through local positive effect of vegetation diversity and the availability of floral resources.

Local habitat management to increase natural enemy fitness and diversity would be expected to be more effective in simplified crop-dominated landscapes than in complex landscapes (Tscharntke et al. 2007). However, this has not always been demonstrated (Vollhardt et al. 2008; Woltz et al. 2012) and the relative importance of local and landscape habitat variables has been observed to change with arthropod group (Shackelford et al. 2013). In a study investigating the impact of sown flower strips on Coccinellidae, both scales were found to increase ladybird diversity but no interaction between local and landscape factors was discovered (Woltz et al. 2012), while local more than landscape habitat structure was found to influence the diversity of natural enemies in overwintering habitats (Sarthou et al. 2014). In a study using path analysis to investigate the effect of landscape complexity on enemy diversity, no significant direct effect was recorded, and the authors associated the negative effect of altitude on enemy diversity to lower plant diversity at higher altitudes (Poveda et al. 2012). Here, we demonstrate that in naturally regenerated field

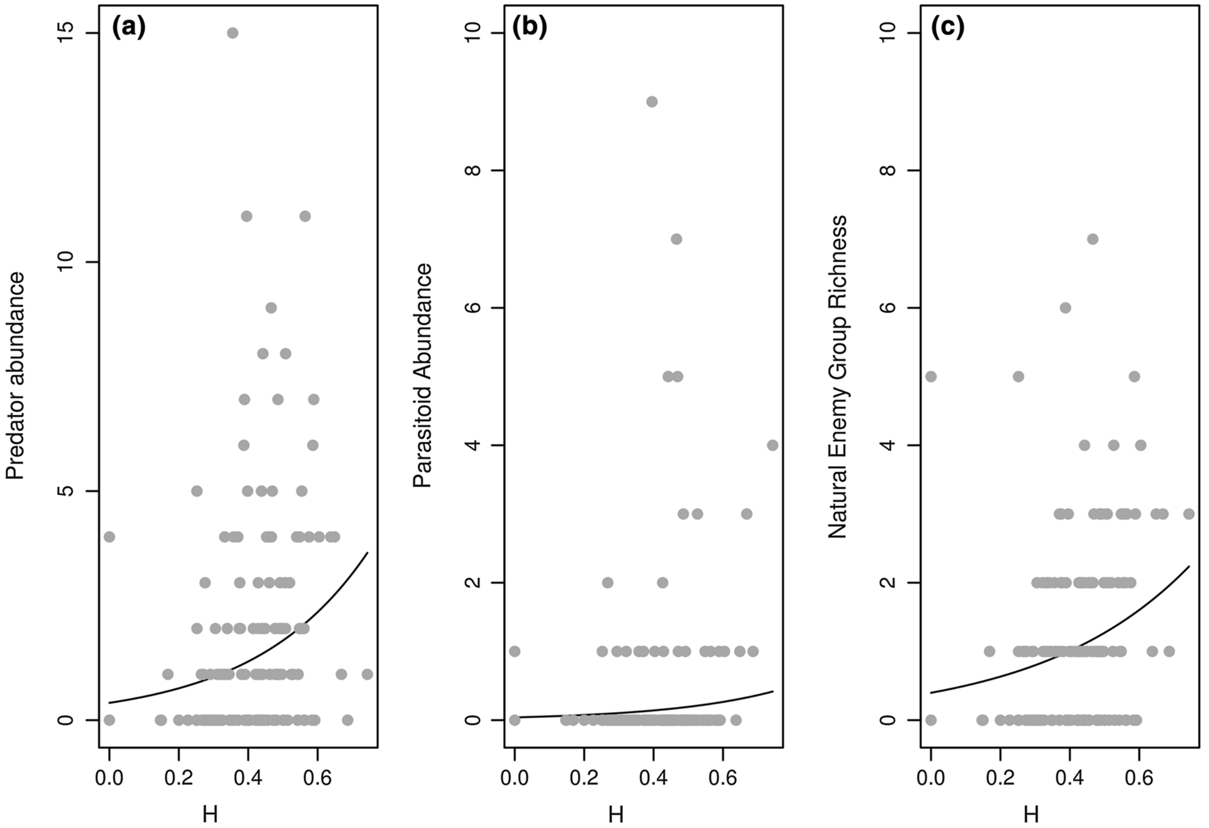

Fig. 1 Scatter plot for (**a**) predator and (**b**) parasitoid groups abundance and (**c**) natural enemy group richness in relation to vegetation diversity (H) in each belt transect (n = 8) for all fields. *Curves* represent estimated abundance/richness of natural enemies in field margins with different vegetation diversity from GLMM with a Poisson error distribution

margins, vegetation diversity appears to be higher in field margins within more complex landscapes and that this is associated with increased natural enemy diversity.

Vegetation diversity at the field scale was positively related to *T. absoluta*-caused fruit injury (Table 4), indicating a benefit obtained from field margins with increased plant diversity. While this effect was not significant within the path analysis ($p = 0.07$, Fig. 3a), *T. absoluta* adults have been previously shown to derive fitness benefits from nectar sources provided by various flowering species under controlled conditions (Balzan and Wäckers 2013). Our results also indicate an important effect of harvest date on crop damage caused by both pests. However, increased vegetation diversity in fields harvested later during the season, that is when higher crop damage is normally observed, was associated with lower *T. absoluta*-caused crop injury. We have also recorded these effects for Noctuidae pests during 2011, indicating that the effect of vegetation on crop injury varies with the harvest date. This might be caused by the dependence of cyclic colonisation of the ephemeral tomato crop and surrounding habitats by natural enemies (Wissinger 1997), and the high biotic potential and ability of these pests to access nectar resources, which might result in comparatively higher derived benefits to crop pests earlier during the crop season. Moreover, results obtained from the path analysis indicate a negative effect of harvest time on vegetation diversity, from which *T. absoluta* was shown to derive benefits. Increased natural enemy abundance and diversity were negatively related to *T. absoluta* fruit injury, but this effect was not significant for noctuid fruit injury and total crop damage. Vegetation complexity, in more species diverse field margins, can mediate multi-predator effects on herbivores by providing micro-habitats that act as a refuge from intra-guild predation,

Table 3 Most abundant flowering species within field margins and GLMM results measuring the influence of floral resources on natural enemies, using a negative binomial error distribution

Species	Family	Number of transects	Flower relative abundance (%)	SE	df	Natural enemy taxonomic group richness		Predator abundance		Parasitoid abundance	
						χ^2	p	χ^2	p	χ^2	p
Chenopodium album	Chenopodiaceae	6	15.39	0.31							
Picrisechioides	Asteraceae	16	10.33	0.26	1			4.29	0.04		
Beta vulgaris	Chenopodiaceae	3	9.10	0.25							
Pulicariadysenterica	Asteraceae	14	7.62	0.23	1	5.18	0.02				
Polygonumaviculare	Polygonaceae	6	6.77	0.22							
Solanum nigrum	Solanaceae	9	5.32	0.19	1					2.96	0.09
Daucuscarota	Apiaceae	27	4.58	0.18	1	6.64	0.01	8.40	0.004		
Coleostephusmyconis	Asteraceae	3	4.04	0.17	1	11.76	0.001			5.42	0.02
Convolvulus arvensis	Convolvulaceae	16	3.37	0.16							
Foeniculum vulgare	Apiaceae	16	2.91	0.15							

Only species that were recorded in three field margin vegetation transects or more are presented and only GLMM fitting results for variables with p-value < 0.1 are shown. The difference in deviance of the two compared models following backward elimination and its significance using a χ^2 test are shown

more effective prey capture and access to alternative resources (Finke and Denno 2002; Langellotto and Denno 2004; Straub et al. 2008).

Landscape complexity appears to influence Lepidoptera-caused crop damage through two concurrent mechanisms (Fig. 3). It is regulated through a direct path, and was lower in fields within landscapes with less arable land. Thus, assuming that increased arable cover is positively related to tomato field area since this is one of the main crops within the study area, our results indicate that pest pressure is associated with higher host crop availability as would be predicted by the resource concentration hypothesis. Landscape complexity also regulates crop damage through an indirect pathway: lower cropped land cover was positively associated with field margin plant species richness, higher plant diversity increased flower and enemy richness in field margins, increased enemy richness was negatively related to *T. absoluta*-caused fruit injury. However, the effect of natural enemy diversity on the crop damage parameter measured here was less consistent than the direct bottom-up effect, indicating that the maintenance of landscape habitat diversity remains crucial for the regulation of crop damage.

Results presented here indicate the importance of local and landscape habitat complexity for the conservation of natural enemies and pest control services. Fields in landscapes with low habitat-type diversity are associated with higher crop damage due to increased resources availability for pests and lower top-down control by natural enemies, the latter being positively related to vegetation diversity of field margins of complex landscapes. Thus, given the unsuitability of margin habitats in landscapes dominated by arable land, management at the local scale should aim at providing resources that enhance natural enemies diversity and pest suppression. Previous results demonstrate how wildflower strips establishment in tomato fields can enhance the conservation of natural enemies, and other functional group such as pollinators (Balzan et al. 2014; Balzan and Moonen 2014), whilst ensuring the suppression of yield loss caused from multiple pests (Balzan and Moonen 2014). Native wildflower strips can be established as Ecological Focus Areas under the ("Pillar 1") European Union Common Agricultural Policy (CAP) for 2014–2020, which should be applied to at least 5 % of arable land of farms where arable land covers more than fifteen hectares. Management recommendations

Table 4 Influence of field margin vegetation and landscape habitat diversity on (a) Noctuidae, (b) *T. absoluta*-caused crop injury and (c) total crop damage, measured using a GLMM with a negative binomial error distribution (H = Shannon vegetation diversity or Shannon-habitat type diversity at r = 1000 m, T = harvest date, and YR = year)

Fixed effects	(a) Noctuidae-caused fruit injury						(b) *T. absoluta*-caused fruit injury						(c) Total Crop damage					
	Vegetation diversity (H)			Landscape habitat diversity (H)			Vegetation diversity (H)			Landscape habitat diversity (H)			Vegetation diversity (H)			Landscape habitat diversity (H)		
	Est (±SE)	Z	p	Est (±SE)	Z	p	Est (±SE)	Z	p	Est (±SE)	Z	p	Est (±SE)	Z	p	Est (±SE)	Z	p
Intercept	−3.77 (3.84)	−0.98	NS	−0.65 (1.05)	−0.62	NS	−18.12 (6.94)	−2.61	0.009	−3.76 (4.08)	−0.92	NS	−3.95 (3.41)	−1.16	NS	−0.98 (2.08)	−0.48	NS
H	0.55 (1.53)	0.36	NS	−1.62 (0.56)	−2.91	0.004	6.87 (2.97)	2.32	0.02	1.60 (3.05)	0.52	NS	1.3 (1.4)	0.94	NS	0.54 (1.59)	0.34	NS
YR_B	−14.27 (8.40)	−1.70	0.09				−12.73 (5.09)	−2.50	0.01	−10.41 (3.67)	−2.83	0.005	−12.96 (7.97)	−1.63	NS	4.38 (2.61)	1.68	0.09
T	0.12 (0.07)	1.70	0.09	0.04 (0.01)	4.08	<0.001	0.38 (0.14)	2.82	0.005	0.14 (0.07)	2.11	0.03	0.14 (0.06)	2.53	0.02	0.09 (0.04)	2.51	0.01
HxT	−0.03 (0.03)	−1.13	NS				−0.14 (0.06)	−2.20	0.03	−0.06 (0.05)	−1.18	NS	−0.05 (0.02)	−1.91	0.06	−0.05 (0.03)	−1.82	0.07
$HxYR_B$	7.72 (3.68)	2.10	0.04										6.42 (3.52)	1.82	0.07	−4.30 (2.15)	−2.01	0.045
YR_BxT	0.53 (0.19)	2.75	0.006				0.20 (0.08)	2.42	0.02	0.16 (0.06)	2.61	0.01	0.51 (0.18)	2.76	0.006	−0.10 (0.04)	−2.22	0.03
$HxYR_BxT$	−0.26 (0.09)	−2.98	0.003										−0.24 (0.08)	−2.9	0.004	0.09 (0.04)	2.38	0.02

Estimated parameters (Est) and Wald test values (Z) from the GLMM are shown ('NS' symbol indicates that the effect is not significant). The GLMM assessing the influence of Shannon habitat-type diversity on *T. absoluta* crop injury is not presented as this parameter was not included within the minimum adequate GLMM (supplementary data table S3)

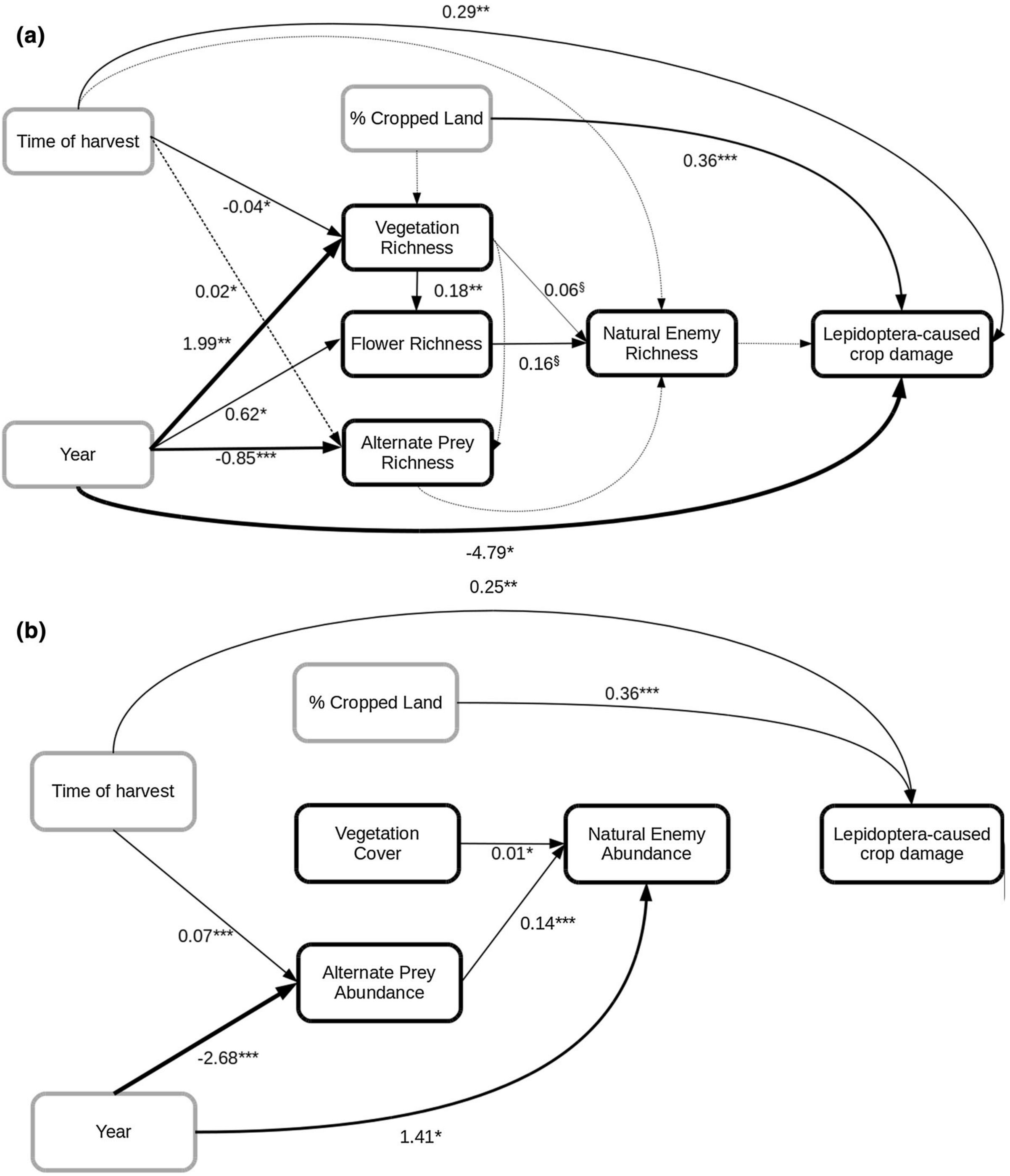

Fig. 2 Path diagram for measuring the direct and indirect effects on total Lepidoptera-caused fruit damage in tomato crop using **a** richness (df = 11, p = 0.42, Satorra–Bentler correction = 1.30) and **b** abundance data (df = 6, p = 0.98, Satorra–Bentler correction = 0.95) for vegetation, alternative prey and natural enemies. *Solid lines* denote significant effects and *dashed lines* represent non-significant effects. Parameters in a *grey box* are exogenous variables whilst those in *black boxes* are endogenous variables. The width of each *line* is used as an indication of the strength of the relationship, while the values represent standardised path coefficients. The path coefficients indicate the amount of expected change in the dependent variable for which the designated factor is directly responsible. $^{\S}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

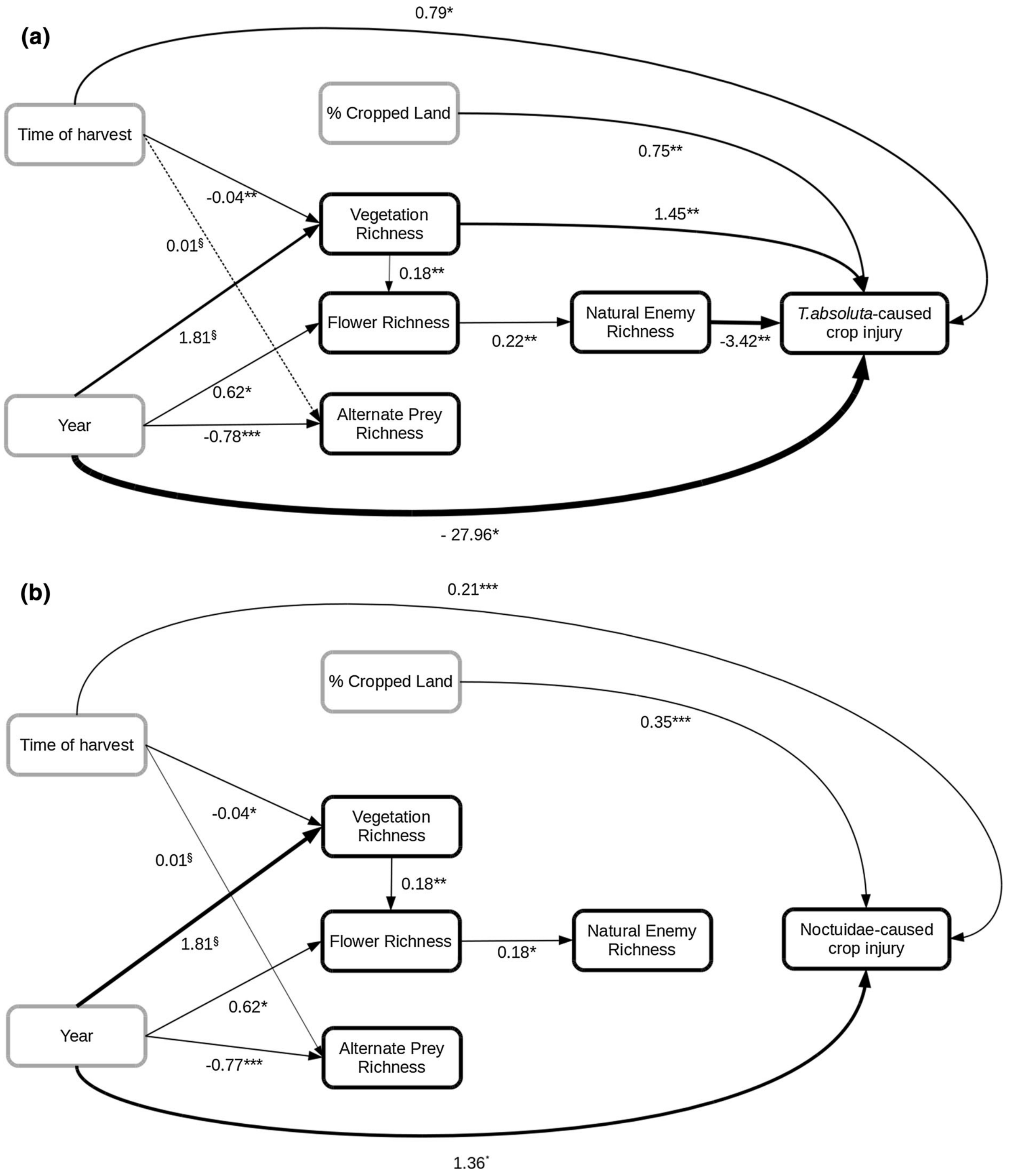

Fig. 3 Path diagram for measuring the direct and indirect effects on **a** *T. absoluta* (df = 11, p = 0.53, Satorra–Bentler correction = 1.71) and **b** Noctuidae-caused (df = 11, p = 0.43, Satorra–Bentler correction = 1.14) fruit injury using richness data. *Solid lines* denote significant effects and *dashed lines* represent non-significant effects. Parameters in a *grey box* are exogenous variables whilst those in *black boxes* are endogenous variables. The width of each *line* is used as an indication of the strength of the relationship, while the values represent standardised path coefficients. The path coefficients indicate the amount of expected change in the dependent variable for which the designated factor is directly responsible. $^{\S}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

would differ for fields in more complex landscapes, which were associated with higher crop damage regulation through lower resource availability and top-down control by natural enemies. Our results demonstrate that field margins in complex landscapes provide flowering resources and alternate prey, necessary for enhancing natural enemies diversity and for reducing Lepidoptera-pest caused crop damage. Hence the conservation of habitat complexity at the either scales should within these landscapes be a priority as non-crop habitats were shown to be important for maintaining plant and insect biodiversity, and to contribute to the suppression of crop damage from multiple pests.

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