Insect Conservation and Diversity

Insect Conservation and Diversity (2017) doi: 10.1111/icad.12249

Environmental heterogeneity effects on predator and parasitoid insects vary across spatial scales and seasons: a multi-taxon approach

DARIA CORCOS,[1,2] DIEGO J. INCLÁN,[2,3,4] PIERFILIPPO CERRETTI,[1,2] MAURIZIO MEI,[1] FILIPPO DI GIOVANNI,[1] DANIELE BIRTELE,[5] PAOLO ROSA,[6] ALESSIO DE BIASE,[1] PAOLO AUDISIO[1] and LORENZO MARINI[2] [1]Department of Biology and Biotechnology 'Charles Darwin', Sapienza University of Rome, Rome, Italy, [2]DAFNAE, University of Padova, Padua, Italy, [3]Instituto Nacional de Biodiversidad, Sección Invertebrados, Quito, Ecuador, [4]Facultad de Ciencias Agrícolas, Universidad Central del Ecuador, Quito, Ecuador, [5]Centro Nazionale Carabinieri Biodiversità di Bosco della Fontana, Mantua, Italy and [6]Bernareggio, Italy

Abstract. 1. As predator and parasitoid insects depend on multiple resources for adult feeding and reproduction, environmental heterogeneity (EH) is expected to be a key driver of their species diversity. In temperate regions, the benefits of EH are expected to vary across spatial scales and seasons, depending on species life-history traits and temporal fluctuations in resources.

2. We tested the importance of EH at multiple spatial scales on diversity and abundance of predator and parasitoid insects, and whether its effects changed across seasons.

3. Insect sampling was carried out in highly fragmented landscapes in a Mediterranean region (Tuscany, Central Italy). We selected 18 semi-natural patches, embedded in an intensive agricultural matrix. For each patch, EH was measured at three spatial scales (micro, patch, and landscape). Five groups of predator and parasitoid insects were sampled 16 times with pan traps between March and November, 2012.

4. EH at the landscape scale positively influenced the diversity of predator and parasitoid insects, while the effects at smaller spatial scales were less evident. The strength and the direction of EH-diversity relationship changed between groups and across seasons, indicating that the mechanisms by which EH affects predators and parasitoids are various and complex.

5. Conservation strategies aimed at maximising the diversity of predators and parasitoids should focus more on increasing EH at the landscape scale than at the local scale.

Key words. Habitat diversity, habitat fragmentation, landscape, scale-dependence, seasonality, temporal dynamics.

Introduction

In recent decades, agricultural intensification has led to the conversion of large areas of natural and semi-natural habitats into simplified landscapes (Weibull *et al.*, 2000; Tilman *et al.*, 2001; Fahrig, 2003; Tscharntke *et al.*, 2005). The fragmentation of the resulting mosaic of semi-

Correspondence: Daria Corcos, Department of Biology and Biotechnology 'Charles Darwin', Sapienza University of Rome, Piazzale Aldo Moro 5, 00185 Rome, Italy.
E-mail: daria.corcos@uniroma1.it

D. Corcos and D. J. Inclán contributed equally to the study.

natural habitats is well-known to strongly affect the diversity of insect communities (Burel *et al*., 2004; Vasseur *et al*., 2013). Although many empirical and theoretical studies have shed light on the effects of habitat fragmentation and habitat loss on populations and communities of primary producers and consumers (Hanski, 1999; Ewers & Didham, 2006), less attention has been paid to the impact of this driver on predators and parasitoids (i.e. the third trophic level; but see Cronin, 2007; Elzinga *et al*., 2007; Holzschuh *et al*., 2010; Coudrain *et al*., 2013; Hicks, 2015).

The effects of habitat fragmentation and habitat loss on the diversity of insect communities have been widely explained using the 'island biogeography theory' (MacArthur & Wilson, 1967) that predicts that bigger and well-connected habitats support communities with higher diversity than small and isolated ones. However, habitat area and connectivity are not always the only predictors of species presence and persistence (Ye *et al*., 2013). Beside semi-natural habitats, also the agricultural matrix can contribute to maintaining insect diversity by providing higher diversity of resources (Bertrand *et al*., 2016; Martin *et al*., 2016). The 'niche theory' (Hutchinson, 1957) predicts that structurally complex environments are likely to provide more niches and diverse ways of exploiting the environmental resources and thus can contribute to increased species diversity (Tews *et al*., 2004; Weisberg *et al*., 2014; Stein & Kreft, 2015). Environmental heterogeneity (EH) is expected to be particularly relevant for the diversity of predators and parasitoids as they depend on the availability of multiple resources such as nectar and pollen and on a variety of prey or hosts (Landis *et al*., 2005; Tscharntke *et al*., 2007; Daoust *et al*., 2012). Considering both spatial and temporal dynamics of EH is hence necessary to fully understand the impacts of habitat fragmentation and habitat loss on the diversity of predator and parasitoid insects (Aranda & Graciolli, 2015).

Although heterogeneous environments can, generally, sustain more species by providing complementary habitats and larger trophic resources (Fahrig *et al*., 2011), those benefits can vary across spatial scales depending on species mobility and degree of resource specialisation (Tamme *et al*., 2010; Bar-Massada & Wood, 2014; Hicks, 2015; Stein & Kreft, 2015). Contrary with the expectations of classical niche theory, Kadmon and Allouche (2007) predicted that increasing EH increases the potential number of species in a given area by providing suitable conditions to a larger number of species, but also reduces the amount of suitable area available for each species. According to this hypothesis, species diversity should increase with EH at large scales, where communities benefit from niche complementarity, while being neutral or decreasing at smaller scales, because of the competition between species (Tews *et al*., 2004; Tamme *et al*., 2010; Gazol *et al*., 2013). At the local scale, many empirical studies have demonstrated that greater plant diversity supports a higher number of insect predators and parasitoids (e.g. Landis *et al*., 2005; Letourneau *et al*., 2012; Bennett & Gratton, 2013). Similarly, at larger spatial scales, complex landscapes composed of different habitats usually support communities with higher diversity compared to more homogeneous landscapes (Tscharntke *et al*., 2005; Chaplin-Kramer *et al*., 2011; Martin *et al*., 2016). In this context, highly mobile predators and parasitoids are expected to respond to EH at relatively large spatial scales (Thies *et al*., 2003) because individuals can switch between habitats where the resources/hosts become available.

In temperate regions, landscapes are dynamic mosaics of habitats whose quality can strongly vary over seasons due to vegetation phenology and landscape management, influencing the insect assemblages differently over time (Jonsen & Fahrig, 1997; Tscharntke *et al*., 2005; Kremen *et al*., 2007). In agricultural landscapes, the high productivity of the crop matrix in certain periods of the year may enhance the amount of available food/prey resources, potentially increasing insect diversity and abundance (Tscharntke *et al*., 2005, 2007; Martin *et al*., 2016). Although many studies have explored the general effects of EH in agricultural landscapes, it is still unclear whether EH effects can vary over seasons (Tews *et al*., 2004).

The purpose of this study was to examine the diversity of five key groups of predator and parasitoid insects in highly fragmented agricultural landscapes. Two groups of dipterans (tachinids and predatory hoverflies) and three groups of hymenopterans (ichneumon, spheciform and cuckoo wasps) were sampled. The adults of these groups feed on nectar and pollen, while the larvae have a wide range of life-styles, spanning from specialist to generalist predators and parasitoids. First, the importance of EH at multiple spatial scales on species richness and abundance was tested. We hypothesised that predators and parasitoids will be more influenced by the increment of EH at the landscape scale rather than at the smaller scales. Second, we tested whether the effects of EH changed over time as a consequence of the temporal fluctuations in resources in both the semi-natural habitats and the crop matrix.

Materials and methods

Study area and site selection

The study was conducted in a highly fragmented area of ca 650 km^2 in the Siena province (Tuscany, Central Italy; Fig. 1a). The climate is temperate Mediterranean with a mean annual temperature of 15 °C and an annual precipitation of 750 mm. The landscape is dominated by intensively farmed crop fields, mainly cultivated with durum wheat (*Triticum durum*). Several remnant patches of semi-natural (open vegetation and forest) habitats are interspersed within the agricultural matrix. Eighteen patches of semi-natural habitat were selected (Fig. 1a; Table S1) with two statistically uncorrelated gradients in

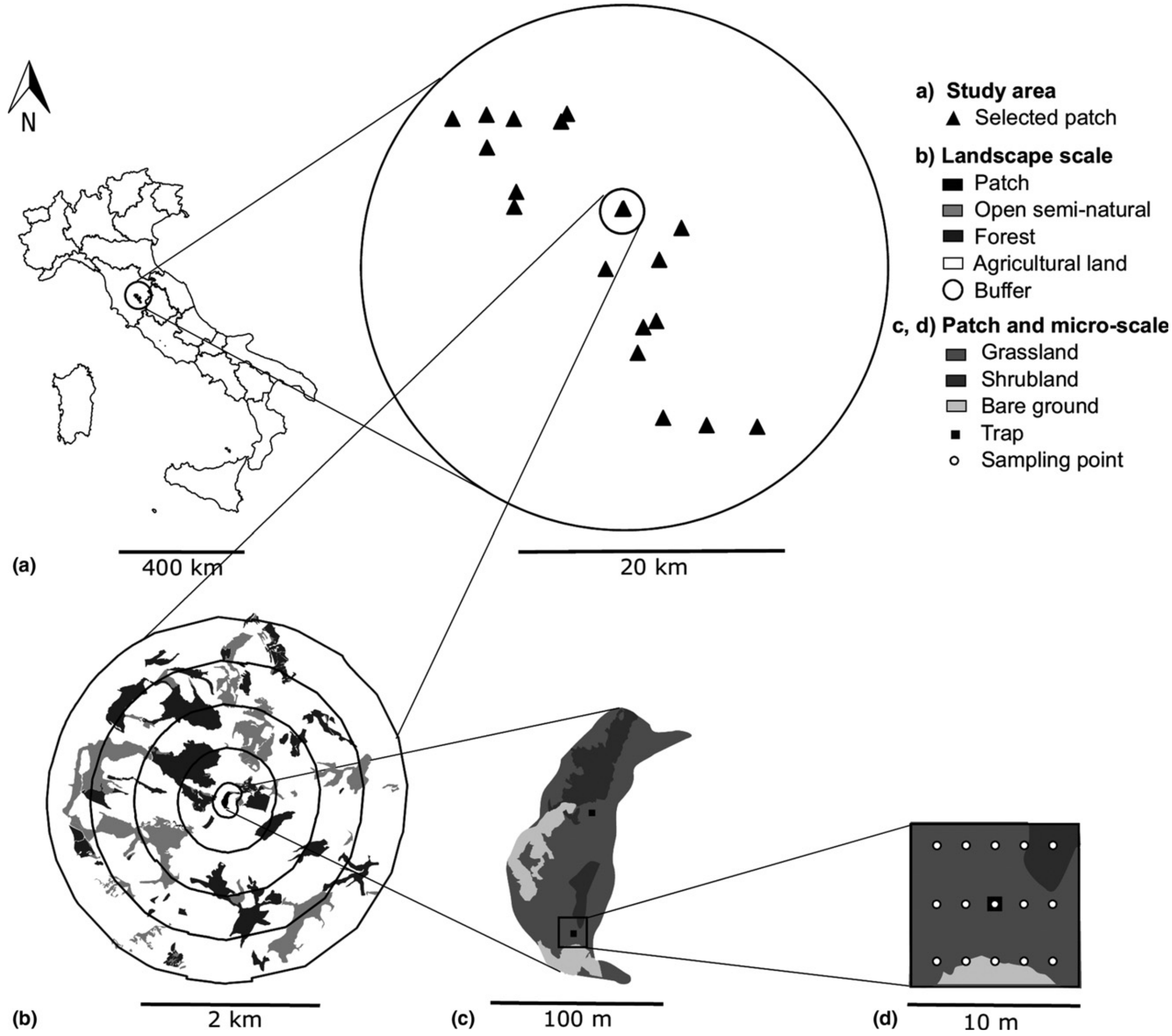

Fig. 1. (a) Study area with the 18 selected patches in the province of Siena and the three spatial scales used to quantify environmental heterogeneity (EH): (b) landscape, (c) patch, and (d) micro-scale. The landscape scale EH was measured by the Shannon index based on the cover of open semi-natural, forest and crop habitats (independently for five buffers of 100, 500, 1000, 1500 and 2000 m). Patch scale EH was measured by the Shannon index based on the cover of grassland, shrubland and bare ground. Micro-scale EH was calculated using the first principal component analysis axis of three micro-scale heterogeneity variables combined.

(i) habitat area and (ii) EH (i.e. Shannon index). These patches were composed of a mosaic of grassland, scrubland and bare ground with little or sparse vegetation (Maccherini *et al*., 2011). The mean minimum distance between focal patches was 2.6 km, and ranged from 0.9 to 4.7 km. The landscape habitat was dominated in spring by wheat and in summer by harvested and ploughed fields. During fall the landscape remained unmanaged until the end of November, when the winter crops were planted. For a detailed description of the study area and site selection see Inclán *et al*. (2014).

Insect sampling

Seven families of insect predators and parasitoids were sampled, belonging to two orders: Diptera (fam. Tachinidae and predaceous Syrphidae) and Hymenoptera (fam. Ichneumonidae, Ampulicidae, Sphecidae, Crabronidae and Chrysididae). The families Ampulicidae, Sphecidae and Crabronidae were pooled as spheciform wasps (Debevec *et al*., 2012). Most species at the adult stage are known to forage on nectar and pollen, behaving as flower-visitors (Leius, 1960; Pagliano & Negrisolo, 2005;

Rosa, 2006; Stireman *et al*., 2006; Speight, 2014). The larvae show different feeding strategies, ranging from generalist to specialist predators or parasitoids. Specifically, tachinid flies, ichneumon wasps and cuckoo wasps are parasitoids (Gauld & Boton, 1988; Kimsey & Bohart, 1991; Stireman *et al*., 2006; Cerretti *et al*., 2014), while spheciform wasps are predators (Pagliano & Negrisolo, 2005). Ichneumon wasps and cuckoo wasps are known to be mostly specialised parasitoids (Fitton *et al*., 1988; Gauld & Boton, 1988; Pärn *et al*., 2014), while tachinid flies have a generally broader host range (Stireman *et al*., 2006; Cerretti *et al*., 2014). Most hoverfly species are predators, but some can be detritivorous or phytophagous (Rotheray, 1993). According to the aim of this study only hoverfly species behaving as predators at the larval stage were included (see Appendix S1 for the feeding behaviour of larvae).

The study was conducted from March to November 2012. Yellow pan traps filled with water and 3% dishwashing detergent (Sole™, Reckitt Benckiser, Milan, Italy) were used to collect adults of the targeted taxa. Pan traps are a reliable, efficient and repeatable method for sampling flying flower-visiting insects when the focus is on a species richness estimate (e.g. Stireman, 2008). Each trap cluster consisted of a set of five pan traps: three standard yellow bowls of 500 ml, with 16 cm diameter, and two UV-yellow plastic bowls of 330 ml, with 10 cm diameter. One UV-yellow and one standard yellow pan traps were held on a wood support and one UV-yellow and two standard yellow pan traps were placed directly on the ground, within a two-meter radius of the wood support. The contents of the five pan traps were pooled in the field obtaining one data point per cluster. The sampling effort was proportional to the patch size: in patches with an area of 1.5 ha or smaller two clusters of pan traps were used and an additional cluster was added every additional ha. All traps were placed at least 20 m from the patch margin and were always positioned in a grassland even if the patch was dominated by shrubs. At each sampling round, the traps were set on day 1 and 2, and collected on day 3 and 4, after 48 h. The sampling was performed every 2 or 3 weeks (depending on the weather, avoiding cloudy and rainy days), covering the period when insect adults were actively flying (from March to November, for a total of 16 sampling rounds). The order in which samples were collected at the sites was randomised across the 16 sampling rounds. Most of the sampled specimens were identified to species level (Appendix S1 for identification literature). Unidentifiable and/or undescribed ichneumon wasps were sorted to morphospecies. Specimens are preserved at the Museum of Zoology, Sapienza University of Rome.

Explanatory variables

Environmental heterogeneity. Micro-scale: Around each trap cluster, we identified a 10 × 10 m grid, composed of three parallel transects of five sampling points (Fig. 1d). Within each grid, the percentage of the three types of open semi-natural habitat (grassland, shrubland and bare ground) was visually assessed, and the Shannon index was calculated. For each sampling point in the grid, the grass height and the ground slope were recorded, and the standard deviation was calculated for both variables. We then combined the three micro-scale heterogeneity variables (i.e. micro-scale Shannon diversity, standard deviation of grass height and standard deviation ground slope) performing a principal component analysis (PCA), and used the first PCA axis to obtain a single micro-scale EH (micro EH). Micro EH accounted for 46% of the variance, and was positively correlated with micro-scale Shannon diversity and standard deviation of ground slope, and negatively correlated with standard deviation of grass height (Pearson's correlation coefficients: 0.80, 0.78, and −0.35, respectively).

Patch scale: Within each of the 18 patches, the area covered by each habitat type was independently calculated using aerial photographs from Google Earth 6.2 (Google Inc., Silicon Valley, CA, USA; Fig. 1c). Patch scale EH (patch EH) was estimated by the Shannon index based on the cover of grassland, shrubland and bare ground (min = 0.40, max = 1.03, median = 0.75).

Landscape scale: The EH at the landscape scale (land EH) was assessed by quantifying the diversity of semi-natural (both open and forest) and crop habitats in the landscape. Polygons of open semi-natural, forest and crop were identified in Google Earth 6.2 (Google Inc.) and the percentage cover of the different habitat types was quantified within five buffers of 100 m, 500 m, 1000 m, 1500 m, and 2000 m (Fig. 1b), using QGIS (Quantum GIS Development Team, 2014). Land EH was measured by the Shannon index based on the cover of open semi-natural, forest and crop (e.g. land EH at 1000 m: min = 0.10, max = 0.95, median = 0.42).

Patch area. The areas of the 18 focal patches of open semi-natural habitat were quantified by digitising the boundaries using aerial photographs in QGIS, and it ranges from 0.29 to 10.82 ha.

Statistical analyses

The effects of the explanatory variables at the three spatial scales (micro, patch and landscape scale) on the five predator and parasitoid groups were analysed using linear mixed-effects models. The response variables were the pooled number of species and abundance sampled in every trap cluster (i.e. five traps pooled) separated by season (spring, summer and fall). For each trap cluster (n = 83), the 16 sampling rounds in three seasons (spring, summer and fall) were grouped by pooling the number of species and abundance. Spring included the first five samplings (16th March–12th May), summer the following six (26th May–8th August) and fall the last five (26th August–24th November). Hence, for each trap cluster there were three repeated measures ($n = 249$). The response variables were log-transformed to improve linearity and to achieve normality and variance homogeneity of model residuals. The explanatory variables were standardised by dividing by two times their standard deviation (Gelman, 2008). All models included trap cluster ID ($n = 83$) nested within patch ID ($n = 18$) as random factors. This random structure accounted for the spatial and temporal dependence in the sampling design. The full model included the following variables:

Response variable (species richness/abundance) ~ area + Land EH + Patch EH + Micro EH + Land EH × season + Patch EH × season + Micro EH × season

The full models were simplified using a backward deletion procedure ($P < 0.05$). The use of model selection based on *P*-values has been widely debated in recent years (Johnson & Omland, 2004; Gelman, 2013). However, the traditional null hypothesis testing approach is still effectively used to test biological accurate hypotheses in effectively designed studies with low collinearity (Gelman, 2013; Murtaugh, 2014). Here, to evaluate the risk of finding biased effects due to our model section procedure we presented the coefficients for both full and reduced models (Table S2). Since the significant variables were very similar, we presented the effects from the reduced models. In order to identify the best landscape scale for each group, the full models were run using the land EH each time measured at a different spatial scale (100, 500, 1000, 1500, and 2000 m), and the model with the best goodness-of-fit (Table S3). The perceived landscape scale differed between groups, but within each group the direction of the effect did not change with different buffer radii. In preliminary analyses, we also tested the effect of semi-natural habitat connectivity instead of landscape scale EH (Table S4), but the model fit was always worse. We did not included the connectivity variable in the model because it was strongly correlated with landscape scale EH (Table S5). All analyses were performed using R3.2.2 (R Core Team, 2015). For the linear mixed-effects model analyses were used 'lme4' (Bates *et al.*, 2014) and 'nlme' (Pinheiro *et al.*, 2013) packages. For the PCA analyses we used the function 'prcomp' from the 'stats' package.

Collinearity between explanatory variables

The selection of the explanatory variables used in the model was designed to minimise the correlation between micro, patch and landscape scale environmental variables, while the five scales of landscape heterogeneity were highly correlated and therefore tested in separate models (Table S6).

Results

A total of 6684 individuals were collected belonging to 450 species: tachinid flies with 1528 individuals and 129 species, hoverflies with 1030 individuals and 17 species, spheciform wasps with 1857 individuals and 76 species, ichneumon wasps with 1056 individuals and 172 species (including 25 morphospecies), and cuckoo wasps with 1212 individuals and 56 species (Appendix S1; Fig. 2). The season with the highest species richness was summer (296 species), followed by fall and spring (261 and 130, respectively). Forty-seven percent of the specimens examined were collected in fall, 40.4% in summer and only 12.3% in spring. Species richness and abundance for each group were always correlated (Pearson's correlation coefficients: tachinids = 0.75; hoverflies = 0.70; spheciform wasps = 0.85; ichneumon wasps = 0.79; cuckoo wasps = 0.79).

The effects of EH largely varied across spatial scales and seasons. We found an overall effect of micro-scale EH only for tachinid flies: both species richness and abundance were higher in habitats with high micro-scale EH (Fig. S1). We did not find an overall effect of patch scale EH on any group. A significant overall effect of landscape scale EH on species richness of tachinid flies, abundance of hoverflies, and species richness and abundance of spheciform and cuckoo wasps was found (Table 1).

We did not find an interaction between micro-scale EH and season for any group. Only, for species richness of hoverflies, an interaction between patch scale EH and season was found, i.e. the number of species was higher in heterogeneous patches in summer and lower in spring and fall (Fig. S2). With the exception of the species richness and abundance of cuckoo wasps, and species richness of spheciform wasps, the relative importance of landscape scale EH varied between seasons (Fig. 3). Generally, a higher species richness and abundance was associated with heterogeneous landscapes in both spring and summer

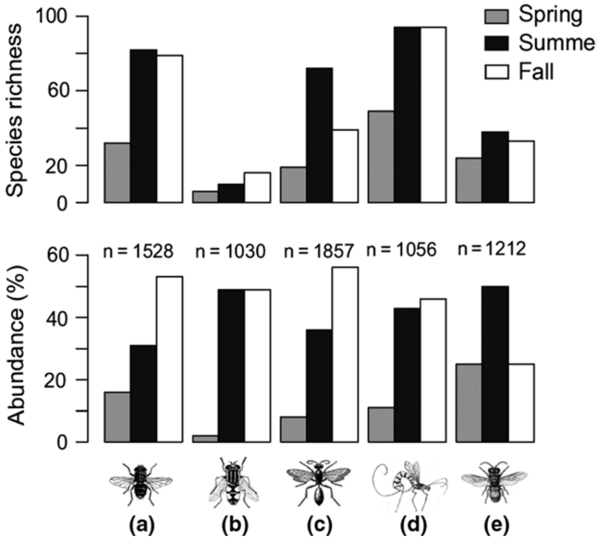

Fig. 2. Species richness and relative abundance (%) of (a) tachinid flies, (b) hoverflies, (c) spheciform wasps, (d) ichneumon wasps and (e) cuckoo wasps across seasons.

Table 1. Results from the mixed-effect models testing patch area, season, environmental heterogeneity (EH) measured at the micro, patch and landscape scale (micro, patch and land EH), and the interaction between EH and season on species richness and abundance of the five groups.

	χ^2	d.f.	P	R^2mar	R^2con		χ^2	d.f.	P	R^2mar	R^2con
(i) Species richness						(ii) Abundance					
(a) Tachinids				0.490	0.700					0.420	0.598
Area	4.604	1	0.032			Area	10.350	1	0.001		
Micro EH	4.573	1	0.032			Micro EH	9.176	1	0.002		
Land EH500	5.442	1	0.020			Land EH500	0.157	1	0.692		
Season	79.192	2	<0.0001			Season	55.927	2	<0.0001		
Land EH500 × season	7.697	2	0.021			Land EH500 × season	5.936	2	0.051		
(b) Hoverflies				0.641	0.686					0.626	0.678
Patch EH	6.368	1	0.012			Land EH1000	5.285	1	0.022		
Land EH1500	4.882	1	0.027			Season	180.410	2	<0.0001		
Season	26.480	2	<0.0001			Land EH1000 × season	47.156	2	<0.0001		
Patch EH × season	15.726	2	<0.0001								
Land EH1500 × season	8.393	2	0.015								
(c) Sphecids				0.549	0.612					0.523	0.688
Land EH1000	23	1	<0.0001			Land EH2000	1.162	1	0.281		
Season	300.5	2	<0.0001			Season	85.49	2	<0.0001		
						Land EH2000 × season	6.425	2	0.040		
(d) Ichneumonids				0.453	0.553					0.450	0.553
Land EH500	0.532	1	0.466			Land EH100	6.584	1	0.010		
Season	90.214	2	<0.0001			Season	178.121	2	<0.0001		
Land EH500 × season	16.143	2	0.000			Land EH100 × season	32.072	2	0.000		
(e) Cuckoo wasps				0.300	0.384					0.313	0.462
Area	4.179	1	0.041			Land EH100	24.92	1	<0.0001		
andSI100	32.390	1	0.000			Season	41.58	2	<0.0001		
Season	41.954	2	0.000								

The buffer used for every group is provided for the landscape scale EH. Only the significant and marginally significant variables after a backward deletion procedure ($P > 0.05$) are presented. The pseudo-R^2's, R^2marginal (R^2mar) and R^2conditional (R^2con) are presented.

(stronger in spring), while the effect in fall was variable. Hoverfly species richness and abundance were higher in heterogeneous landscapes in spring, and lower in summer.

We found a linear positive effect of semi-natural patch area only on species richness and abundance of tachinid flies and species richness of cuckoo wasps.

Discussion

Dispersal and foraging of insect predators and parasitoids can occur at large spatial scales and across multiple habitats (Letourneau *et al*., 2012; Ekroos *et al*., 2013) and there is a growing consensus that investigating EH at multiple spatial and temporal scales might help to fully understand the negative effects of environmental simplification on insect communities (Weibull *et al*., 2000; Vasseur *et al*., 2013; Bertrand *et al*., 2016). EH at the landscape scale was the main driver of diversity and abundance of predators and parasitoids, while the effects at smaller spatial scales were less evident. The strength and direction of the EH-diversity relationship, however, changed across groups and seasons, indicating that the mechanisms by which EH affects the diversity of predator and parasitoid insects are various and complex.

Spatial variations in the effects of EH

According to the expectations of the classical niche theory (Hutchinson, 1957), a positive diversity-EH relationship was found for most of the investigated groups. Micro-scale EH (i.e. high micro-scale habitat diversity and ground slope variation, and low grass height variation) only influenced species richness and abundance of tachinid flies. A high micro-scale habitat diversity is often associated with an increased diversity of herbaceous plants, and can be a major factor in determining diversity of species feeding on flowers (Bennett & Gratton, 2013). Furthermore, several species of tachinid flies perch on landmarks, such as hilltops, to mate (Stireman, 2008) and are probably positively influenced by ground slope variation. Considering that this group was also positively influenced by semi-natural habitat area (linear increase in

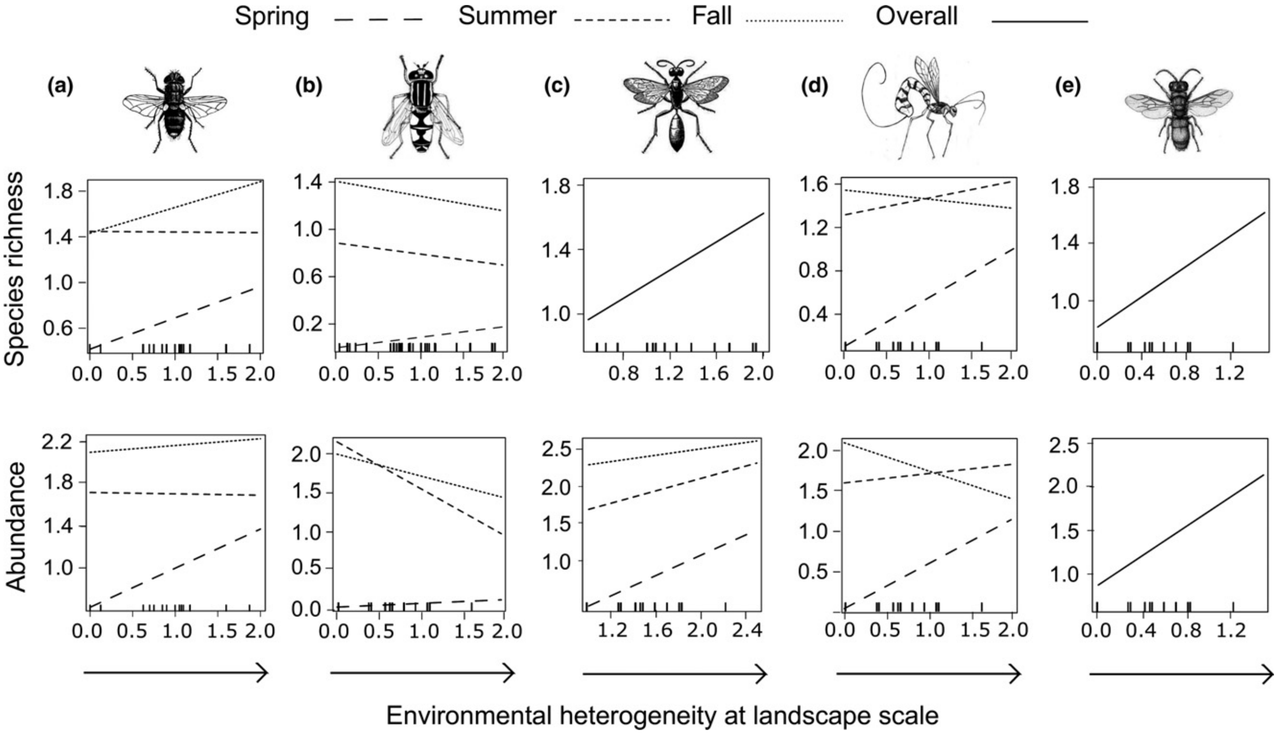

Fig. 3. Plots showing the relationship between landscape scale environmental heterogeneity and species richness/abundance of (a) tachinid flies, (b) hoverflies, (c) spheciform wasps, (d) ichneumon wasps and (e) cuckoo wasps across season. Both species richness and abundance were log-transformed. Plots were drawn using the 'effect' function from the library 'effects' in R.

abundance as the patch area increased), this may suggest that heterogeneous non-crop areas can provide more suitable habitats and resources for this parasitoid family, compared to the wheat dominated agricultural matrix. Those results are consistent with other studies (Letourneau *et al*., 2012; Inclán *et al*., 2014, 2015) that found, for this parasitoid group, a strong dependence on semi-natural habitats. According to our first hypothesis, the EH benefits were stronger at the landscape scale than at the local (patch and micro) scale. Predators and parasitoids depend on multiple and interacting resources and often use more than one habitat type to feed and reproduce (Landis *et al*., 2005). As trophic resources (e.g. plant and prey/hosts) are unevenly distributed between semi-natural and crop habitats, heterogeneous landscapes likely support higher resources throughout the seasons (Landis *et al*., 2005). Furthermore, flying insects can easily move between patches and will benefit from the complementary trophic resources and nesting sites between semi-natural and crop habitats (Letourneau *et al*., 2012).

Seasonal variations in the EH effects at the landscape scale

Quality of both semi-natural habitats and the matrix strongly fluctuate over time due to the temporal turnover of plant communities, crop or vegetation phenology and farm management (Burel *et al*., 2004; Vasseur *et al*., 2013). As predators and parasitoids use diverse resources during their life cycle (Landis *et al*., 2005), they strongly depend on the phenology, activity and reproduction of their prey and hosts (Bianchi *et al*., 2010). Our results support our second hypothesis of a seasonality in the EH effect, but the response varied between groups. In spring, landscape scale EH always had a strong positive influence on all the groups of predators and parasitoids, because many species can benefit from the complementarily of resources between semi-natural and crop habitats. In summer, the agricultural matrix is less permeable due to crop harvest, and predators and parasitoids can use only semi-natural habitats to locate alternative food sources. The effect of landscape-scale EH depends on how insects use the different habitat types: groups that use mainly semi-natural habitats can still benefit from a high landscape heterogeneity, while insects that rely mostly on crop habitats may be negatively affected. For example, for spheciform and cuckoo wasps the positive effect of landscape scale EH was consistent over time, indicating that these groups may be less susceptible to the temporal fluctuation in resources in the agricultural matrix. Spheciform wasps exhibit a variety of nesting behaviours. Some species dig galleries in the ground (56% of the species collected), others build their nests in vegetation (30%), or are cleptoparasitoids of other nests (14%; Pagliano & Negrisolo, 2005). They are more likely to benefit from the high diversity in semi-natural habitats, where they can find suitable nesting sites, rather than the more homogeneous crop. Cuckoo wasps are parasitoids of other hymenopterans, among which many spheciform wasps (e.g. one of the most abundant species collected, *Hedychrum niemelai* Linsenmaier 1959, parasitises spheciform species belonging to the genus *Cerceris*, among which *Cerceris quadricincta* (Panzer 1799), also collected in this study (Agnoli & Rosa, 2017). Their distribution in the landscape probably follow one of their hosts. On the contrary, we found a negative effect of landscape scale EH on both the number of species and abundance of hoverflies in summer. This result might be explained by the fact that, unlike the other groups, hoverflies are more common in crop than in semi-natural habitats (Ekroos *et al*., 2013). Among the hoverflies collected, 84% belonged to the three highly anthropophilic species *Sphaerophoria scripta* (Linnaeus, 1758; 49%), *Eupeodes corollae* (Fabricius, 1794; 21%), and *Episyrphus balteatus* (De Geer, 1776; 14%), whose larvae feed on aphids attacking a wide range of plants, including crops (Speight, 2014). In spring adult hoverflies may feed on flowers in semi-natural habitats and use the agricultural matrix to lay eggs. Their abundance is therefore expected to benefit from heterogeneous landscapes. In summer, when the crop is harvested, the main food resource for the larvae is lost, causing the disruption of resource acquisition. Hence, the high landscape EH can be perceived more as habitat fragmentation than as an increased number of suitable habitats, resulting in lower species richness and abundance (Bertrand *et al*., 2016). Quite interesting, we found that in summer, when the matrix is unsuitable due to crop harvesting, the effect of patch scale EH become important for predator hoverflies (Fig. S2), suggesting that when the landscape is disturbed by farming practices hoverflies may avoid this habitat. Finally, in the fall, the low disturbance levels in the fields and the large presence of weeds in the fallows together with the loss of flower resources in the semi-natural patches (due to the end of the flowering season) probably homogenised the landscape mosaics, causing a weaker EH effect.

We showed that various groups of predators and parasitoids were positively influenced by EH and that the effects changed across groups, spatial scales and seasons. The same mosaic of semi-natural and crop habitats can be perceived both as resources and disturbed habitats according to the season and the investigated group. Most of the groups benefited from a heterogeneous environment. However, negative EH-diversity relationships were also observed for aphidophagous species that strongly rely on simplified landscapes dominated by crops. When the agricultural matrix in the landscape is unsuitable due to crop harvest, an increased landscape scale EH may still benefit species that forage on both semi-natural and crop habitats, while EH is associated with a lower number of species closely associated with the agricultural matrix. Species closely associated with semi-natural habitats, on the contrary, may be less susceptible to EH over time. Our findings agree with other recent studies (e.g. Bianchi *et al*., 2010; Holzschuh *et al*., 2010; Thornton *et al*., 2011; Bertrand *et al*., 2016) and clearly demonstrate that management strategies aimed at maximising diversity of predators and parasitoids should focus on the landscape scale. Our multi-taxon approach showed no consistent response of the groups to EH, meaning that other variables such as dispersal ability and the spatial arrangement of resources in the landscape have to be considered (Bianchi *et al*., 2010; Ekroos *et al*., 2013). However, precise information on the dispersal ability and prey/host specialisation are not documented for most species, and more research is needed to fully understand such complex interactions.

Acknowledgements

We thank Dr. James E. O'Hara (Ottawa) who revised linguistically the manuscript, and Dr. Martin Schwarz (Linz) for his help in identifying Cryptinae. We are grateful to three anonymous reviewers for their constructive suggestions, which greatly improved the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12249:

Figure S1. Plots showing the effects of micro-scale environmental heterogeneity on species richness and abundance of tachinid flies.

Figure S2. Plot showing the relationship between environmental heterogeneity at patch scale and species richness of hoverflies over seasons.

Table S1. Description of the sampled patches with the indication of area (ha), coordinates, environmental heterogeneity (EH; micro, patch and landscape scale), and micro-scale structural variables (standard deviation of grass height, ground slope and the first principal component analysis (PCA) axis, PC1, of micro-scale structural variables and EH combined).

Table S2. Table with the coefficients for each of the full model and final reduced model, for each of the 10 responses depicted in Fig. 3.

Table S3. Akaike information criterion (AICs) obtained running the full models with area, environmental heterogeneity (EH) at the three spatial scales (micro, patch and landscape scale), season and the interactions EH and season, as explanatory variables.

Table S4. Results from the models testing the effects of semi-natural patch area, semi-natural habitat connectivity (SI), micro and patch scale environmental heterogeneity (micro and patch EH), season, and the interaction between micro and patch EH and season, on (i) species richness and (ii) abundance of the five natural enemy groups.

Table S5. Correlation between landscape scale environmental heterogeneity (land EH) and semi-natural habitat connectivity (SI), measured at five buffers of respectively 100, 500, 1000, 1500 and 2000 m.

Table S6. Collinearity (Pearson's correlation) between semi-natural patch area, and micro, patch and landscape scale environmental heterogeneity (micro, patch and land environmental EH).

Appendix S1. Natural enemy groups: species list, their relative abundance in the study area and feeding behaviour of the larvae.

References

Agnoli, G.L. & Rosa, P. (2017) *Hedychrum niemelai* Linsenmaier, 1959. Chrysis.net Database of the Italian Chrysididae, interim version 24 March 2017. < http://www.chrysis.net/database/ > 13th March 2017.

Aranda, R. & Graciolli, G. (2015) Spatial–temporal distribution of the Hymenoptera in the Brazilian Savanna and the effects of habitat heterogeneity on these patterns. *Journal of Insect Conservation*, **19**, 1173–1187.

Bar-Massada, A. & Wood, E.M. (2014) The richness–heterogeneity relationship differs between heterogeneity measures within and among habitats. *Ecography*, **37**, 528–535.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: Linear Mixed-Effects Models Using Eigen and S4. R Package Version* 1.0–6. <https://cran.r-project.org/web/packages/lme4/index.html> 17th November 2016.

Bennett, A.B. & Gratton, C. (2013) Floral diversity increases beneficial arthropod richness and decreases variability in arthropod community composition. *Ecological Applications*, **23**, 86–95.

Bertrand, C., Burel, F. & Baudry, J. (2016) Spatial and temporal heterogeneity of the crop mosaic influences carabid beetles in agricultural landscapes. *Landscape Ecology*, **31**, 451–466.

Bianchi, F.J.J.A., Schellhorn, N.A., Buckley, Y.M. & Possingham, H.P. (2010) Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. *Ecological Applications*, **20**, 2322–2333.

Burel, F., Butet, A., Delettre, Y.R. & Millan-Pena, N. (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landscape Urban Planning*, **67**, 195–204.

Cerretti, P., O'Hara, J.E., Wood, D.M., Shima, H., Inclán, D.J. & Stireman, J.O. III (2014) Signal through the noise? Phylogeny of the Tachinidae (Diptera) as inferred from morphological evidence. *Systematic Entomology*, **39**, 335–353.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, **14**, 922–932.

Coudrain, V., Herzog, F. & Entling, M.H. (2013) Effects of habitat fragmentation on abundance, larval food and parasitism of a spider-hunting wasp. *PLoS ONE*, **8**, e59286.

Cronin, J.T. (2007) From population sources to sieves: the matrix alters host-parasitoid source-sink structure. *Ecology*, **88**, 2966–2976.

Daoust, S., Belisle, M., Savage, J., Robillard, A., Baeta, R. & Brodeur, J. (2012) Direct and indirect effects of landscape structure on a tri-trophic system within agricultural lands. *Ecosphere*, **3**, 94.

Debevec, A.H., Cardinal, S. & Danforth, B.N. (2012) Identifying the sister group to the bees: a molecular phylogeny of Aculeata with an emphasis on the superfamily Apoidea. *Zoologica Scripta*, **41**, 527–535.

Ekroos, J., Rundlöf, M. & Smit, H.G. (2013) Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. *Landscape Ecology*, **28**, 1283–1292.

Elzinga, J.A., van Nouhuys, S., van Leeuwen, D.J. & Biere, A. (2007) Distribution and colonization ability of three parasitoids and their herbivorous host in a fragmented landscape. *Basic and Applied Ecology*, **8**, 75–88.

Ewers, R.M. & Didham, R.K. (2006) Continuous response functions for quantifying the strength of edge effects. *Journal of Applied Ecology*, **43**, 527–536.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Fitton, M.G., Shaw, M.R. & Gauld, I.D. (1988) Pimpline ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). *Hand-Books for the Identification of British Insects* (ed. by Royal Entomological Society), Vol. 7, part 1, pp. 1–110. Royal Entomological Society of London, London, UK.

Gauld, I.D. & Boton, B. (1988) *The Hymenoptera*. Oxford University Press, Ottawa, Canada.

Gazol, A., Tamme, R., Price, J.N., Hiiesalu, I., Laanisto, L. & Partel, M. (2013) A negative heterogeneity-diversity relationship found in experimental grassland communities. *Oecologia*, **173**, 545–555.

Gelman, A. (2008) Scaling regression inputs by dividing by two standard deviations. *Statististics in Medicine*, **27**, 2865–2873.

Gelman, A. (2013) The problem with p-values is how they're used. < http://andrewgelman.com/2014/05/17/forum-ecology-p-values-model-selection/ > 2nd June 2017.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, New York City, New York.

Hicks, J.P., Hails, R.S. & Sait, S.M. (2015) Scale-dependent, contrasting effects of habitat fragmentation on host-natural enemy trophic interactions. *Landscape Ecology*, **30**, 1371–1385.

Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, **79**, 491–500.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.

Inclán, D.J., Cerretti, P. & Marini, L. (2014) Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes. *Landscape Ecology*, **29**, 879–889.

Inclán, D.J., Cerretti, P. & Marini, L. (2015) Landscape composition affects parasitoid spillover. *Agriculture, Ecosystems and Environment*, **208**, 48–54.

Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.

Jonsen, I. & Fahrig, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology*, **12**, 185–197.

Kadmon, R. & Allouche, O. (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. *The American Naturalist*, **170**, 443–454.

Kimsey, L.S. & Bohart, R.M. (1991) *The Chrysidid Wasps of the World*. Oxford University Press, New York City, New York.

Kremen, C., Williams, M.N., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J. & Ricketts, T.H. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.

Landis, D.A., Menalled, F.D., Costamagna, A.C. & Wilkinson, T.K. (2005) Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, **53**, 902–908.

Leius, K. (1960) Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Canadian Entomologist*, **92**, 369–376.

Letourneau, D.K., Bothwell Allen, S.G. & Stireman, J.O. (2012) Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. *Journal of Applied Ecology*, **49**, 1405–1416.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Maccherini, S., Marignani, M., Gioria, M., Renzi, M., Rocchini, D., Santi, E., Torri, D., Tundo, J. & Honnay, O. (2011) Determinants of plant community composition of remnant biancane badlands: a hierarchical approach to quantify species-environment relationship. *Applied Vegetation Science*, **14**, 378–387.

Martin, E.A., Seo, B., Park, C.-R., Reineking, B. & Steffan-Dewenter, I. (2016) Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, **26**, 448–462.

Murtaugh, P.A. (2014) In defense of P values. *Ecology*, **95**, 611–617.

Pagliano, G. & Negrisolo, E. (2005) *Fauna d'Italia. HymenopteraSphecidae*. Edizioni Calderini, Bologna, Italy.

Pärn, M., Soon, V., Vallisoo, T., Hovi, K. & Luig, J. (2014) Host specificity of the tribe Chrysidini (Hymenoptera: Chrysididae) in Estonia ascertained with trap-nesting. *European Journal of Entomlogy*, **112**, 91–99.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D.; the R Development Core Team (2013) *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version* 3.1–111. <https://cran.r-project.org/web/packages/nlme/index.html> 17th November 2016.

Quantum GIS Development Team (2014) *Quantum GIS Geographic Information System*. Open Source Geospatial Foundation Project. < http://qgis.osgeo.org/ > 17th November 2016.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. < https://www.R-project.org/ > 17th November 2016.

Rosa, P. (2006) I Crisidi della Valle d'Aosta. *Monografie del Museo Regionale di Scienze Naturali di Saint-Pierre*, **6**, 368.

Rotheray, G.E. (1993) Colour guide to hoverfly larvae (Diptera, Syrphidae) in Britain and Europe. *Dipterist Digest*, **9**, 156.

Speight, M.C.D. (2014) Species accounts of European Syrphidae (Diptera). *Syrph the Net, the Database of European Syrphidae* (ed. by Syrph the Net Publications), Vol. 78, pp. 1–321. Syrph the Net Publications, Dublin, Ireland.

Stein, A. & Kreft, H. (2015) Terminology and quantification of environmental heterogeneity in species-richness research. *Biological Review*, **90**, 815–836.

Stireman, J.O. III (2008) α and β diversity of a tachinid parasitoid community over space and time. *Annals of the Entomological Society of America*, **101**, 362–370.

Stireman, J.O. III, O'Hara, J.E. & Wood, D.M. (2006) Behavior, ecology and evolution of tachinid parasitoids. *Annual Review of Entomology*, **51**, 525–555.

Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R. & Pärtel, M. (2010) Environmental heterogeneity, species diversity and co-existence at different spatial scales. *Journal of Vegetation Science*, **21**, 796–801.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18–25.

Thornton, D.H., Branch, L.C. & Sunquist, M.E. (2011) The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology*, **26**, 7–18.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D. & Swackhamer, D. (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S. & Vidal, S. (2007) Conservation biological control and enemy diversity on a landscape scale. *Biological Control*, **43**, 294–309.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, **8**, 857–874.

Vasseur, C., Joannon, A., Aviron, S., Burel, F., Meynard, J.-M. & Baudry, J. (2013) The cropping systems mosaic: how does the hidden heterogeneity of agricultural landscapes drive arthropod populations? *Agriculture Ecosystems and Environment*, **166**, 3–14.

Weibull, A.-C., Bengtsson, J. & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, **23**, 743–750.

Weisberg, P.J., Dilts, T.E., Becker, M.E., Young, J.S., Wong-Kone, D.C., Newton, W.E. & Ammon, E.M. (2014) Guild-specific responses of avian species richness to liDAR-derived habitat heterogeneity. *Acta Oecologica*, **59**, 72–83.

Ye, X., Skidmore, A.K. & Wang, T. (2013) Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. *Landscape Ecology*, **28**, 135.

Accepted 27 June 2017

Editor: Raphael Didham
Associate editor: Philip Barton