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**HETEROGENEITY IN AGRICULTURAL LANDSCAPES:  
An analysis of its effects on the diversity and biological  
interactions of aerial-nesting wasp and bee communities  
(Hymenoptera: Apoidea) as sensitive indicators of  
environmental quality.**

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# Introductory chapter

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## 1. INTRODUCTION

Europe has an important diversity of agricultural landscapes that differ markedly in the type of land use, the size and shape of croplands, and in the abundance and model of seminatural elements (Billeter *et al.* 2008).

Although many of these agroecosystems were originally rich in biodiversity (Edwards *et al.* 1999), in recent decades many species that used to be common have become rare or have even disappeared, leading to a sharp decline in species richness (Robinson & Sutherland 2002).

There is a considerable body of evidence to suggest that the decrease in biodiversity of these zones is related to changes in agricultural practices, affecting many aspects of cultivated habitats. Economic incentives and technological initiatives to increase productivity have led to a rapid intensification of farming practices. As a result, we are now seeing a loss of ecological heterogeneity at multiple spatial and temporal scales (Benton *et al.* 2003), which has been replaced by homogeneity in habitat structure.

From the perspective of classical conservation, this anthropogenic matrix has usually been treated as a sterile extension, an area considered biologically uniform, uninhabitable and hence ecologically irrelevant (Jules & Shahani 2003; Ricketts 2001). In fact, however, a large proportion of European biodiversity is preserved on agricultural landscapes (Benton *et al.* 2003; Dauber *et al.* 2003; Fahrig & Jonsen 1998; Krebs *et al.* 1999), converting them into a conservation

focus to be taken into account at both small and large scale (Browne *et al.* 2000; Chamberlain *et al.* 1999; Weibull *et al.* 2000).

Landscape structure is particularly important when species mainly prefer one type of habitat but are able to use different landscape resources (Lin & Batzli 2004; Norton *et al.* 2000; Ricketts 2001), and their characteristics may contribute differently to the survival of populations and species richness (Debinsky & Holt 2000; Norton *et al.* 2000; Zschokke *et al.* 2000). The required use of spatially separated resources is related to the concept of landscape complementation, which occurs when the landscape structure permits access among multiple required resources (Dunning *et al.* 1992).

Study of mobile organisms and the services they provide to the ecosystem demands the use of both a local scale and a landscape perspective, which would reflect the spatial distribution of resources and foraging and dispersive movements of the organisms themselves, considering spatial factors or characteristics and those of the area cultivated (Kareiva 1990; Ricketts 2001; Roland & Taylor 1997; Thies *et al.* 2003; Tischendorf & Fahrig 2000; Turner & Gardner 1991). Different authors (Menalled *et al.* 1999; Thies & Tschardtke 1999) have indicated that certain concrete processes occur at particular spatial scales and that this spatial scale at which organisms interact may depend both of the type of landscape and on the traits of the species involved. Only a multiscale analysis can detect the importance of the landscape context for pollinating species (Steffan-Dewenter *et al.* 2002) and for establishing a basis for a better handling and management of agricultural landscapes (Tschardtke *et al.* 2005a).

From the point of view of landscape, different studies performed mainly over the past two decades have highlighted the influence of different variables in the maintenance of diversity: habitat heterogeneity, complexity, fragmentation, the degree of management of the agroecosystems... Landscape ecology provides a broad variety of parameters to quantify landscape structure (e.g. Turner & Gardner 1991). Changes in landscape structure can be characterized by the proportion of habitats available (Andrén 1994), habitat diversity and the size and spatial features of the habitats within a landscape (Gustafson 1998).

Despite structural diversity, two general parameters of the landscape can be distinguished as the most significant contributors to explaining species richness across different taxonomic groups. The most important is the proportion of surrounding seminatural habitats, followed by the habitat diversity prevailing in the matrix (Billeter *et al.* 2008). At local level, although species are affected by habitat fragmentation in different ways, both the structure of the community and interspecific interactions and ecological functions may change (Didham *et al.* 1996; Ewers & Didham 2007; Holt *et al.* 1999), the context of the fragment within the spatial structure of the landscape being very significant (Chacoff & Aizen 2006; Westphal *et al.* 2003). The abiotic characteristics of these habitat patches (due to geological and hydrographic differences) and adjacent zones (known as zones of emigration and immigration) differ at geographic scales (Tschardtke *et al.* 2002). The series of small- and medium-sized fragments capture a broader heterogeneity of habitats and of microclimates than large areas. The groups of species found in these zones differ, since the quality of the habitat and the structure of the community vary

with location or the geography of the fragment (Quinn & Harrison 1988; Tschardtke *et al.* 2002).

Agricultural ecosystems are related to their surroundings more than other types of habitat since part of the plant cover has been cleared or eliminated through agricultural practices, such that much of their biodiversity depends on recolonization from surrounding perennial habitats (Roschewitz *et al.* 2005; Tschardtke & Kruess 1999). When habitat patches begin to decline in size and become separated from one another, the ranges of local extinction cannot be compensated by recolonization if the abilities of the species involved to disperse are low (Fahrig 2003; Thomas 2000). It is assumed that the dispersion of seminatural habitats within a given intensive agricultural area will improve the heterogeneity of the agricultural ecosystem in general, which implies high biodiversity and an improvement in the aesthetic properties of the area (Stein *et al.* 1999).

From a multi-scale perspective, the surrounding matrix may significantly affect the structural connectivity of habitat patches and cause an increase or decline in population density at local level and hence the risk of extinction (Gonzales *et al.* 1998; Ricketts 2001). Biological corridors, often formed by uncultivated zones or the residual zones of a seminatural habitat, permit connections between different habitat fragments, facilitating the access of organisms to numerous resources within the landscape matrix (Boren *et al.* 1999; Hanski 1998; Norderhaug *et al.* 2000). The remaining natural habitats, surrounded by agricultural croplands, pastures or urban settlements, maintain a degree of terrestrial connectivity through the surrounding modified habitats (Chacoff & Aizen 2006). Thus, spatial ordering in the landscape is also a



variable to be taken into account, since it reflects greater or lesser accessibility to additional resources in the matrix by the organisms persisting in a local habitat.

Additionally, the interaction between spatial and temporal heterogeneity should be taken into account. Thus, since modern agricultural practices induce spatial uniformity, they also involve temporal uniformity, mainly because the time in which the soil is productive has been expanded and non-productive periods have been reduced. However, the often high productivity of cultivated areas, in comparison with that of natural systems, may provide more resources (such as plants, flowers and fruits). Thus, the value of the habitat of agroecosystems is often determined by the amplitude of food resources, resulting from their high productivity (and not only from the high levels of perturbation) (Tscharntke *et al.* 2005b). Crop diversity has proved to be an important variable, positively associated with arthropod richness (Tscharntke *et al.* 2005b). Accordingly, the maintenance of spatial variability in agricultural landscapes would act as a buffer to the temporal variation of resources, providing habitats that could remain unexploited under more favourable circumstances (Benton *et al.* 2003; Payne & Wilson 1999).

Reductions in the diversity and abundance of insects that visit flowers have attracted a good deal of attention in recent years (Buchmann & Nabham 1996), mainly because pollination represents a critical service for both natural and agricultural ecosystems (Costanza *et al.* 1997). For many plants, the success of pollination depends on the availability of bees, which play a crucial role as pollinators. Effective pollination increases the production of many crops (Corbet 1987; Williams 1996) and contributes to the conservation of many

species of plants threatened by extinction (Kwak *et al.* 1996). Moreover, wasps can be considered beneficial insects in that they may be effective predators of other insects (Harris 1994). The existence of these groups depends on the proportion of suitable habitats within a local sector of the landscape and also on the diversity of habitat types at a larger spatial scale (Tscharntke *et al.* 1998).

Both in plants and in vertebrates studies have been conducted to address the relationship between landscape complexity and species richness and the density of individuals (Atauri & De Lucio 2001; Metzger 2000), although insect communities and their trophic interactions have received little attention (Cane 2001; Holt *et al.* 1999; Steffan-Dewenter & Tscharntke 2000). In agricultural zones, the effects of landscape complexity on insect communities are almost unknown (Kareiva & Wennergren 1995; Steffan-Dewenter & Tscharntke 2000), and also little is known about the influence of the surrounding landscape on the reproduction and life of these organisms (Gustafson 1998; Tscharntke *et al.* 1998).

Accordingly, studies aimed at clarifying these aspects are essential for assessing the loss of biological diversity due to the decline in the quality of the environment and ecosystems and the status of derived ecological services such as pollination or biological control. A more exhaustive knowledge, at different spatial scales, of the influence of the agricultural landscape on communities and their services through the quality of the habitat and its structures is of huge importance in decision making as regards policies aimed at land use and the development of agroenvironmental schemes by agents responsible for the management of the territory.

## 2. GENERAL METHODOLOGY

### 2.1. Study organisms

This study addresses aerial nesting bee and wasp communities, which account for about 5% of all wasp and bee species (Krombein 1967). They play a crucial role in ecosystems and can be considered as a reflection of ecological change through their species richness and related parameters and, also, through their ecological functions or interactions: pollination, predation and mortality due to their natural enemies. The community of bees and wasps nesting in trap-nests is known to include species with specific habitat demands and different authors have reported the potential ecological application of these groups (Tscharntke *et al.* 1998).

### 2.2. Study areas

The studies carried out in this work were performed in agricultural landscapes of the province of La Rioja (Northern Spain) in 2007, 2008 and 2009. This province was chosen because, within a relatively reduced area, it has different types of Mediterranean crops with different types of land use intensity.

In the case of the investigations reported in chapters 1, 2 and 3 (2007), we chose plots from two study regions. The first includes the riverside areas of the Ebro River, characterized by vineyard crops and vegetable crop areas, with a mean altitude of 450 m AMSL. The second, with a mean altitude of 634 m, is located parallel to the first one and is dominated by cereal crops. Other plots located in these regions were used for the studies described in chapters 4 and 5 (2008). The research reported in chapter 6 (2009) was carried out in the

surrounding of Cenicero (42° 28' N, 2° 38' W) (La Rioja). This zone is characterized by a major presence of crop areas managed on an intensive basis, with a predominance of vineyards and a patchy distribution of fragments of natural and seminatural habitats among the crop fields (Fig. 1)



**Figure 1.-** Agricultural landscape dominated by vineyards, characteristic of the surroundings of Cenicero (La Rioja).

### **2.3. Sampling methods**

During the three years of the study we used standardized trap-nests, whose efficiency has already been confirmed by other research teams (Steffan-Dewenter 2002; Tschardtke *et al.* 1998; Tylianakis *et al.* 2005). Each trap nest comprised a metal post 1.5 m in length that held two PVC tubes (63 mm diameter) at the top on each side and a wooden roof above. Each tube



**Figure 2.-** Trap-nest model used in the study and detail of one of the tubes containing stems.

contained 50 stems of *Phragmites australis* (Cav.) Trin ex Steud y *Arundo donax* L. (17 cm in length; 2.10 mm in diameter), and the same number of stems per diameter was placed in all the tubes. The backs of the tubes were covered with a plastic lid, offering only one access for nesting purposes. All the trap-nests were emplaced with a NE orientation (Martín 2006) at a height of 1 m above the ground (Fig. 2).

The trap-nests remained in the field from mid-April to mid-September of each of the study years. After their retrieval, the tubes were taken to the laboratory, where the groups of stems were removed and placed in a refrigerator at 4-6 °C until later processing. Each stem was opened, extracting the cell contents (bee and wasp larvae), which were deposited in vials (Fig. 3).

During the opening, we recorded the number of brood cells per nest, natural mortality (measured as the number of cells whose occupant(s) had already died before the stems were opened) and the number of cells attacked by natural enemies. In order to calculate the biological efficiency of the species

of natural enemies we checked the viability of their cells, recording natural deaths at the time of opening the stems.



**Figure 3.-** Aspect of the brood cells of (A) bees, and (B) eumenine wasps at the time of opening the stems.

The vials were coded and returned to the refrigerator until the following spring, when they were subjected to room temperature until the adults emerged after the winter diapause. Then, the specimens -both the host species and the parasitoids- were identified at species level. After the emergence and identification of the adults, we recorded and calculated species richness, diversity (Simpson index,  $1-\lambda' = 1 - \sum(N_i^*(N_i-1))/(N*N-1)$ ), the percentage of natural mortality (measured as the number of cells whose occupant(s) had died at the time of opening the stems against the total number of brood cells) and the percentage of parasitism (measured as the percentage of cells attacked by natural enemies against the total number of brood cells) for both groups, separated into the community of bees and the community of wasps, the latter

subdivided into the community of Spheciformes wasps and the community of eumenine wasps.

In the case of the studies reported in chapters 4 and 5, the species of the bee community were separated into oligolectic (bees that collect pollen from a limited number of plants), and polylectic (not specialized in the collection of pollen, using many plants of different groups) species. Additionally, for the community of natural enemies we calculated species richness and diversity. We also calculated their biological efficiency (measured as the percentage of parasitized cells whose occupants reached adulthood: i.e., the % of cells that were not subject to natural death) for the study reported in chapter 3.

Regarding the research described in chapters 4 and 5, in order to gain insight into the wasp and bee communities present at the study plots, hand-net samplings were performed, in three annual replicates, distributed between the end of spring and the end of summer (approximately every 30 days). The capture of wasp and bee species was performed along linear transects over 15 min by two collectors, using the adjacent uncultivated edge of each of the 18 plots studied. The specimens collected in each of the monthly samples were prepared and labelled for later identification, down to generic level in the case of the bees and down to species level for most of the wasps. The data recorded for each locality were grouped with those from the trap-nests to calculate the richness and diversity of the general community of bees and of the general community of wasps on each of the study plots. To estimate the communities of parasitoids present, sampling were performed with sweep netting, with the same frequency as those used for bees and wasps and for each of the 18 plots. In each replica we chose 5 points at random at the edge of the plots performing

10 consecutive sweeps, all by the same person (collector). After the sweeps, the specimens captured in the net were taken out with an aspirator (pooter) (Fig. 4).



**Figure 4.-** Collection of specimens of parasitoids using an aspirator (pooter), after sampling with a sweep net.

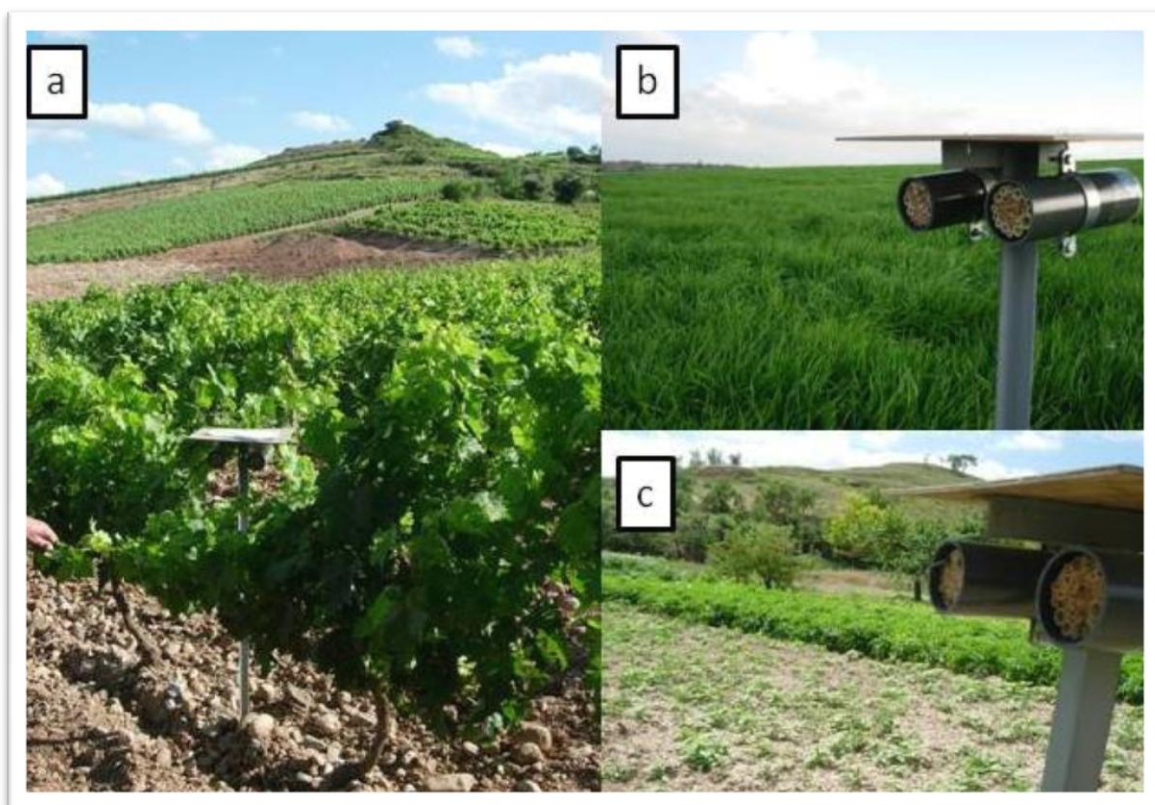
The specimens collected in each of the monthly samples were mounted and labelled for later identification at species level. The data recorded for each locality were grouped with those recorded for the natural enemies from the trap-nests in order to calculate the richness and diversity of the general community of parasitoids at each study plot.

## **2.4. Study designs**

In order to develop chapters 1, 2 and 3 (2007) and chapters 4 and 5 (2008), we chose 8 plots with three crop types (vineyard crops, cereal crops and vegetable crop areas) and two types of farming intensity (low-intensity vs. high-intensity). Vineyard and cereal crops are mono-crops, the former being



perennial and the latter annual. The vegetable crop areas are polycrops characterized by showing a broad variety of different crops over space and time (Fig. 5). For each combination of type of crop/farming intensity, 3 replicates were made, using a total of 18 study sites. We attempted to maintain homogeneity regarding both plot size, for each crop type/farming intensity combination, and the type of management used, in order to standardize the possible local effects of the habitat and facilitate study of the effects of the landscape context (Steffan-Dewenter 2002).



**Figure 5.-** Trap-nests used in the three crop types analyzed: (A) vineyard), (B) cereal, (C) vegetable crop areas.

To select agricultural landscapes with two types of intensity, we addressed three numerical variables that characterize the intensity of use of agricultural land: (1) the PAR (perimeter/area ratio) fragmentation index, which

is calculated as the quotient between the summatory of the perimeters and the summatory of the areas of all the plots included in the study area; this is a reflection of the dominant structural shape of the plots (high values correspond to more linear shapes) (Salas *et al.* 2003); its value was lower in the system with high-intensity farming (ANOVA,  $F_{1,16}=35.588$ ;  $P<0.0001$ ; Tukey *a posteriori* test, low-intensity (mean=0.062 m/m<sup>2</sup>) vs. high-intensity (mean=0.035 m/m<sup>2</sup>),  $P<0.0001$ ); (2) the total number of plots (ANOVA,  $F_{1,16}=11.131$ ;  $P=0.004$ ; Tukey *a posteriori* test, low-intensity (mean=318.56 plots per sector) vs. high-intensity (mean=160.78 plots per sector),  $P=0.004$ ); and (3) mean plot size (ANOVA,  $F_{1,16}=7.389$ ;  $P=0.015$ ; Tukey *a posteriori* test, low-intensity (mean=0.649 ha) vs. high-intensity (mean=1.878 ha),  $P=0.015$ ). The zones with high-intensity land use had the lowest number of plots, with greater mean sizes than the lower-intensity agricultural zones (Table I).

**Table I.-** Values recorded for the variables defining the degree of farming intensity: Perimeter/area ratio (PAR); total number of crop plots and their mean size (in ha), for the localities studied, by crops, under high- and low-farming intensity.

Study site	LOW FARMING INTENSITY			HIGH FARMING INTENSITY		
	PAR	Num. Fields	Mean size	PAR	Num. Fields	Mean size
Vineyard 1	0.045	210	1.070±1.077	0.037	136	1.520±1.194
Vineyard 2	0.058	267	0.701±0.728	0.033	129	1.832±1.496
Vineyard 3	0.051	243	0.799±0.854	0.037	152	1.441±1.297
Cereal 1	0.065	170	0.635±0.564	0.024	95	2.883±3.022
Cereal 2	0.066	253	0.650±0.714	0.018	74	5.042±5.521
Cereal 3	0.071	383	0.48±0.515	0.033	151	1.499±2.001
Veg. crop 1	0.061	359	0.588±0.515	0.042	246	0.826±1.073
Veg. crop 2	0.081	586	0.327±0.377	0.043	240	0.963±0.629
Veg. crop 3	0.064	396	0.591±0.567	0.043	224	0.900±0.997

At each of the plots selected for each study year, we placed two standardized trap-nests: one at the centre of the crop area and the other at one of the edges (Fig. 6). The data from the stems from the two tubes present on each trap were analyzed jointly, since their position (left-right) is not considered to be relevant from the ecological perspective. We also performed preliminary analyses to check the influence of the trap position (edge or centre) on the study plots for each year; we failed to detect a significant effect of position on the dependent variables analyzed (2007: ANOVA, N° of brood cells:  $F_{1,35}=0.104$ ;  $P=0.794$ ; total richness:  $F_{1,35}=3.073$ ;  $P=0.089$ ; total host richness:  $F_{1,35}=2.854$ ;  $P=0.100$ ; and parasitoid richness:  $F_{1,35}=1.737$ ;  $P=0.100$ ; 2008: ANOVA, N° of brood cells:  $F_{1,35}=3.035$ ;  $P=0.091$ ; total host richness:  $F_{1,35}=3.137$ ;  $P=0.086$ ; wasp richness:  $F_{1,35}=3.646$ ;  $P=0.065$ ; bee richness:  $F_{1,35}=0.513$ ;  $P=0.479$ ; percentage of mortality:  $F_{1,35}=0.756$ ;  $P=0.391$ ; percentage of parasitoidism:  $F_{1,35}=0.053$ ;  $P=0.820$ ), such that the data from the traps located at each study site were analyzed together both study years.



**Figure 6.-** Trap-nest established at the edge of a vineyard.

For the study addressed in chapter 6, we selected 6 localities that were at least 1 km distant from each other, with a size of 0.8-2 km<sup>2</sup>, distributed over a total area 6 x 6 km. At each locality we set up 6 trap-nests, separated by at least 500 m and each trap was considered an independent replication. In order to analyze the effect of the different types of structure present in the agricultural matrix of the vineyards, the trap-nests were positioned at: (1) the edge of the natural habitat; (2) hedgerows and (3) grass strips (Fig. 7).



**Figure 7.-** Trap-nests placed on one of the grass strips of the agricultural matrix of vineyard selected for the study.

The natural habitats present in the zone are forests of *Quercus ilex* L. or their successional states, with a mean size of  $24 \pm 22.55$  ha; the trap-nests were positioned at the edges, between the natural habitat and the vineyard plots. The hedgerows, with vegetation similar to that found in the natural habitat, were at least 150 m long ( $251.33 \pm 66.4$  m), and had a mean width of  $26.8 \pm 12.5$  m and they did not form part of a network in the landscape. The trap-nests were

established at the longitudinal centre of the hedgerow, in the zone between the hedgerow and the vineyard plot. In turn, the grass strips consisted of narrow strips with herbaceous vegetation: their mean width was  $5.05 \pm 1.58$  m and they did not form part of a network of bands within the landscape either; the traps were placed at their centre.

To analyze the effect of the presence of corridors between the natural habitat and the trap-nests on occupation, we compared two types of hedgerows (connected and slightly isolated) and 3 types of grass strips (connected, slightly isolated, and isolated). The connected hedgerow ended at the natural habitat and the slightly connected hedgerow was arranged parallel to this habitat, at a distance of 300 m. Likewise, the connected strip ended at the natural habitat; the slightly connected strip was parallel to this at a distance of 300 m and the isolated strip was located at a distance of 600 m from the natural habitat (Table II).

**Table II.** Types of structures analyzed with different combinations for the distance to the natural habitat and degree of isolation/connectivity intensity. In brackets: number of replications for each combination.

structure type		distance	connectivity/isolation
Natural habitat edge	(n=6)	0 m	–
Hedgerow	(n=6)	300 m	connected
Hedgerow	(n=6)	300 m	slightly isolated
Grass strip	(n=6)	300 m	connected
Grass strip	(n=6)	300 m	slightly isolated
Grass strip	(n=6)	>600 m	highly isolated

In these landscapes there were no isolated hedgerows (at more than 600 m from the natural habitat), which is why for the present study this type was not

selected. The distances were chosen according to data reported by other authors regarding the maximum distances of foraging by bees (Gathmann & Tscharrntke 2002) and attending to observations concerning the richness of wasps and bees from the trap-nests, which is greater between 0 and 300 m distance to the natural habitats (Klein *et al.* 2006).

## **2.5. Local and landscape context analysis**

### **2.5.1. Landscape variables**

In order to analyze the landscape matrix, for the studies reported in chapters 1, 2 and 3, we used aerial photographs (Regional Government of La Rioja) corresponding to each of the study zones. Around each plot selected we established a sector of 1 km in radius, attending to the maximum foraging distances recorded in other studies for the groups analyzed (Gathmann & Tscharrntke 2002; Steffan-Dewenter *et al.* 2002). The landscape sectors of the different study sites did not overlap, the distance between them varying between 2.3 and 67.2 km. For each sector, the total area of each type of habitat was quantified separately using Geographic Information Systems, with the ARCGIS 9.3 package (ESRI) (Fig. 8). The habitat types were classified as follows: (a) forest, (b) sequential habitats (zones close to natural forest, not very disturbed and with a successional vegetation), (c) vegetation along inshore waters (canopy forests, vegetation associated with water courses), (d) water areas (rivers, lakes, large irrigation canals), (e) hedgerows and the edges of croplands, (f) agricultural tracks (bare soil with vegetation at the edges), (g) vineyard plots, (h) cereal plots, and (i) plots with vegetable crops.



**Figure 8.-** Example of landscape sector (1 km radius) highlighting the following: (A) surface area of seminatural habitats, and (B) surface area of crop lands.

From the covers of each crop type (vineyard, cereal and vegetable crop areas) we calculated the percentage of cover of cultivated fields for each landscape sector. We also estimated the percentage of cover of seminatural habitats, including habitats suitable for these communities in that they provide nesting sites and food resources. Thus, in the calculation of the percentage of cover of seminatural habitats in each sector, we included the proportions of forests, sequential habitats, riverside vegetations, hedgerows and edges of croplands, and agricultural tracks.

From the areas (%) corresponding to each type of habitat we calculated the total diversity of habitats, using the Shannon-Wiener index ( $H's = -\sum p_i \times \log(p_i)$ ) (Krebs 1989), excluding the cultivated areas for its calculation. Finally, we calculated the size of each plot for its inclusions as a possible variable in the analysis.

We performed a Principal Components Analysis (PCA) as an exploratory analysis to assess, among all the landscape variables measured, those that were correlated and could not be included simultaneously in the analysis. The first two principal components, which were orthogonal to each other, explained 41% of the global variance, one of the variables with the greatest factor loading by each of these components being selected. In the case of the first component, the percentage cover of seminatural habitats showed a significant positive correlation with habitat diversity ( $H'$ ) (factor loading,  $R=0.819$ ;  $P < 0.0001$ ), with the percentage of sequential habitats (factor loading,  $R=0.809$ ;  $P=0.0003$ ) and with the percentage of forests (factor loading,  $R=0.799$ ;  $P=0.0001$ ), and was negatively correlated with the percentage of cover of croplands (factor loading,  $R=-0.895$ ;  $P < 0.0001$ ). In the second component, the farming intensity variable did not show significant correlations with the other landscape variables ( $R < 0.483$ ;  $P > 0.05$ ). We also tested the relationship between the percentage of cover of seminatural habitats and agricultural intensity landscape variables. The percentage of seminatural habitats did not vary significantly between the two degrees of the intensity of land use (ANOVA,  $F_{1,16}=2.301$ ;  $P=0.149$ ).

We then performed a PCA to assess the correlation between the local variables recorded: type of local crop (the type of crop in which the trap-nests were placed; i.e. vineyard, cereal, vegetable plot) and plot size. The analysis revealed a strong correlation between plot size and the type of local crop variables, especially with the cereal cultures (factor loading,  $R=0.704$ ;  $P=0.001$ ) and vegetable crop plots (factor loading,  $R=-0.501$ ;  $P=0.034$ ).

The possible influence of the type of local crop variable on the landscape variables did not reveal significant differences between the three types of local



crop analyzed (ANOVA,  $F_{1,16}=0.219$ ;  $P=0.80$ ). Additionally, with a view to exploring the effect of the type of local crop variable (used in chapter 1) or of the local crop system variable (monocrops vs. polycrops) (used in chapter 2) on the farming intensity variable, in the analysis we used the numerical variables employed to define it. Neither the PAR (perimeter/area ratio) (ANOVA,  $F_{1,16}=0.870$ ;  $P=0.439$ ) nor mean plot size (ANOVA,  $F_{1,16}=1.758$ ;  $P=0.206$ ) were significantly different for the types of crop system analyzed. Only the total number of plots showed a marginal relationship (ANOVA,  $F_{1,16}=3.935$ ;  $P=0.042$ ).

### 2.5.2. Local variables

To develop the study reported in chapter 4, we measured the edge density ( $m^2$ ) adjacent to each of the study plots, using aerial photographs and the ARCGIS 9.3 (ESRI) package. This density remained constant throughout the study period. Likewise, we calculated the size of each plot to include it as a possible variable in the analysis.

From three inspections, made from the end of spring to the end of summer (approximately every 30 days), we quantified a series of local variables for the edge of each plot studied (Fig. 9). Using a tape measure, we estimated the total surface of the cover of flowering plants ( $m^2$ ) and we recorded by inspection the richness of flowering plants during each of the replications, grouping the data thus obtained during the three samples. From the edge density of each of the study plots, we quantified the total percentage of flowering plant cover (i.e., total availability of flowering plants during the study period) and from the species richness of each sample we calculated the total

richness of flowering plants (i.e., total species richness during the study period) for each of the edges analyzed (Table III).



**Figure 9.-** Image of one of the marginal habitats adjacent to a vegetable crop plot, where the inspections performed to calculate the local variables were performed.

In order to assess those variables that were correlated and could not be included simultaneously in the analysis, we performed an exploratory analysis with PCA among all the local variables. The first three principal components, which were orthogonal to one another, accounted for 83% of the global variance; variables with a high factor loading for each of these three components were selected. In the first component, the percentage of flower cover (factor loading,  $R=0.788$ ) was positively correlated with field size ( $R=0.862$ ;  $P<0.05$ ). On the second axis, edge density (factor loading,  $R=-0.724$ )

did not show a significant relationship with any other variable (all  $P > 0.05$ ), among them the types of local crop. In the third component, the flowering plant richness (factor loading,  $R = 0.651$ ) was not correlated with the other variables (all  $p > 0.005$ ,  $N = 18$ ).

**Table III.** Total values recorded in the 8 crop plots under two different degrees of farming intensity for the local variables: edge density (ha), percentage of flowering plant cover, richness (S) of flowering species and size of crop plot (ha).

Study site	Farming intensity	Edge density	%Cover flowering plants	S flowering plants	Field size
Vineyard 1	Low	1430.00	50.11	13	0.60
Vineyard 2		3364.00	35.67	14	0.36
Vineyard 3		2174.40	50.88	11	0.53
Vineyard 4	High	217.50	53.73	17	2.12
Vineyard 5		357.50	53.21	14	2.25
Vineyard 6		23.00	63.06	9	1.55
Cereal 1	Low	1709.00	30.51	14	1.65
Cereal 2		5814.00	11.83	24	1.41
Cereal 3		292.00	22.78	13	1.68
Cereal 4	High	107.50	25.33	3	6.96
Cereal 5		181.00	42.64	9	6.22
Cereal 6		8600.00	41.06	14	5.96
Veg. crop 1	Low	668.00	48.64	8	0.11
Veg. crop 2		68.00	49.84	11	0.17
Veg. crop 3		2567.00	49.32	15	0.62
Veg. crop 4	High	140.00	34.02	15	0.38
Veg. crop 5		378.58	5.60	6	0.76
Veg. crop 6		195.18	20.26	14	0.45

### 2.5.3. Crop field isolation

In chapter 5 we analyze the spatial isolation of the crop fields. Using aerial photographs corresponding to each of the study localities, with the ARCGIS 9.3 (ESRI) package, in the landscape surrounding each of the study sites we located the closest seminatural and natural habitat, recording the distances from the centre of the plot to each of them. As seminatural habitats

we considered the edges of plots, fields or sequential habitats with low vegetation and bushes; as natural habitats, we considered the fragments of natural forests present in the zone, normally composed of Holm-oaks and reforested pine. Although the maximum foraging distance recorded for these communities is 1.5 km, the distance to the closest natural habitat was significantly greater in the case of three localities corresponding to cereal crop plots in high-intensity systems.

We chose habitats greater than 0.36 ha since patches of this size were sure to have types of habitat based on soil types and that would be sufficiently large to harbour characteristic vegetation (Williams & Kremen 2007). The size (i.e., area) of the seminatural habitats and of the closest natural habitats was measured for inclusion as a variable in the analysis (Table IV). Likewise, the size of each study field was calculated.

**Table IV.** Total values recorded, at the 18 crop plots, with two degrees of farming intensity, for the isolation variables: distance to the natural habitat (IFSH) (in metres); size of seminatural habitat (Size SN) (ha); distance to the natural habitat (IFNH) (in metres) and size of natural habitat (Size N) (ha).

Study site	Farming intensity	DSH	Size SH	DNH	Size N
Vineyard 1	Low	115	2.28	1138	47.77
Vineyard 2		45	11.23	200	1.77
Vineyard 3		91	4.77	319	23.57
Vineyard 4	High	296	0.44	390	11.15
Vineyard 5		230	0.40	968	13.58
Vineyard 6		728	5.11	1473	10.40
Cereal 1	Low	33	0.85	415	11.19
Cereal 2		35	5.63	264	2.55
Cereal 3		47	0.44	584	11.19
Cereal 4	High	305	2.70	2645	15.57
Cereal 5		206	1.33	3276	15.57
Cereal 6		146	9.20	2158	65.45
Veg. crop 1	Low	75	3.60	849	11.35
Veg. crop 2		80	0.65	270	12.17
Veg. crop 3		23	1.94	274	7.95
Veg. crop 4	High	27	0.95	177	9.37
Veg. crop 5		243	1.79	1550	17.51
Veg. crop 6		466	0.91	428	11.81

Among all the variables measured, using PCA we assessed those that were correlated and could not be included simultaneously in the analysis. The first two principal components, orthogonal to each other, explained 65% of the overall variance, variables with a high factor loading for each of these two components being selected. In the first component, the distance to the seminatural habitat (factor loading,  $R=0.853$ ) was positively correlated with plot size ( $R=0.690$ ;  $P<0.05$ ) and the distance to the natural habitat (factor loading,  $R=0.740$ ) was not correlated with other variables (all  $P>0.05$ ,  $n=18$ ). On the second axis, the size of the seminatural habitat (factor loading,  $R=0.536$ ) and the size of the natural habitat (factor loading,  $R=0.658$ ) were not significantly correlated with the other variables or with each other (all  $P>0.5$ ).

## 2.6. Statistical analyses

The variables that did not show a normal distribution were transformed. The variables and interactions that did not contribute to the models with a  $p<0.05$  were removed by the stepwise backward procedure. Statistical analysis of the data was carried out using XIStat 2009 (Addinsoft). To calculate the diversity indices, PRIMER 5.2 (PRIMER-E Ltd) was used.

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## Objectives

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The main aim of this work was to analyze the effects of the degree of heterogeneity of agricultural landscapes on the trap-nesting bee and wasp communities and on the interactions with their natural enemies at different scales. To accomplish this, we established a series of objectives for each of the studies carried out.

1. Analysis of the effects, at landscape level, of the presence of seminatural habitats and of the degree of farming intensity, in combination with the effect of local crop type, on the trap-nesting bee and wasp communities, both of them groups with different functions in the ecosystem (Chapter 1).
2. Assessment of the effects of the type of farming intensity in two types of crop system –monocrop and polycrop- on the trap-nesting bee and wasp communities (Chapter 2)
3. Identification, at landscape level, of which variables are the driving factors of the persistence of the natural enemies of the trap-nesting bee and wasp communities in intensified agricultural landscapes (Chapter 3)
4. Detection of which factors associated with agricultural plots model the communities of bees and wasps and their natural enemies (Chapter 4).
5. Analysis of the effects of the isolation of the crop field with regards to distance to natural and seminatural habitats on the richness and diversity of bee and wasp communities and their natural enemies (Chapter 5).

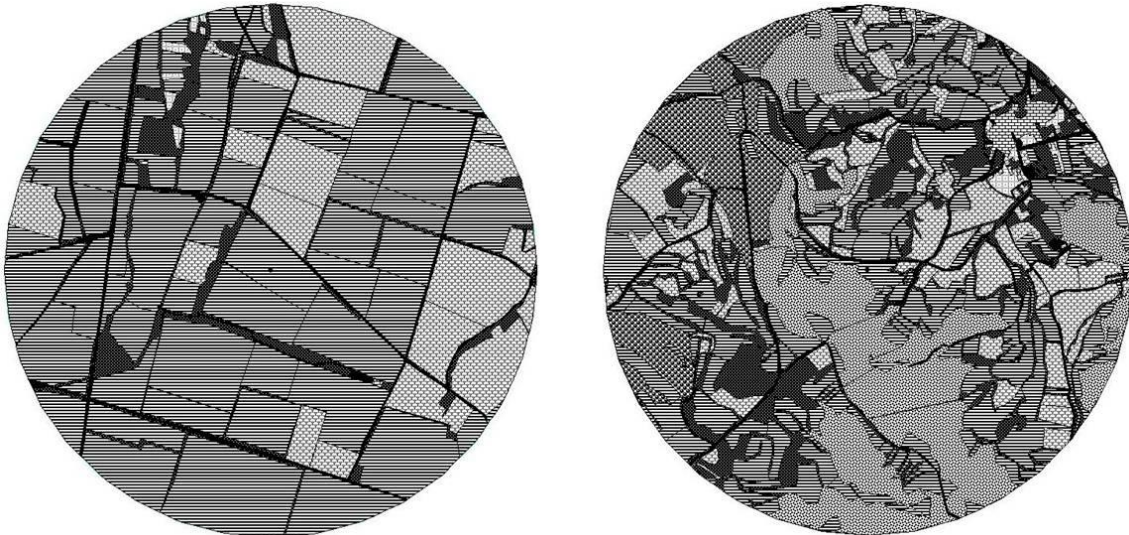
6. Assessment of the effects of different types of structure present in agricultural landscapes harbouring vineyards on the richness and abundance of bee and wasp communities, and on the interactions with their natural enemies, together with their role as promoters of the connectivity of the agricultural matrix (Chapter 6).

## Chapter 1

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### **Pollinators and predators: different functional groups take advantage of the Mediterranean agricultural landscape in different ways**

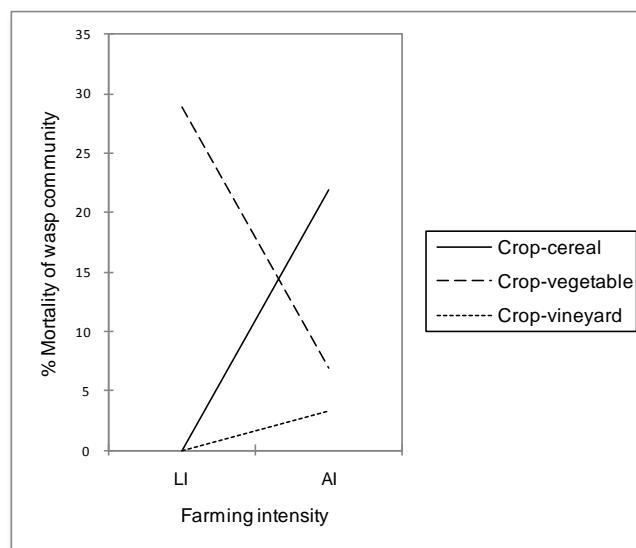
Due mainly to the intensification of land use, Mediterranean agricultural landscapes are very complex, ranging from heterogeneous landscape matrices, with a balance between crop areas and the remains of seminatural habitats, to uniform matrix, where most of the surface area is cultivated. Understanding the role of certain specific habitats within those landscapes and the effect of the crops themselves and the type of farming intensity is essential for the preservation of many insect communities associated with these agroecosystems.



**Figure 1.-** Examples of landscape sectors (1 km radius) corresponding to: (A) high-intensity farming system (cereal growing at the “Montenegro” plot in Rodezno (La Rioja)) and, (B) low farming intensity system (cereal growing at “Idesa” in Ventosa (La Rioja)).

Using trap-nests established on three types of Mediterranean crop lands (vineyard, cereal, vegetable crops areas), together with two types of farming intensity (low- vs. high-intensity) (Fig. 1) we analyzed the communities of bees, Spheciformes wasps and eumenine wasps nesting aerially, through the relationship among different biological parameters and selected landscape and local variables related to the agricultural landscape, the degree of farming intensity, and the crops themselves.

The groups of trap-nesting predators and pollinators gain different benefits from the structures present in the agricultural landscape matrix and are affected differently by the type of crop and farming intensity. The abundance and richness of the wasp community (especially in the case of the Spheciformes wasps) are mainly affected by the percentage of seminatural habitats present in the matrix (Table I). A high percentage of presence of these habitats may buffer the negative effect exerted by farming intensity and the crops themselves at local level (Figs. 2).



**Figure 2.-** Plot showing the interactions between the farming intensity and local crop type variables for the percentage of mortality of wasps community (LI, low- farming intensity; HI, high- farming intensity)

**Table I.-** GLMs of the relationship between the number of brood cells, species richness, percentage of natural mortality and percentage of parasitism of the wasp community in general and of Spheciformes wasps in particular, and the agricultural landscape variables and local crop type. Only the significant variables and interactions are included (ns: not significant; LI, low- farming intensity; HI, high- farming intensity; H: vegetable crop plots; V, vineyards).

Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
<b>NUM. BROOD CELLS</b>					
Wasp community	Seminatural habitats (%)	1.85	8.83	0.009	0.316
Spheciformes wasps	Seminatural habitats (%)	1.99	13.36	0.002	0.421
<b>SPECIES RICHNESS</b>					
Wasp community	Seminatural habitats (%)	0.066	6.14	0.025	0.232
Spheciformes wasps	Seminatural habitats (%)	0.064	22.03	0.000	0.553
<b>NATURAL MORTALITY (%)</b>					
Wasp community	Farming intensity (LI _HI)	LI 21.889	6.46	0.039	0.801
	Local crop type	Veg 28.928	7.74	0.017	
		V 0.000			
		LI _HI*Crop type	LI*Veg -43.908	15.70	0.003
		LI*V -18.556			
Spheciformes wasps	Seminatural habitats (%)	1.96	39.01	0.025	0.983
	Farming intensity (LI _HI)	LI 54.592	186.33	0.005	
	Local crop type	Veg 476.406	82.56	0.012	
		V 10.211			
		Seminatural habitats (%)*LI _HI	LI -1.396	94.97	0.010
	Seminatural habitats (%)*Crop type	Veg -12.322	50.18	0.020	
		V -0.571			
	LI _HI*Crop type	LI*Veg -155.908	20.83	0.045	
<b>PARASITISM (%)</b>					
Wasp community	—	—	—	ns	—
Spheciformes wasps	—	—	—	ns	—

However, the abundance of the bee community is strongly dependent upon the presence of vegetable crop plots (the only polycrop analyzed) as the local crop type, and species richness is determined by the predominating type of farming intensity in the matrix, reflecting the need for heterogeneous landscapes (Table II).

The maintenance of quality habitats, such as forests, sequential habitats, vegetation along inshore waters and the edges of crop fields, the last remnants of suitable habitats in intensified Mediterranean landscapes, is determinant for the bee and wasp communities nesting in trap-nests.

**Table II.-** GLMs of the relationship between the number of brood cells, species richness, percentage of natural mortality and percentage of parasitism of the bee community and the agricultural landscape variables and local crop type. Only the significant variables and interactions are included (ns: not significant; LI, low- farming intensity; HI, high- farming intensity; H: vegetable crop plots; V, vineyards).

Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
BEE COMMUNITY					
Total number of brood cells	Local crop type	Veg 172,1€ V 31,000	4.93	0.023	0.317
Species richness	Farming intensity (LI _HI)	LI 1,667	5.29	0.035	0.202
Natural mortality (%)	—	—	—	ns	—
Parasitism (%)	—	—	—	ns	—

Bearing in mind the importance of the presence of these structures in the agricultural matrix and the influence exerted by the crops in different degrees of farming intensity, it is possible to establish some directives for the preservation of these communities and the services they provide to the ecosystem within intensified Mediterranean agricultural landscapes.



## Chapter 2

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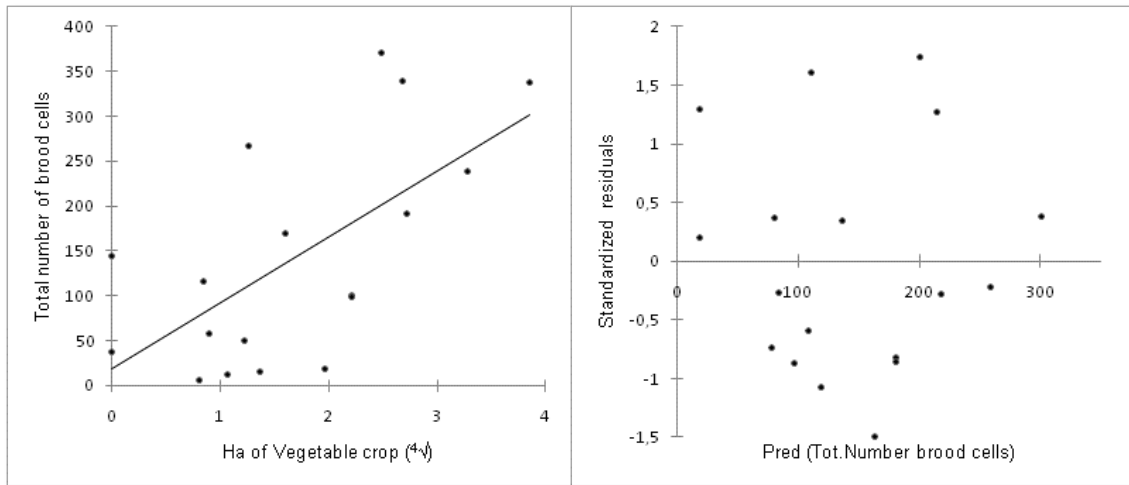
### **Polycrops vs. monocrops: additional resources favour nest colonization and the progeny of pollinator communities**

At landscape level, the diversity of crops, together with spatial heterogeneity, connectivity, and the proportion of natural elements, is an important factor in the agricultural matrix. The amplitude of resources, derived from the high productivity associated with cultivated land, in agricultural landscapes made up of mosaics of small elements and low-intensity agricultural systems could favour certain populations of species.

Using communities of solitary bees that nest in trap-nests, which have specific needs related to the nesting site (an important element in the structuring of their communities), we assessed the effect of two types of farming intensity (high- vs. low-intensity) in two Mediterranean monocrops (vineyards and cereals) and one polycrop (vegetable crop areas) on nest occupation and population structure. We also analyzed the relationship between the *sex ratio* of the most abundant species- *Osmia caerulescens*- and the two crop systems.

Polycrops were found to favour nest occupation (number of brood cells) (Fig. 1) and the efficiency of generalist species, regardless of the farming intensity dominant in the agricultural system (Table I). Species richness in both systems and nest occupation in monocrops are favoured by a low-intensity land use. In the case of *Osmia caerulescens*, stem diameter and the degree of farming intensity affect the production of male and female progeny (Table II). In

certain agricultural systems, the presence of different types of crop would buffer the lack of seminatural spaces as sources of resources.



**Figure 1.-** Regression plot and standardized residuals of the total number of brood cells of the bee community as a function of the surface area of vegetable cropland (ha).

**Table I.-** ANOVA for the effects of the crop system (monocrops vs. polycrops) and, within the monocrops, of the degree of farming intensity (low-farming intensity vs. high-farming intensity) on the following variables: number of brood cells and species richness of the communities of trap-nesting solitary bees (Mono c: cereal monocrop; Mono v: vineyard monocrop; LI, low-farming intensity; HI, high-farming intensity).

		Dependent variables									
		Total number of brood cells					Species richness				
		Value	F	P	R <sup>2</sup> Adj.	DF	Value	F	P	R <sup>2</sup> Adj.	DF
Crop system (Mono vs. Poly)	Poly	156.66	11.79	<b>0.004</b>	0.444	2,15	-0,33	0.18	0.679	0,158	2,15
Farming intensity (LI vs. HI)	HI	-83,660	3.78	0.071			-1,67	5.02	<b>0.041</b>		
		Value	F	P	R <sup>2</sup> Adj.	DF	Value	F	P	R <sup>2</sup> Adj.	DF
Monocrop (Mono v vs. Mono c)	Mono v	31.00	0.56	0.471	0.304	2,9	1,000	0.97	0.349	0.280	2,9
Farming intensity (LI vs. HI)	HI	-103,00	6.23	<b>0.034</b>			-2,333	5.31	<b>0.047</b>		

**Table II.-** GLM of the relationship between the sex ratio of *Osmia caerulescens* and the nesting and landscape variables. Only the significant explanatory variables are included (LI\_HI, low intensity \_high intensity)

Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
Sex ratio from <i>Osmia caerulescens</i>	Diameter (mm)	-0,25	33.60	<0.0001	0.151
	Seminatural habitats (%)	0.01	6.01	0.015	
	Farming intensity (LI_HI)	HI -0.18	4.79	0.03	

## Chapter 3

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### **The abundance of hosts and the structure of the landscape determine the persistence of natural enemies of trap-nesting communities in intensified Mediterranean agroecosystems**

The expansion of agriculture, the increase of plot sizes, and the clearing of cultivated land through different practices have given rise to a simplification of the agricultural landscapes, small fragments of seminatural and natural habitats persisting in some cases.

Many insect populations that persist in the interface between cultivated fields and the remnants of natural habitats include important functional groups, among which natural enemies are of great relevance since they act as parasitoids of the nesting communities of other insects.

Using standardized trap-nests we analyzed the effect of different factors characteristic of agricultural landscapes, such as the degree of farming intensity, the type of Mediterranean crop (vineyards, cereal, vegetable crops areas), and the presence of natural habitats in the matrix on the biological parameters of the populations of natural enemies of trap-nesting bee and wasp communities, together with the nature of their relationship to the abundance of hosts.

The persistence of natural enemies in the agricultural landscapes analyzed is determined by the abundance of their hosts and by the composition of the agricultural matrix (Table I). The activity, richness and diversity of the

species of the community of natural enemies are positively related to the number of trap-nesting host cells (Table II).

**Table I.-** GLMs of the relationship between the explanatory variables (landscape and local) related to the community of hosts and the parameters of the community of natural enemies: (A) total number of cells attacked, (B) species richness; (C) diversity, and (D) biological efficiency. Only the significant variables are included (type of local crop: c, cereal; veg, vegetable crops).

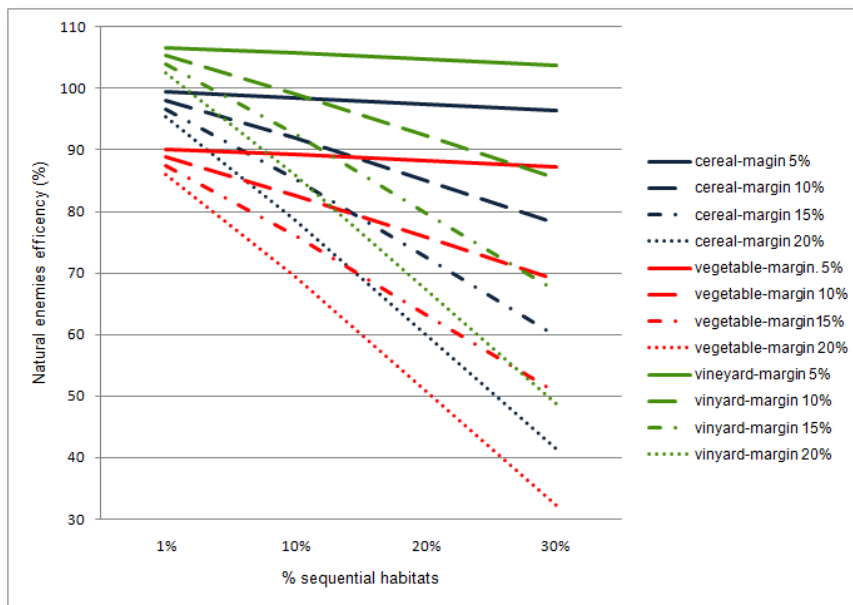
Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
<b>(A) Attacked cells</b>	Seminatural habitats (%)	0.359	4.62	0.048	0.473
	Total number of host brood cells	0.186	12.66	0.003	
<b>(B) Species richness</b>	Seminatural habitats (%)	0.053	19.82	0.000	0.693
	Total number of host brood cells	0.008	20.46	0.000	
<b>(C) Diversity(1-<math>\lambda</math>)</b>	Forest (%)	0.012	6.41	0.023	0.459
	Total number of host brood cells	0.001	10.02	0.006	
<b>(D) Efficiency</b>	Margin habitats (%)	-0.16	13.66	0.004	0.837
	Sequential habitats (%)	0.482	15.56	0.002	
	Local crop type	c -7.239	20.32	0.000	
		veg -16.496			
	Margin habitats*Sequential habitats	-0.117	17.45	0.002	

**Table II.-** Relationship between the number of cells attacked in a nest by natural enemies and nest occupancy. The number of stems occupied and the number of brood cells correspond to the total recorded in the groups of 50 stems (tubes) selected at random for each study site.

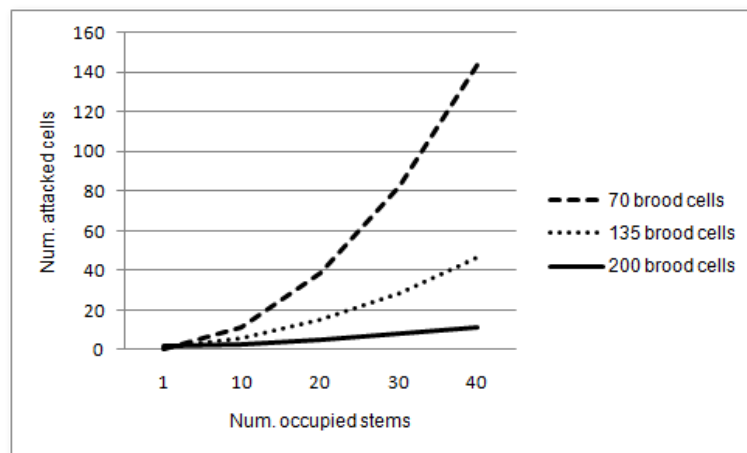
Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
<b>PARASITISM</b>	<b>NEST COLONIZATION</b>				
Tot. number of attacked cells	Total number occupied stems	1.07	20.55	0.000	0.67
	Total number of host brood cells	—	—	ns	
	Occupied stems*Host brood cells	-0.273	16.38	0.001	

Moreover, the number of cells attacked is affected by the number of stems occupied by hosts (Fig. 1). The presence of seminatural habitats in the agricultural matrix, such as forests, sequential habitats and the edges of croplands, affects the activity, richness and diversity parameters of the

community of natural enemies positively. Finally, efficiency is strongly affected by the type of local crop and by the presence of specific habitats in the agricultural landscape (Fig. 2). Efforts directed at the conservation of natural enemies in agroecosystems should focus on the maintenance of the remnants of habitats suitable for these populations and those of their hosts, together with restoration practices that will promote their connectivity.



**Figure 1.-** Model of the effect of % of edges and % of sequential habitats (for cereal, vegetable, and vineyards crops) on the efficiency of natural enemies. In the model, the range of records for both variables in the landscapes associated with these crops were used.



**Figure 2.-** Model of the effect of the number of occupied stems and number of brood cells of hosts on the number of cells attacked by natural enemies.

## Chapter 4

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### **Which local factors of the crop plot drive the communities of bees, wasps and their natural enemies?**

In recent decades, the expansion of agriculture has given rise to a reduction in uncultivated habitats adjacent to croplands, and the surface area of the former has decreased considerably. At local scale, agricultural intensification has affected biodiversity through changes in agricultural practices, modifying the spatial and temporal distribution of floristic and nesting resources of the marginal habitats, which are important for the dynamics of the populations and the composition of many insect communities. The structure and composition of the vegetation associated with marginal habitats, the physical habitat of many organisms, is determinant for many groups of insects, although the influence of local factors associated with crop plots on communities is little known.

Using standardized trap-nests and net sampling, we analyzed the relationship between different local variables associated with edges (edge density, percentage of floral cover and species richness of plants with flowers) and the type of local crop (vineyards, cereal and vegetable crops areas), and the biological parameters characterizing the communities of bees, wasps and their natural enemies in Mediterranean agroecosystems under two types of farming intensity.

The cover of flowering plants and the richness of flowering plants contribute to the patterns observed for the trap-nesting bee community. The abundance of polylectic species in terms of the establishment of brood cells is

negatively related to the floral cover while the percentages of mortality and parasitism are determined by the richness of flowering plants and the type of local crop (Table I).

**Table I.-** GLMs of the relationship between the total number of brood cells, the percentage of natural mortality and the percentage of parasitism of the community of trap-nesting bees and local variables: percentage of flowering plant cover, richness (S) of species of flowering plants and type of local crop. Only the significant variables and interactions are included (ns, not significant; Tot, total number of bee species; Oligo, oligolectic species; Poly, polylectic species; veg, vegetable crops; v, vineyard).

TRAP-NEST BEE COMMUNITY						
Dependent variable	Variable in model		Value	F	P	R <sup>2</sup> Adj.
Total number of brood cells	Tot	% Cover of flowering plants	-6.967	10.986	0.004	0.370
	Oligo	—	—	—	ns	—
	Poli	% Cover of flowering plants	-6.591	26.234	0.000	0.597
% Natural mortality	Tot	—	—	—	ns	—
	Oligo	S flowering plants	-1.162	5.069	0.044	0.238
	Poli	—	—	—	ns	—
% Parasitism	Tot	S flowering plants	—	—	ns	—
		Local crop type	—	—	ns	—
		S flowering plants*Local crop type	Sflor*veg 2.414 Sflor*v -0.972	4.14	0.040	0.408
	Oligo	—	—	—	ns	—
	Poli	—	—	—	—	ns

The percentage of floral cover governs both natural mortality in communities of trap-nesting wasps (through the availability of quality prey associated with the vegetation) and the percentage of parasitism by natural enemies (with respect to an increase in the availability of alternative hosts in the marginal habitat) (Table II). Both the richness of trap-nesting natural enemies and that of the general community persisting in the agricultural plots analyzed are determined by the edge density adjacent to them (Table III, Figs. 1 and 2), supporting the notion that the presence of such refuge habitats is essential for the persistence of parasitoids in agroecosystems.

**Table II.-** GMLs of the relationship between the total number of brood cells, the percentage of mortality and the percentage of parasitoidism of the trap-nesting wasps and local variables: percentage of flowering plant cover, richness (S) of flowering plants and type of local crop. Only the significant variables and interactions are included (ns= not significant).

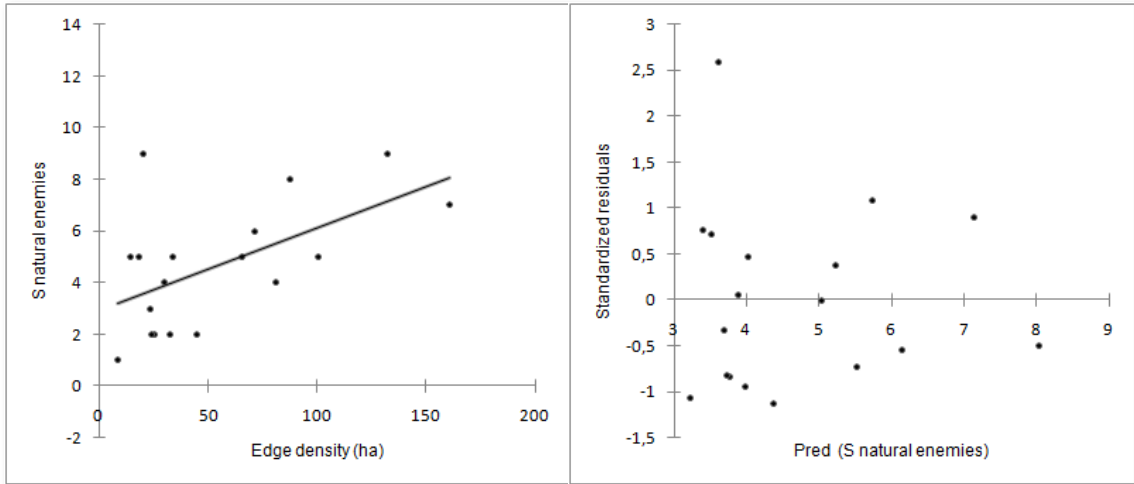
TRAP-NEST WASP COMMUNITY					
Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
Total number of brood cells	—	—	—	ns	—
% Natural mortality	% Cover of flowering plants	-0.035	5.221	0.035	0.202
% Parasitism	% Cover of flowering plants	-0.532	6.94	0.018	0.259

**Table III.-** GMLs of the relationship between species richness, diversity and biological efficiency (%) of the community of trap-nesting natural enemies and of the richness and diversity of the general community of parasitoids (trap-nests and net captures) and local variables: percentage of flowering plant cover, richness (S) of flowering plants and type of local crop. Only the significant variables and interactions are included (ns= not significant).

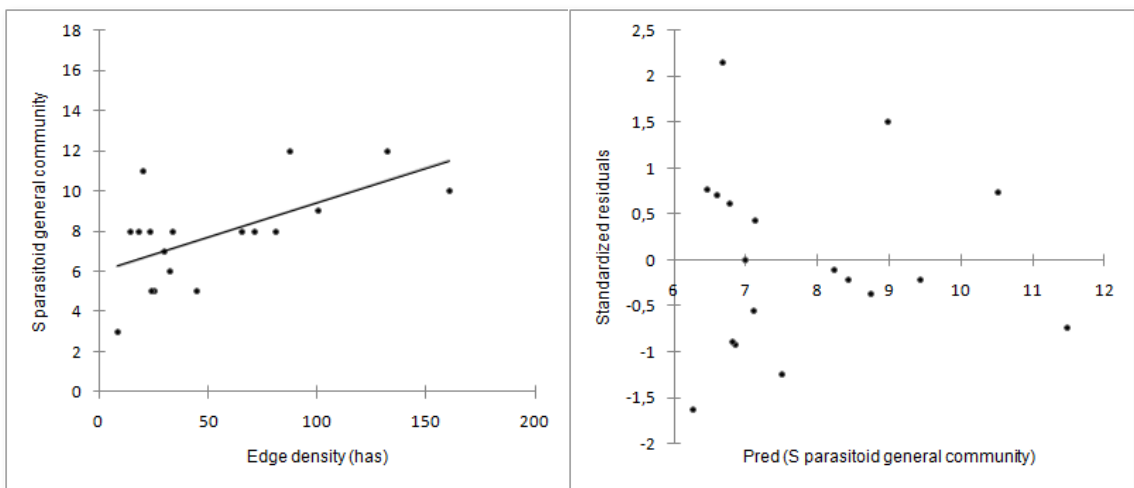
NATURAL ENEMY COMMUNITY					
Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
Species richness	Edge density	0.032	7.399	0.015	0.273
Diversity (1- $\lambda'$ )	—	—	—	ns	—
Efficency (%)	—	—	—	ns	—
GENERAL PARASITOID COMMUNITY					
Dependent variable	Variable in model	Value	F	P	R <sup>2</sup> Adj.
Species richness	Edge density	0.034	9.388	0.007	0.330
Diversity (1- $\lambda'$ )	—	—	—	ns	—

Knowledge of the local factors that drive the parameters of the communities of bees, wasps and their natural enemies could help to establish suitable agroenvironmental schemes for their conservation and hence the maintenance of their ecological functions in agricultural landscapes.





**Figure 1.-** Regression plot and standardised residuals of the species richness of natural enemies of trap-nests as a function of the edge density adjacent to the plot (ha).



**Figure 2.-** Regression plot and standardised residuals of the species richness of parasitoids of the general community (trap-nests and net captures) as a function of the edge density adjacent to the plot (ha).

## Chapter 5

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### **Spatial isolation of crop fields: the distance to the closest natural or seminatural habitat determines the species richness of communities of bees, wasps and their natural enemies**

The destruction, alteration, and fragmentation of natural habitats by agricultural intensification are considered to be the main agents responsible for the loss of biodiversity at local and global level. Both the size and the spatial configuration of these habitats seem to be decisive for the maintenance of certain species, acting as hibernation habitats and a source of alternative resources for many arthropods.

Different authors have analyzed the effects of the isolation and size of natural and seminatural habitats on the populations of insects living in them. However, the effect of the processes of isolation of crop fields themselves on communities that nest or forage in them is little known. Using standardized trap-nests and net samplings, we analyzed the effect of the distance of the crop fields to the closest natural and seminatural habitats, and the size of these habitat fragments on the richness and diversity of the species of communities of bees, wasps and their natural enemies.

The species richness of bees and wasps nesting in trap-nests is lower on the crop fields that are more isolated with respect to the closest seminatural habitat. However, the combined richness for the species caught with nets and trap-nests does not show this relationship with isolation, in comparison with the

seminatural habitats, but is determined by natural habitats, being less marked on the fields at a greater distance from the closest natural habitat (Table I). These differences are a reflection of the different composition of species integrating the two communities, with specific requirements as regards their choice of prey, their floristic resources, and nesting sites.

**Table I.-** Linear regressions between species richness and the diversity of trap-nesting bee and wasp communities, and of their general communities (trap-nest and insect net) and the isolation variables: distance to seminatural habitat, (IFSH), distance to natural habitat (IFN), size of seminatural habitat (Size SN) and size of natural habitat (Size N). Only the significant variables and interactions are included; Tot, total species of bees; Oligo, oligolectic species; Poly, polylectic species.

Dependent variable	Variable in model	Value	F	P	R2 Adj.	
<b>TRAP-NEST BEE COMMUNITY</b>						
Diversity (1- $\lambda'$ )	Tot	IFSH	-0.133	5.671	0.03	0.216
	Oligo	—	—	—	ns	—
	Poli	IFSH	-0.097	5.302	0.035	0.202
	Tot	—	—	—	ns	—
	Oligo	—	—	—	ns	—
	Poli	—	—	—	ns	—
<b>GENERAL BEE COMMUNITY</b>						
Species richness	IFN	-0.003	9.925	0.006	0.344	
Diversity (1- $\lambda'$ )	IFN	3.0 <sup>-5</sup>	9.745	0.008	0.471	
	Size N	—	—	ns	—	
	IFN*Size N	0,000	7.621	0.015	—	
<b>TRAP-NEST WASP COMMUNITY</b>						
Species richness	—	—	—	ns	—	
Diversity (1- $\lambda'$ )	—	—	—	ns	—	
<b>GENERAL WASP COMMUNITY</b>						
Species richness	IFN	-0.002	7,962	0,012	0,291	
Diversity (1- $\lambda'$ )	—	—	—	ns	—	

In turn, the community of trap-nesting natural enemies and the general community of parasitoids are strongly determined by the isolation of the crop plot, both as regards seminatural habitats and the natural ones present in the matrix; sites that govern the search for hosts and the resources necessary for the insects

to complete their life cycles (Table II). These observations suggest that the greatest contribution to the total species biodiversity in agroecosystems comes from the presence of these habitats, both natural and seminatural, and that the conservation of communities rich in species requires the maintenance of such areas, less isolation, and the fostering of connectivity among the fragments.

**Table II.-** Linear regressions between species richness and the diversity of trap-nesting natural enemies and of their general community (trap-nest and insect net) and the isolation variables: distance to seminatural habitat, (IFSH), distance to natural habitat (IFN), size of seminatural habitat (Size SN) and size of natural habitat (Size N). Only the significant variables and interactions are included (ns: not significant).

Dependent variable	Variable in model	Value	F	P	R2 Adj.
<b>NATURAL ENEMY COMMUNITY</b>					
Species richness	IFSH	-0.275	15.228	0.001	0.456
Diversity (1-λ')	IFSH	-0.034	11.111	0.005	0.492
	IFN	1.49 <sup>-4</sup>	7.375	0.016	
<b>GENERAL PARASITOID COMMUNITY</b>					
Species richness	IFSH	-0.288	18.22	0.001	0.503
Diversity (1-λ')	—	—	—	ns	—

## Chapter 6

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### **Analysis of the role of hedgerows and grass strips, in vineyard agricultural matrix, for the persistence of trap-nesting bees and wasps**

The fragmentation of habitats is one of the main causes of the decline in species, owing to its effects on interspecific interactions, the movement of the individuals, and the genetic composition of the local populations. The degree of connectivity of the fragments of natural habitats affects the ability of some species to persist in fragmented landscapes. The remaining linear habitats, surrounded by crops, maintain a degree of connectivity through the modified surrounding habitats, and the different nature of these structures can exert a strong effect on the communities, modifying the availability of resources. Corridors have been recognised as a potential way to reduce the effects of habitat fragmentation, which seems to be particularly severe when the matrix between the fragments involves cultivated land.

Using trap-nests established in agricultural landscapes dominated by vineyards, we analyzed the effect of different natural structures (edges of natural habitats, hedgerows and grass strips) on the richness and abundance of communities of bees and wasps, and the impact of their natural enemies. Regarding these variables, we also assessed the role of hedgerows and grass strips with different degrees of isolation (connected, slightly isolated and isolated) on the connectivity of the vineyard agricultural matrix.

The effects of the type of structure were only significant in the case of the richness and abundance of the community of trap-nesting bees (Table I). The number of brood cells was significantly different between the edge of the natural habitat and the strip. The species richness of bees was significantly different between the edge of forest and the strip and between the hedgerow and the grass strip, with the observation of a significant effect of the type of structure on the richness of this group. The presence of a greater availability of resources, for both feeding and nesting, favours the presence of different species and of a greater number of cells established at the edges of forests and hedgerows, with a more complex plant composition than that existing on the grassy strips. Neither the richness and abundance of the community of wasps nor the percentage of parasitism by natural enemies were related to the type of structure where the trap-nests had been placed.

The results obtained failed to reveal a clear corridor effect of the structures with different degrees of isolation on the colonization of trap-nests by bee and wasp communities (Tables II and III). Only the richness of wasps showed significant differences between the connected hedgerows and the slightly connected hedgerows, supporting the findings of other authors. However, the degree of connectivity/isolation of hedgerows and stripes present between crop fields does not determine the parameters of the bee community, which may have different dispersion strategies than wasps, entering the crop matrix to move towards their foraging habitats. The interactions between parasitoids and hosts were not related to the types of structure or the degrees of isolations, presumably owing to the generalist condition of the natural enemies recorded.

Avoiding the degradation of existing linear elements and favouring the creation of new structures in highly fragmented landscapes may be beneficial to favouring the persistence of many species in agroecosystems.

**Table I.-** Linear mixed-effects models for the effect of type of structure (habitat edge, hedgerow, grass strip) in richness and abundance of bees and wasps and on the percentage of parasitism by natural enemies. Structure type was included as a fixed factor and the locality study as the random block factor.

<b>Bee community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Structure type</b>	<b>2, 33</b>	<b>5.92</b>	<b>0.006</b>
	<i>Forest edge vs. grass strip</i>			0.031
	<i>Hedgerow vs. grass strip</i>			0.003
	<i>Hedgerow vs. forest edge</i>			ns
Num. Brood cells	Model	DF	F	P
	<b>Structure type</b>	<b>3, 33</b>	<b>2.57</b>	<b>0.092</b>
	<i>Forest edge vs. grass strip</i>			0.036
	<i>Hedgerow vs. grass strip</i>			ns
	<i>Hedgerow vs. forest edge</i>			ns
% Parasitism	Model	DF	F	P
	<b>Structure type</b>	<b>2, 31</b>	<b>0.99</b>	<b>0,381</b>
	<i>Forest edge vs. grass strip</i>			ns
	<i>Hedgerow vs. grass strip</i>			ns
	<i>Hedgerow vs. forest edge</i>			ns
<b>Wasp community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Structure type</b>	<b>2, 33</b>	<b>0.11</b>	<b>0.897</b>
	<i>Forest edge vs. grass strip</i>			ns
	<i>Hedgerow vs. grass strip</i>			ns
	<i>Hedgerow vs. forest edge</i>			ns
Num. Brood cells	Model	DF	F	P
	<b>Structure type</b>	<b>2, 33</b>	<b>0.29</b>	<b>0.747</b>
	<i>Forest edge vs. grass strip</i>			ns
	<i>Hedgerow vs. grass strip</i>			ns
	<i>Hedgerow vs. forest edge</i>			ns
% Parasitism	Model	DF	F	P
	<b>Structure type</b>	<b>2, 27</b>	<b>0.27</b>	<b>0.762</b>
	<i>Forest edge vs. grass strip</i>			ns
	<i>Hedgerow vs. grass strip</i>			ns
	<i>Hedgerow vs. forest edge</i>			ns

**Table II.-** Linear mixed-effects models for the effect of the type of grass strip with different degrees of isolation (connected, slightly isolated and highly isolated) on the richness and abundance of bees and wasps, and on the percentage of parasitism by natural enemies. The grass strip type was included as the fixed factor and the study locality as the random block factor.

<b>Bee community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Grass strip type</b>	<b>2, 15</b>	<b>0.02</b>	<b>0.979</b>
	<i>Connected vs. highly isolated</i>			ns
	<i>Slightly isolated vs. highly isolated</i>			ns
	<i>Slightly isolated vs. connected</i>			ns
Num. Brood cells	Model	DF	F	P
	<b>Grass strip type</b>	<b>2, 15</b>	<b>1.63</b>	<b>0.228</b>
	<i>Connected vs. highly isolated</i>			ns
	<i>Slightly isolated vs. highly isolated</i>			ns
	<i>Slightly isolated vs. connected</i>			ns
% Parasitism	Model	DF	F	P
	<b>Grass strip type</b>	<b>1, 10</b>	<b>1.41</b>	<b>0.262</b>
	<i>Connected vs. highly isolated</i>			ns
	<i>Slightly isolated vs. highly isolated</i>			ns
	<i>Slightly isolated vs. connected</i>			ns
<b>Wasp community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Grass strip type</b>	<b>2, 15</b>	<b>1.62</b>	<b>0.230</b>
	<i>Connected vs. highly isolated</i>			ns
	<i>Slightly isolated vs. highly isolated</i>			ns
	<i>Slightly isolated vs. connected</i>			ns
Num. Brood cells	—	—	—	—
% Parasitism	Model	DF	F	P
	<b>Grass strip type</b>	<b>2, 12</b>	<b>0.06</b>	<b>0.937</b>
	<i>Connected vs. highly isolated</i>			ns
	<i>Slightly isolated vs. highly isolated</i>			ns
	<i>Slightly isolated vs. connected</i>			ns



**Table III.-** Linear mixed-effects models for the effect of the type of hedgerow with different degrees of isolation (connected and slightly isolated) on the richness and abundance of bees and wasps, and on the percentage of parasitism by natural enemies. The hedgerow type was included as the fixed factor and the study locality as the random block factor.

<b>Bee community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Hedgerow type</b>	<b>1, 10</b>	<b>1.87</b>	<b>0.201</b>
	<i>Connected vs. slightly isolated</i>			ns
Num. Brood cells	—	—	—	—
% Parasitism	Model	DF	F	P
	<b>Hedgerow type</b>	<b>1, 10</b>	<b>1.41</b>	<b>0.262</b>
	<i>Connected vs. slightly isolated</i>			ns
<b>Wasp community and parasitism</b>				
Species richness	Model	DF	F	P
	<b>Hedgerow type</b>	<b>1, 10</b>	<b>5.00</b>	<b>0.049</b>
	<i>Connected vs. slightly isolated</i>			0.045
Num. Brood cells	Model	DF	F	P
	<b>Hedgerow type</b>	<b>1, 10</b>	1.76	0.213
	<i>Connected vs. slightly isolated</i>			ns
% Parasitism	—	—	—	—

## Conclusions

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**First.-** The bee and wasp communities nesting in trap-nests benefit differently from the characteristics of the matrix of the Mediterranean agricultural landscape. The type of local crop, the degree of farming intensity and the presence in the landscape of seminatural structures affect the population parameters characterizing both groups in different ways.

**Second.-** In intensified agricultural landscapes, the conservation of quality seminatural habitats, such as forests, sequential habitats, riverside vegetation and the edges of crop lands favours the persistence of trap-nesting wasp communities and the ecological function of the group as predators.

**Third.-** The persistence of the bee communities is determined by both local and landscape factors. The crop system (local) and the degree of farming intensity (landscape scale) affect species abundance and richness significantly.

**Fourth.-** The polycrop system, typical in the riverside area of the Ebro river and characterized by having a high heterogeneity of resources in both space and time, favours the occupation of nests by the bee community, regardless of the farming intensity prevailing in the zone. Thus, vegetable crops buffer the high level of disturbance to which agricultural landscapes are subject due to their management and to a reduction in seminatural habitats, derived from the increase in the surface area cultivated.

**Fifth.-** Apart from the diameters of the stems where the insect nests, the sex ratio of the species *Osmia caerulescens* is governed by the degree of farming intensity in the landscape.

**Sixth.-** In agricultural landscapes, the presence of seminatural habitats determines the richness and diversity of species of natural enemies of the communities of trap-nesting bees and wasps. Their activity and efficiency are also favoured by these habitats, whose presence increases the abundance of host populations, on whose density the natural enemies depend strongly.

**Seventh.-** The presence of margin habitats adjacent to crop plots, with a dense structure and a composition rich in species of flowering plants, favours the trap-nesting bee and wasp communities and those of their natural enemies and the general community of parasitoids associated with areas close to cultivated fields. These characteristics increase the availability of floral resources, both for bees and for the potential preys of wasps and alternative hosts of natural enemies.

**Eighth.-** The richness of trap-nesting natural enemies and of the general community of parasitoids is favoured by the increase in edge density associated with crop plots, suggesting that these places act as important refuges and that their presence is essential for the persistence of this group and its functions in agricultural landscapes.

**Ninth.-** The important relationship seen in the richness and diversity of the species of the communities of bees, wasps and natural enemies and the isolation of the crop fields with respect to the surrounding natural and seminatural habitats indicate that the presence of these uncultivated quality habitats in the landscape contribute in an important way to the total biodiversity of agroecosystem species.

**Tenth.-** Conservation of the species of bees, wasps and specialized parasitoids in agricultural areas can be benefited by the maintenance of a mosaic formed by natural habitats intercalated among crop fields, reducing isolation and favouring the connectivity of the fragments.

**Eleventh.-** Habitats such as hedgerows and the edges of forests present in the agricultural matrix of vineyards favour the richness and abundance of the communities of trap-nesting bees. These natural structures, with more complex plant communities than the grass strips, provide more resources for the establishment of brood cells and for nesting.

**Twelfth.-** Hedgerows, as linear habitats present among crop fields, favour the species richness of trap-nesting wasps, increasing the connectivity of the vineyard agricultural matrix.

**Thirteenth.-** The communities of bees and wasps nesting in trap-nests and their natural enemies respond to both local factors and landscape variables, and analyses should be performed at many different scales if we are to fully understand the functioning of these communities in agricultural landscapes.

**Fourteenth.-** The increase in farming intensity carried out in the agroecosystems analyzed has given rise to a decrease in the number of crop fields, with an increase in their size and less linear shapes. Agricultural systems with low intensity land-use, favour trap-nesting bee and wasp communities and their natural enemies, affording more heterogeneous landscapes, which are required for the persistence of these hymenoptera.

**Fifteenth.-** The heterogeneity of agricultural landscapes, with a balanced presence of seminatural habitats and crop plots, is essential for the persistence of the communities of trap-nesting bees and wasps and their natural enemies and for the preservation of their functions in the agroecosystem. The presence of natural and seminatural habitats is important at both landscape and local level owing to the maintenance of marginal habitats. Accordingly, an agrarian policy aimed at regulating management practices at local level and favouring the maintenance of quality habitats, by promoting their connectivity, is crucial if we are to ensure the balance of the communities associated with agricultural landscapes.