Agriculture, Ecosystems and Environment 312 (2021) 107345

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Landscape and agri-environmental scheme effects on ant communities in cereal croplands of central Spain

Hodei Zumeaga [a,*], Francisco M. Azcárate [b,c], Elena D. Concepción [d], Violeta Hevia [e], Mario Díaz [d]

[a] *Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain*
[b] *Terrestrial Ecology Group (TEG). Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain*
[c] *Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain*
[d] *Department of Biogeography and Global Change, National Museum of Natural Sciences, Spanish National Research Council (BGC-MNCN-CSIC), C/ Serrano 115 bis, E-28006, Madrid, Spain*
[e] *Social-Ecological Systems Laboratory, Department of Ecology, Universidad Autónoma de Madrid, Madrid, Spain*

ARTICLE INFO

Keywords:
Harvester ants
Ecosystem services
Field edges
Landscape complexity
Landscape constraints

ABSTRACT

Agri-environmental schemes (AES) of the Common Agricultural Policy (CAP) aims at reversing the negative effects of agricultural intensification on biodiversity and ecosystem services. Landscape context may modulate, and even constraint, AES effectiveness. We evaluate AES effectiveness on ant abundance, diversity and community composition. Ants are an ecologically dominant group whose response to conservation efforts in farmland has been rarely evaluated, despite its role in weed control, particularly in Mediterranean farmland.

Ants were sampled in the edge and in the centre of paired cereal fields, managed with and without AES in three study areas along a landscape complexity gradient. AES application had no significant effects on ant species richness or ant community composition. Richness increased in fields and landscapes with higher amounts of complex edges and decreased towards the centre of the fields. Specialist granivorous ants (harvester ants, *Messor* spp.) were the most abundant. Abundance of foraging ants increased with the amount of complex edges around fields and in the landscape. AES application increased ant abundance close to field edges but not in field centers. AES fields had less specialist granivorous foraging in their centers than in control field centers.

Ant communities in Mediterranean cereal cropland were mostly constrained by the availability of complex edges, needed for nest building. AES increased the abundance of foraging ants, mostly specialist harvester ants, and its potential service of weed control, but close to field edges mainly. Measures promoting the abundance of stable edges rather than of ephemeral headlands in the landscape are essential to enhance the potential of AES for increasing ant-mediated ecosystem services of weed control.

1. Introduction

The loss of taxonomic and functional biodiversity is one of the biggest consequences of worldwide land use changes (Foley et al., 2005; Sala et al., 2000). Such changes occurred principally along the 20th century, due to the transformation of large amounts of land into croplands (MA, Millennium Ecosystem Assessment, 2005). In Europe, where agricultural expansion occurred much earlier, intensification of agricultural land use from the mid-20th century onwards was the main driver of biodiversity loss and its impact on ecosystem functioning and structure (Cardinale et al., 2012). Therefore, the conservation of biodiversity and its associated ecosystem services in Europe and in other countries with a long agricultural history, depends critically on the management of human-modified landscapes (Díaz and Concepción, 2016).

Management of actual agroecosystems is highly dependent of various synthetic supplies, as fertilizers (Altieri, 1999) and pesticides (Altieri and Nicholls, 2011). Agri-environmental schemes (AES) of the Common Agricultural Policy (CAP) finance the reduction of those supplies, as well as a limitation of farming activities in some periods, and are nowadays the main conservation tool in European agroecosystems (Batáry et al., 2015). The evaluation of the effectiveness of these

---

[*] Corresponding author.
E-mail address: hzumeagasuarez@gmail.com (H. Zumeaga).

https://doi.org/10.1016/j.agee.2021.107345
Received 10 November 2020; Received in revised form 20 January 2021; Accepted 25 January 2021

measures, however, has not been included in political evaluations, despite the key role of environmental benefits to justify CAP subsidies (Batáry et al., 2015; Concepción et al., 2020; Díaz and Concepción, 2016; Kleijn et al., 2006; Pe'er et al., 2019).

Effectiveness of AES is constrained by the surrounding landscape (Concepción et al., 2008, 2012a) and depend on the level of agricultural extensification (ecological contrasts) they achieved (Batáry et al., 2015; Kleijn et al., 2006; Tarjuelo et al., 2020). As a result of the interaction between local and landscape factors related to agricultural intensification, AES effectiveness is expected to be highest in agroecosystems of intermediate landscape complexity and land use intensity (Batáry et al., 2011, 2015; Concepción et al., 2008, 2012a; Díaz and Concepción, 2016; Kleijn et al., 2011; Tscharntke et al., 2012). Interactive effects of intensification-related factors at distinct spatial scales are expected to vary among species groups, ecosystem services' provision and regions (Díaz and Concepción, 2016). Differential perception of landscapes by organisms differing in size and mobility imply different responses of different groups to the same landscape structure. Further, non-linearity of landscape effects limits the generalization of responses to local- and landscape-scale management to different species groups (Concepción et al., 2008, 2012a, 2020; Díaz and Concepción, 2016).

Surprisingly, very few studies have investigated the effects of AES on ants, despite they are considered as a key group because of their usually large biomass share (Höldobler and Wilson, 2009) and their dominant role in terrestrial ecosystem function (Folgarait, 1998). Ants play a major role in the provision of ecosystem services and in the maintenance of ground functionality, and are key nodes in interaction networks (House et al., 2012; Lobry De Bruyn, 1999). A very high number of myrmecophiles and social parasites, many of them included in insect red lists, are dependent on ants (Thomas, 2005). Furthermore, ants are sensible to a variety of environmental perturbations or ground conditions in agroecosystems (Peck et al., 1998). This ecological relevance, combined with the fact that ants are organisms thoroughly extended and easy to sample make ant monitoring a useful tool for evaluating the conservation state of terrestrial ecosystems (Agosti et al., 2000).

Several additional reasons support the use of ants for monitoring the effect of AES and agricultural management on agroecosystem state. Apart from their role in other ecosystem services, ants have a strong effect in weed control, due to the impact of granivorous ants on weed seed banks, especially in Mediterranean croplands (Baraibar et al., 2009). Seed predation rates are however highly dependent on ant's nest distribution across the farmed landscape (Diaz, 1991), that determines local abundance of foraging harvester ants (Díaz, 1992). Therefore, the response of ants to agroecosystem and landscape management is expected to be high, and probably different from those observed for other groups of terrestrial invertebrates. All ants are eusocial insects that depend on stable, usually large and long-lived, permanent nests (Höldobler and Wilson, 2009). Hence, its sensitivity to management in periodically disturbed systems such as croplands would be stronger than sensitivity of the short-lived or solitary arthropod groups best studied to date, bees, butterflies or carabids, mainly (Albrecht et al., 2020; Batáry et al., 2011; Mader et al., 2018, 2017; Martin et al., 2019; Scheper et al., 2013), which could be more sensitive to year-to-year weather fluctuations (Pollard, 1991; Roy et al., 2001) and less indicative of background trends.

Here we analyze the effects of AES and landscape context on species richness, species composition and abundance of ant communities in dry cereal croplands of central Spain. Specifically, we aim to analyze ant abundance and species richness in fields where AES were implemented and in control fields along a landscape complexity gradient. Also, we explore the potential influence of the landscape and AES application on weed control ecosystem service in croplands, mediated by ant community composition according to ants' diet.

2. Material and methods

2.1. Study area

Sampling fields were located in the municipalities of Retuerta del Bullaque (Ciudad Real), Huecas (Toledo) and La Guardia (Toledo) (Fig. 1). These three study regions are dominated by extensively managed cereal croplands (Concepción et al., 2012b, 2012a, 2008). The three regions are close to each other (60−80 km) but differ in landscape configuration. Retuerta del Bullaque represents the most complex, fine-grained landscape, Huecas an intermediate landscape and La Guardia is the simplest, most coarse-grained landscape (Concepción and Díaz, 2011). Weed communities of study fields were previously studied (Concepción et al., 2012b).

2.2. Sampling design

Seven field pairs were selected in each study region. Each pair was composed by a field in which AES had been applied during at least 5 years and a field cultivated in the usual way, that was used as a control (Concepción et al., 2008). The evaluated schemes are aimed at protecting steppe birds in extensively managed cereal fields and consists in limitations to fertilizer and pesticide applications as well as restrictions of agricultural activities to certain periods to avoid disturbance to breeding birds (Kleijn et al., 2006).

Fields within pairs were cultivated with the same cereal species (mostly barley *Hordeum vulgare* or wheat *Triticum aestivum*) and were selected close to each other, minimizing differences between them in size, shape, soil type, and landscape context (Concepción et al., 2012b).

Foraging ants were sampled by means of pitfall traps 15 cm of diameter and 11 cm deep (Duelli et al., 1999). Traps were buried to soil level and covered with an elevated roof to avoid effects of rainfall or sunshine on the preserving liquid (2/3 of 70° ethanol and 1/3 of glycerine, filling 1/3 of the trap). One trap was set 50 m away from the nearest edge (centre trap hereafter) and the other trap was set near the edge, on the first furrow parallel to the edge and more than 50 m away from the field's corners. Sampling was done from early May to late June 2003. Traps were set for three 2-week periods: two consecutive 2-week periods and a final 2-week period after a 2-week interval in which traps were closed (6 weeks in total; (Duelli et al., 1999)). Trap contents were preserved in 70° ethanol.

Collected ants (foraging workers) were identify to species with a binocular microscope using the dichotomy keys from Lebas et al. (2017) and Gómez and Espadaler (2007). Species richness and abundance of foraging workers were computed by pooling data for the three trapping periods. Overall abundance and richness, and abundance and richness of granivorous ants, either overall granivores or only specialist ants, were computed for each trap. Species' diets were taken from Lebas et al. (2017).

The abundance of all species and the abundance of granivorous species (specialist and generalist) were analyzed separately because of the potential key role of granivorous ants in weed control (Baraibar et al., 2009). Number of ant foragers trapped were taken as a direct estimate of food search intensity of ants nesting nearby (Baraibar et al., 2009; Díaz, 1992).

The landscape metric selected to estimate landscape complexity around trap location was total length of boundaries with natural or seminatural vegetation (mostly grassy strips between fields with shrubs or scattered trees), based on previous studies (Concepción et al., 2012a, 2012b, 2008). Length of such boundaries was measured at the scale of the fields sampled (*i.e.*, boundaries surrounding study fields) and in 500 m-radius circular buffers centered in such fields (Concepción et al., 2008). Measures were done on digitalized aerial photographs using ArcView 3.2 (ESRI, 2000).

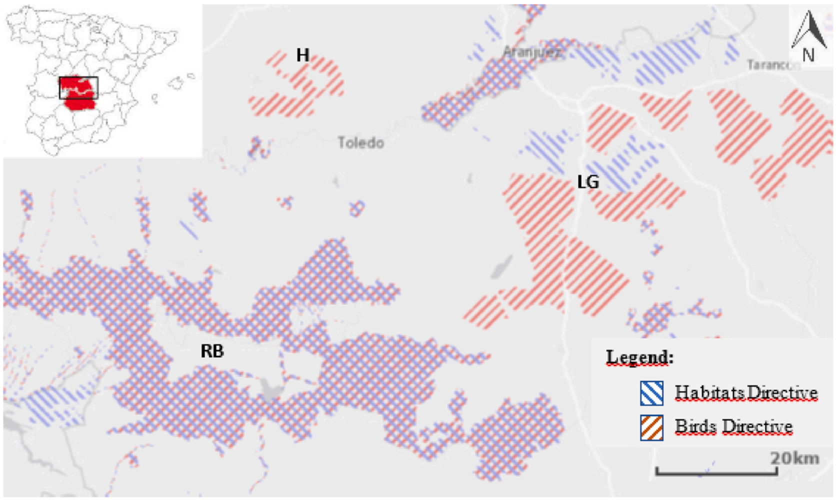

Fig. 1. Location of the sampled municipalities (H: Huecas, LG: La Guardia, RB: Retuerta de Bullaque). Natura 2000 sites protected under the Habitats and Birds Directives, (http://natura2000.eea.europa.eu/), where the analysed AES were applied, are shown.

2.3. Statistical analysis

Generalized Lineal Mixed Models (GLMM) with logarithmic link and Poisson distribution of errors were used to analyze the effects of AES and landscape context on ant communities. Random factors were field pairs nested in study regions. Fixed factors were management type (AES application *vs*. control) and trap location (edge *vs.* centre). Log-transformed lengths of field boundaries both around focal fields and in buffers were included in the models as explanatory variables, testing its main effects on ant species richness and abundance and its interactive effects with AES application (see Concepción et al., 2008 for more details).

The GLMM used were selected based on a complete model with all the explanatory variables and their interactions. Then, non-significant interactions were eliminated. Next, non-significant variables that were neither included in significant interactions were step-wisely eliminated after verifying model improvement in accordance to the Akaike's Information Criterion (AIC) (Burnham and Anderson, 2004).

A Non-Metric Multidimensional Scaling (NMDS) was used to compare graphically ant community composition in relation to the management (AES or control), trap location (edge or centre) and the study area. Ant communities were compared with a PERMANOVA in relation to the same explanatory variables (Legendre and Legendre, 2012).

3. Results

We collected 20,481 ant workers belonging to 26 species, 15 genera and three subfamilies in the 18 pairs of fields (Supplementary Table 1). Three out of the seven pairs selected in La Guardia could not be sampled due to logistic constraints (Kleijn et al., 2006). *Messor* (specialist harvester ants; Lebas et al., 2017; Díaz, 1992, 1991) was, by far, the most diverse and abundant genus in our samples; being *M. barbarus* the most abundant (56% of total individuals) and the most prevalent (86% of the traps) ant species. Four species were exclusive of AES fields (*Cardyocondila batesii*, *Formica cunicularia*, *M. capitatus* and *Oxyopomyrmex saulcyi*) and one was unique to control fields (*Temnothorax fuentei*; Supplementary Table 1).

Species richness was not affected by the type of farmland management. Only trap location and landscape variables showed significant effects. Specifically, the overall species richness and overall granivorous richness was higher in the edge traps. Length of complex margins in the surrounding landscape had also positive effects on overall species richness. This landscape variable was also significant at the field scale, but for specialist granivorous ants only (Table 1).

Effects on ant abundances were more complex than for species richness. Management had no significant effect, but in interaction with trap location had a positive effect on ant abundance: they were more abundant on edge traps of control fields (Fig. 2). Interestingly, location effects, by itself, were only significant for the granivorous ants, both overall and specialist, which indicates that these foraging ants were more abundant close to edges. Length of complex edges at field scale was positively associated to overall species and specialist granivorous ant's abundance (Table 1). Abundance increases differed according to trap location: edge traps capture more individuals as edge length increased (Fig. 3). Therefore, AES effectiveness was constrained by landscape variables.

The NMSD results did not show any difference in ant community composition neither in relation to management nor to management x location interactions. Species composition was more homogeneous for the centre than for the edge traps ($F_{1,70} = 2.55$; $p = 0.007$; Fig. 4). Edge traps presented eight unique species while centre traps just one.

4. Discussion

Responses of ant communities to AES in Mediterranean cereal cropland were strongly constrained by landscape structure, as found for grasslands (Pérez-sánchez et al., 2018). Complex field edges with low shrubs and scattered trees at both field and landscape scales shaped ant community composition. Positive effects of AES on ant abundance were concentrated close to such edges and were enhanced by edge length at both field and landscape scales. Measures promoting the abundance of stable field edges in the landscape would thus be essential to enhance AES effects on ants. Such measures are not currently implemented in most Spanish AES (Concepción et al., 2020; Concepción and Díaz, 2019).

Landscape influence on biodiversity has been attributed to either landscape structure or landscape configuration effects, or to biotic conditions such as local climate or soil attributes in grassland (Pérez-sánchez et al., 2018). Habitat diversity in complex landscapes would enable source populations inhabiting stable habitats to repeatedly rescue sink populations in nearby cropped lands (Benton et al., 2003)It is shown that invertebrate species richness and abundance were positively correlated with landscape complexity (Gonthier et al., 2014), and also that ant species richness was influenced by landscape structure (Dauber et al., 2003). Overall, arthropods were most abundant in landscapes that combine high edge density with high proportion of semi-natural habitat (Martin et al., 2019).

Table 1
Results of Generalized Lineal Mixed Models analysing AES and landscape effects on the species richness and abundances of overall, overall granivorous and specialist granivorous ants. Significant fixed factors were Management (Man; AES or control fields), Location (Loc; edge or centre traps) and length of complex edges at field scale (L3f) and in 500 m buffer areas around focal fields (L3b).

		Random effects		Fixed effects			
			σ^2		Estimate	z	P
RICHNESS	**Overall species**	Region:Field	0	Intercept	1.767	19.92	
	AIC = 316.310			Location	−0.434	−4.32	1.5×10^{-5}
	d.f. = 4			L3 buffer	0.100	3.10	1.9×10^{-3}
	Overall gran.	Region:Field	0	Intercept	1.344	15.78	
	AIC = 263.515 d.f. = 3			Location	−0.254	−1.975	0.048
	Specialist gran.	Region:Field	1.97×10^{-17}	Intercept	0.078	0.63	
	AIC = 181.394 d.f. = 3			L3 field	1.2×10^{-3}	2.43	0.015
ABUNDANCE	**Overall species**	Region:Field	0.613	Intercept	5.088	22.49	
	AIC = 8424.954			Management	0.067	0.25	0.801
				Location	0.042	1.54	0.125
				L3 field	3.2×10^{-3}	3.67	2.4×10^{-4}
	d.f. = 9			L3 buffer	0.015	0.16	0.847
				Man × Loc	−0.641	−20.21	$<2 \times 10^{-6}$
				Loc × L3f	-6.3×10^{-4}	−9.03	$<2 \times 10^{-6}$
				Loc × L3b	−0.058	−4.92	8.8×10^{-7}
	Overall gran.	Region:Field	0.911	Intercept	4.700	19.61	
	AIC = 263.515			Management	0.218	0.68	0.495
				Location	0.248	11.68	$<2 \times 10^{-16}$
	d.f. = 3			L3 field	2.4×10^{-3}	2.51	0.012
				Man × Loc	−1.069	−31.23	$<2 \times 10^{-16}$
	Specialist gran.	Region:Field	1.986	Intercept	4.128	10.11	
	AIC = 6462.362			Management	0.389	0.81	0.416
				Location	0.133	4.13	3.6×10^{-5}
				L3 field	4×10^{-3}	2.59	9.5×10^{-3}
	d.f. = 8			L3 buffer	−0.126	−0.73	0.463
				Man × Loc	−1.390	−33.95	$<2 \times 10^{-16}$
				Loc × L3b	0.040	3.19	1.4×10^{-3}

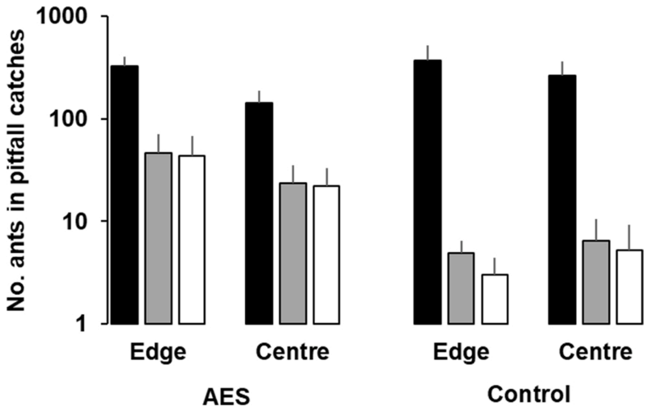

Fig. 2. Ant abundance (+SD) in relation to the management and trap location. Black: all ants; grey: generalist granivores; white: specialists granivores. Note logarithmic scale.

Pesticide applications can reduce the taxonomic and functional diversities of local insect communities (Brittain et al., 2010). Ant species richness did not respond to AES despite they include significant reductions in pesticide and fertilizer applications (Kleijn et al., 2012). Low species richness (Concepción and Díaz, 2019), or resilience to pesticides of the ant communities that occupy disturbed Mediterranean habitats to pesticides (Hevia et al., 2019), may be alternative explanations to this lack of effect. Fertilization has no significant effect on ant species richness on temperate grasslands, only affecting indirectly ants by altering plant communities (Heuss et al., 2019).

Ant communities occupying field centers were subsets of the ant communities of field edges, a fact that may be explained by a continuous spill over of colony founders or foragers from the surrounding landscape (Kleijn et al., 2011). Ant community composition should then be strongly dependent on community dynamics in the areas surrounding fields (Crist, 2009). Ecotones with large structural heterogeneity, such as hedgerows, have been found to improve regional biodiversity of both insects (Martin et al., 2019; Duelli, 1997) and weeds (Concepción et al., 2012b).

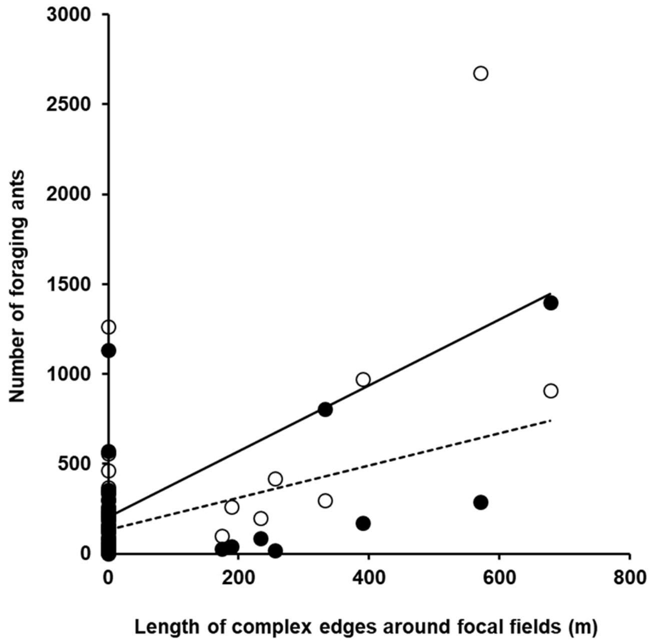

Fig. 3. Abundance of foraging ants in relation to the length of complex edges, with low shrubs and scattered trees, around focal fields. Black dots, pointed line: centre traps; white dots, continuous line: edge traps.

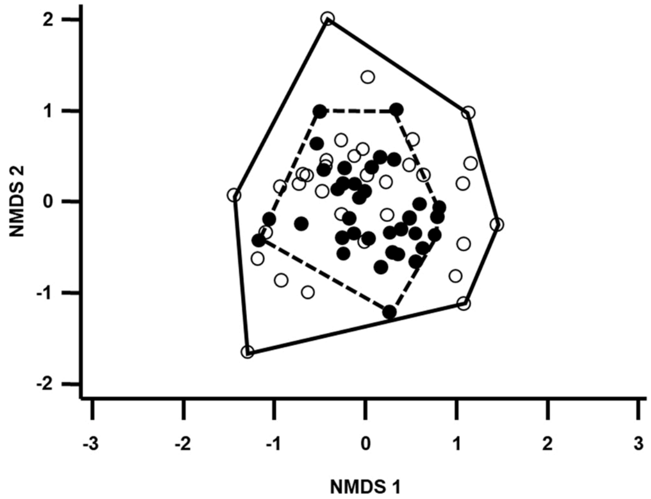

Fig. 4. Results of the non-Metric multivariant dissimilarity analysis comparing ant community composition according to trap location. Black dots, pointed line: centre traps; white dots, continuous line: edge traps. Polygons group samples according to trap location.

Field boundaries, together with uncultivated habitats, provide additional food resources and safer nesting places within agricultural landscapes (Concepción et al., 2012a, 2012b). Unploughed ground has been found essential for nest building in bee species (Steffan-Dewenter and Schiele, 2008), as well as for harvester ants in Mediterranean dry cropland (Diaz, 1991). Low shrubs within unploughed habitats are selected by ants, probably because shrubs enhance soil conditions for nest maintenance (Díaz, 1991). This fact may explain the key role of complex edges for ant distribution.

Landscape effects on arthropod communities are in turn related to provision of key ecosystem services (Bennett et al., 2006; Martin et al., 2019). Hevia et al. (2016) highlighted the importance of drove roads, complex lineal landscape structures typical of Mediterranean regions, on bee abundance and richness and on the pollination service in adjacent sunflower fields. Edge management for ants would enhance natural weed control in dry cereal croplands, as shown by the strong dominance of harvester ants. Seed predation rates of ants in these landscapes are much higher than those of other granivores such as birds or mice (Díaz, 1994). Seed predation by ants may be enough to control the populations of some weeds (Baraibar et al., 2009; Westerman et al., 2012), and would offset yield losses of cereals taken by foraging ants (Baraibar et al., 2011). However, seed removal rates strongly decline with distance to ant nests due to the central place foraging strategy of ants (Díaz, 1992), a fact that explain why foraging activity is concentrated near field edges. Higher weed abundance in AES fields that in controls (Concepción et al., 2012b), together with central place foraging from nests located mostly at complex field edges, may explain why harvester ants concentrate even more its foraging activity in AES fields than in controls.

Edge management plays a central role in many European conservation programs for agrarian landscapes (Dauber and Wolters, 2004), but it is essentially focused on maintaining conservation headlands, strips of ploughed land along field borders that are not sowed and harvested, or are sowed with seed mixtures of wild flowers to favor pollinators. As ploughing eliminates both nests and woody vegetation, conservation headlands would not be suitable to preserve ant communities in farmland and its potential service of weed control.

Preserving wildlife in croplands, and enhancing the ecosystem services they provide, requires incorporation of wildlife requirements into AES and evaluation of their performance (Díaz and Concepción, 2016). An increasing number of studies emphasize the need to adopt multi-scale approaches to evaluate the effect of AES on farmland biodiversity conservation (Concepción et al., 2012b). Guidelines to adapt policy tools to this reality must consider the necessities of defined target groups within landscape constraints (Díaz and Concepción, 2016). Our findings suggest that the conservation of the complexity of agrarian landscape could allow the maintenance of a greater richness and abundance of ants, potentially enhancing weed control. The promotion of uncultivated habitats within croplands for biodiversity and ecosystem service conservation, the so-called new “green architecture”, using compulsory tools of the CAP Pillar I, may be an even better alternative to tackle landscape-scale constraints (Concepción et al., 2020). A change in edge management prescriptions within agri-environmental policy is needed, promoting complex and stable edges rather than ephemeral headlands.

5. Authors’ contributions

MD and EDC designed the methodology and coordinated field and landscape data collection; HZ and FMA identified ant species; HZ, FMA, VH and EDC analyzed the data; HZ led the writing of the manuscript; all authors contributed to the drafts and to the final version of the manuscript and gave final approval for publication.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

This paper is a contribution to the EU Project QLK5-CT-2002–1495 ‘Evaluating current European Agri-environment Schemes to quantify and improve Nature Conservation efforts in agricultural landscapes (EASY)’. EDC is recipient of a Juan de la Cierva - Incorporación postdoctoral fellowship (IJCI-2016-30964).

References

Agosti, D., Majer, J.D., Alonso, L.E., Schultz, T.R., 2000. Standard methods for measuring and monitoring biodiversity. Biol. Divers. Handb. Ser.

Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., McKerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharntke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. Ecol. Lett. 23 https://doi.org/10.1111/ele.13576.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agric. Ecosyst. Environ. 74 https://doi.org/10.1016/S0167-8809(99)00028-6.

Altieri, Miguel Ay, Nicholls, C., 2011. Cambio climático y agricultura campesina : impactos y respuestas adaptativas. Rev. Agroecol. LEISA 24.

Baraibar, B., Westerman, P.R., Carrión, E., Recasens, J., 2009. Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. J. Appl. Ecol. 46 https://doi.org/10.1111/j.1365-2664.2009.01614.x.

Baraibar, B., Ledesma, R., Royo-Esnal, A., Westerman, P.R., 2011. Assessing yield losses caused by the harvester ant Messor barbarus (L.) in winter cereals. Crop Prot. 30 https://doi.org/10.1016/j.cropro.2011.05.010.

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: A meta-analysis. Proc. R. Soc. B Biol. Sci. 278 https://doi.org/10.1098/rspb.2010.1923.

Batáry, P., Dicks, L.V., Kleijn, D., Sutherland, W.J., 2015. The role of agri-environment schemes in conservation and environmental management. Conserv. Biol. 29 https://doi.org/10.1111/cobi.12536.

Bennett, A.F., Radford, J.Q., Haslem, A., 2006. Properties of land mosaics: implications for nature conservation in agricultural environments. Biol. Conserv. 133 https://doi.org/10.1016/j.biocon.2006.06.008.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. (Amst.). https://doi.org/10.1016/S0169-5347(03)00011-9.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. Basic Appl. Ecol. 11 https://doi.org/10.1016/j.baae.2009.11.007.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. https://doi.org/10.1177/0049124104268644.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature. https://doi.org/10.1038/nature11148.

Concepción, E.D., Díaz, M., 2011. Field, landscape and regional effects of farmland management on specialist open-land birds: does body size matter? Agric. Ecosyst. Environ. 142 https://doi.org/10.1016/j.agee.2011.05.028.

Concepción, E.D., Díaz, M., 2019. Varying potential of conservation tools of the Common Agricultural Policy for farmland bird preservation. Sci. Total Environ. 694 https://doi.org/10.1016/j.scitotenv.2019.133618.

Concepción, E.D., Díaz, M., Baquero, R.A., 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. Landsc. Ecol. 23 https://doi.org/10.1007/s10980-007-9150-2.

Concepción, E.D., Díaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012a. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49 https://doi.org/10.1111/j.1365-2664.2012.02131.x.

Concepción, E.D., Fernandez-González, F., Díaz, M., 2012b. Plant diversity partitioning in Mediterranean croplands: effects of farming intensity, field edge, and landscape context. Ecol. Appl. 22 https://doi.org/10.1890/11-1471.1.

Concepción, E.D., Aneva, I., Jay, M., Lukanov, S., Marsden, K., Moreno, G., Oppermann, R., Pardo, A., Piskol, S., Rolo, V., Schraml, A., Díaz, M., 2020. Optimizing biodiversity gain of European agriculture through regional targeting and adaptive management of conservation tools. Biol. Conserv. 241 https://doi.org/10.1016/j.biocon.2019.108384.

Crist, T.O., 2009. Biodiversity, species interactions, and functional roles of ants (hymenoptera: Formi-cidae) in fragmented landscapes: a review. Myrmecol. News 12.

Dauber, J., Wolters, V., 2004. Edge effects on ant community structure and species richness in an agricultural landscape. Biodivers. Conserv. 13 https://doi.org/10.1023/B:BIOC.0000014460.65462.2b.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agric. Ecosyst. Environ. 98 https://doi.org/10.1016/S0167-8809(03)00092-6.

Diaz, M., 1991. Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of Central Spain. Insectes Soc. 38 https://doi.org/10.1007/BF01241871.

Díaz, M., 1992. Spatial and temporal patterns of granivorous ant seed predation in patchy cereal crop areas of central Spain. Oecologia 91. https://doi.org/10.1007/BF00650332.

Díaz, M., 1994. Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. Oecologia 99. https://doi.org/10.1007/BF00317076.

Díaz, M., Concepción, E.D., 2016. Enhancing the effectiveness of CAP greening as a conservation tool: a plea for regional targeting considering landscape constraints. Curr. Landsc. Ecol. Rep. https://doi.org/10.1007/s40823-016-0017-6. Reports 1.

Duelli, P., Obrist, M.K., Schmatz, D.R., 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. Agric. Ecosyst. Environ. 74 https://doi.org/10.1016/S0167-8809(99)00029-8.

ESRI, 2000. ArcView GIS 3.2a. Environmental Systems Research Institute, Redlands, California, USA.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science (80-.). https://doi.org/10.1126/science.1111772.

Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodivers. Conserv. https://doi.org/10.1023/A:1008891901953.

Gómez, G., Espadaler, X., 2007. Hormigas Ibéricas. http://hormigas.org/.

Gonthier, D.J., Ennis, K.K., Farinas, S., Hsieh, H.Y., Iverson, A.L., Batáry, P., Rudolphi, J., Tscharntke, T., Cardinale, B.J., Perfecto, I., 2014. Biodiversity conservation in agriculture requires a multi-scale approach. Proc. R. Soc. B Biol. Sci. 281 https://doi.org/10.1098/rspb.2014.1358.

Heuss, L., Grevé, M.E., Schäfer, D., Busch, V., Feldhaar, H., 2019. Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. Ecol. Evol. 9 https://doi.org/10.1002/ece3.5030.

Hevia, V., Bosch, J., Azcárate, F.M., Fernández, E., Rodrigo, A., Barril-Graells, H., González, J.A., 2016. Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields. Agric. Ecosyst. Environ. 232 https://doi.org/10.1016/j.agee.2016.08.021.

Hevia, V., Ortega, J., Azcárate, F.M., López, C.A., González, J.A., 2019. Exploring the effect of soil management intensity on taxonomic and functional diversity of ants in Mediterranean olive groves. Agric. For. Entomol. 21 https://doi.org/10.1111/afe.12313.

Höldobler, B., Wilson, E.O., 2009. The Superorganism: the Beauty, Elegance, and Strangeness of Insect Societies. WW Norton & Company, London.

House, A.P.N., Burwell, C.J., Brown, S.D., Walters, B.J., 2012. Agricultural matrix provides modest habitat value for ants on mixed farms in eastern Australia. J. Insect Conserv. 16 https://doi.org/10.1007/s10841-011-9389-4.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. https://doi.org/10.1111/j.1461-0248.2005.00869.x.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H.G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends Ecol. Evol. (Amst.). https://doi.org/10.1016/j.tree.2011.05.009.

Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. B Biol. Sci. 276 https://doi.org/10.1098/rspb.2008.1509.

Lebas, C., Galkowski, C., Blatrix, C., Wegnez, P., 2017. Guía De Campo De Las Hormigas De Europa Occidental, first ed. Omega, Barcelona.

Legendre, P., Legendre, L., 2012. Numerical Ecology. Developments in Environmental Modeling. Elsevier.

Lobry De Bruyn, L.A., 1999. Ants as bioindicators of soil function in rural environments. Agric. Ecosyst. Environ. 74 https://doi.org/10.1016/S0167-8809(99)00047-X.

MA, Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Current Status and Trends, Vol. 1. Island Press, New York.

Mader, V., Diehl, E., Fiedler, D., Thorn, S., Wolters, V., Birkhofer, K., 2017. Trade-offs in arthropod conservation between productive and non-productive agri-environmental schemes along a landscape complexity gradient. Insect Conserv. Divers. 10 https://doi.org/10.1111/icad.12220.

Mader, V., Diehl, E., Wolters, V., Birkhofer, K., 2018. Agri-environmental schemes affect the trophic niche size and diet of common carabid species in agricultural landscapes. Ecol. Entomol. 43 https://doi.org/10.1111/een.12671.

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M.V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A.C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. https://doi.org/10.1111/ele.13265.

Pe’er, G., Zinngrebe, Y., Moreira, F., Sirami, C., Schindler, S., Müller, R., Bontzorlos, V., Clough, D., Bezák, P., Bonn, A., Hansjürgens, B., Lomba, A., Möckel, S., Passoni, G., Schleyer, C., Schmidt, J., Lakner, S., 2019. A greener path for the EU common agricultural policy. Science (80-.). https://doi.org/10.1126/science.aax3146.

Peck, S.L., Mcquaid, B., Campbell, C.L., 1998. Using Ant Species (Hymenoptera: Formicidae) as a Biological Indicator of Agroecosystem Condition. Environ. Entomol. 27 https://doi.org/10.1093/ee/27.5.1102.

Pérez-sánchez, A.J., Zope, D., Klimek, S., Dauber, J., 2018. Differential responses of ant assemblages (Hymenoptera: Formicidae) to long-term grassland management in Central Germany. Myrmecol. News 27.

Pollard, E., 1991. Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. Oikos 60. https://doi.org/10.2307/3544985.

Roy, D.B., Rothery, P., Moss, D., Pollard, E., Thomas, J.A., 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. J. Anim. Ecol. 70 https://doi.org/10.1046/j.1365-2656.2001.00480.x.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L.R., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science (80-.). https://doi.org/10.1126/science.287.5459.1770.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. Ecol. Lett. 16 https://doi.org/10.1111/ele.12128.

Steffan-Dewenter, I., Schiele, S., 2008. Do resources or natural enemies drive bee population dynamics in fragmented habitats? Ecology 89. https://doi.org/10.1890/06-1323.1.

Tarjuelo, R., Margalida, A., Mougeot, F., 2020. Changing the fallow paradigm: a win–win strategy for the post-2020 Common Agricultural Policy to halt farmland bird declines. J. Appl. Ecol. 57 https://doi.org/10.1111/1365-2664.13570.

Thomas, J.A., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos. Trans. R. Soc. B. https://doi.org/10.1098/rstb.2004.1585.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Westerman, P.R., Atanackovic, V., Royo-Esnal, A., Torra, J., 2012. Differential weed seed removal in dryland cereals. Arthropod. Interact. 6 https://doi.org/10.1007/s11829-012-9211-6.