Crops modify habitat quality beyond their limits

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ABSTRACT

Edge effect is a strong driver of change in fragmented landscapes. In the last few decades, agricultural land-use intensity at field scale has increased and, consequently, the edges between crops and natural vegetation matrix have sharpened. Interspersed crops produce now negative effects not only by direct habitat destruction, but also by inputs of agrochemicals that may spread their effects on the surroundings. These processes are taking place worryingly in steppe habitats in Iberian Peninsula where the high diversity of bird communities and other taxa they hold is at risk. The aims of this study were to evaluate the edge effect of crops on i) the microhabitat quality of a natural landscape matrix and ii) the space use of a threatened habitat-specialist steppe bird, the Dupont's lark (Chersophilus duponti). We carried out microhabitat sampling and bird surveys within and around crops interspersed in a typical Iberian shrub-steppe matrix during spring and autumn 2016 and spring 2017. Microhabitat quality was measured by sampling vegetation structure and arthropod biomass (as proxy of food availability) within and at increasing distances (1, 10 and 50 m) to seven crops. The intensity of space use by the Dupont's lark was estimated applying a Kernel density function on the spatial point pattern of the males' territories. Vegetation structure variables were summarized by Principal Components Analysis. Linear Mixed Models and model averaging were used to test for effects of distance to crop on microhabitat quality and space use by the Dupont's lark. Distance to crop significantly affected microhabitat quality. A patchy structure of herbaceous and shrub was found outside crops in all sampling dates, with more shrub cover and less herbaceous cover as the distance to crops increased. Biomass of hypogeous arthropods significantly decreased when the distance to crops was lower than 50 m. The intensity of space use by Dupont's lark varied according to the sampling date, being higher in spring, and as the distance to crops and the biomass of hypogeous arthropods increased. Negative effects of crops on the space use of this bird species might be shaped both by the effect of the crop itself and by its edge effect on hypogeous arthropods. Our results point to an edge effect of crops of 10–50 m on natural vegetation structure, arthropod availability and use of space by the Dupont's lark, which suggests that the effective area of optimal habitat available for true steppe species could be overestimated.

1. Introduction

Habitat fragmentation is a main research theme in conservation biology (Fischer and Lindenmayer, 2007) because it is one of the major threats to biodiversity (Bennett and Saunders, 2010). The negative effects of habitat fragmentation have been reported for community composition (Ewers and Didham, 2006), interpatch connectivity (Fagan, 2002), plant genetic diversity (González et al., 2020), vegetation dynamics (Pueyo and Alados, 2007), predator–prey dynamics (Batáry and Báldi, 2004), invertebrate richness and abundance (Parker and Mac Nally, 2002), suitable habitat for different species (Andrén, 1994), and lower productivity and breeding success of birds (Sheridan et al., 2020),

among others. Habitat fragmentation due to land-use changes have effects at different scales. On the one hand, a formerly continuous landscape is fragmented into multiple patches, thus breaking landscape continuity (Emmerson et al., 2016). On the other hand, the more is the intensity of land-use change, the higher is the difference between the patch itself and the surroundings (Moilanen and Cabeza, 2002; Fahrig, 2003). At this local scale, land-use change results in edge effects (Barbosa and Marquet, 2002), which is the result of the interaction between two adjacent ecosystems separated by an abrupt transition, called edge (Murcia, 1995). The edge effect may alter the structure and diversity of plant and animal communities in natural habitats surrounding the perturbation (Fahrig, 2003; Ewers and Didham, 2006). For example,

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previous studies have found that beetle abundance decreased from the patch center towards the edge (Barbosa and Marquet, 2002), and similar results were found for species number of Orthoptera, with a negative impact of edge effect up to 30 m from the edge (Bieringer and Zulka, 2003).

Agriculture is an example of land-use change and the main factor driving habitat fragmentation in Europe (Stoate et al., 2009). In the last few decades, agrarian intensification has transformed crops toward a higher productivity and profitability (Fernández and Corbelle, 2017; Serra et al., 2014) through a wider use of machinery and agrochemicals, among other farming practices (Concepción and Díaz, 2013) that increase homogenization at local scale. At a field-scale, these increases in land-use intensity suppose a drastic modification of habitat within the crops but also in their surroundings due to edge effect (Fahrig, 2003). In this sense, organisms can be affected by the presence of borders due to changes in abiotic (i.e. environmental conditions) and biotic conditions (i.e. food availability and habitat structure) (Murcia, 1995), which leads the species to occupy the central parts of the optimal habitat spots (Schlossberg and King, 2008). In the last few decades, several studies have demonstrated a direct link between crop-edge effect and habitat fragmentation (see Davies et al., 2001; Fletcher and Koford, 2002; Sheridan et al., 2020), reporting negative effects of intensification on different ecosystem components as plant diversity at local scale (Kleijn et al., 2009; Sans, 2007), plant taxonomic and functional diversity (Carmona et al., 2020), and animals in general (Emmerson et al., 2016).

Plant structure and food availability (i.e. arthropods in the case of insectivorous) are commonly used as direct indicators of habitat quality (e.g. Morales et al., 2008), as they are key drivers defining species distribution and population dynamics in birds (Oro et al., 2004; Perrig et al., 2014) and mammals (Barr and Wolverton, 2014; Hohmann et al., 2006). Thus, changes on habitat quality due to crop-edge effects should have effects on space use and population density of organisms, as the dramatic declines in both range and abundance of many farmland species along Europe (Hole et al., 2005), especially birds (Gayer et al., 2019), suggest. Indeed, there is broad knowledge that the agrarian intensification at landscape scale and the increase in land-use intensity at field scale are main drivers to steppe birds declines (Bowler et al., 2019; Suárez-Seoane et al., 2002; Traba and Morales, 2019). This fact is not only through a direct effect on bird numbers, but also on invertebrates abundance (Matsuda et al., 2001), which constitute a substantial part of the diet of many species during the breeding season and are indispensable for raising offspring (Boatman et al., 2004; Cramp and Perrins, 1994).

The Iberian shrub-steppes are one of the most singular habitats in the European Union (Suárez et al., 2006) and represent an important habitat of Iberian steppes (Ollero and van Staalduinen, 2012) due to the singular communities of plants, arthropods and birds they contain (Gajón, 2007; Suárez-Álvarez et al., 2000). Iberian shrub-steppes are landscapes where human activity (e.g. grazing, fire, pine afforestation and crops among others) have traditionally intervened (Suárez et al., 1992). Crops have been historically embedded into the shrub-steppes natural vegetation, generating a fragmented landscape with soft edges between crops and the surroundings due to the traditional low land-use intensity. This heterogeneous landscape provided spatial and trophic resource variability (Vasseur et al., 2013) that can be used by steppe birds (i.e. use of stubbles during summer, Suárez et al., 2008). In recent years, increases in land-use intensity as the use of machinery and agrochemicals have altered this traditional landscape. Recent studies have reported an increase in the surface of agricultural fields and in the use of agrochemicals as glyphosate in Iberian shrub-steppe (Traba, 2020) and suggested an association between crops, habitat fragmentation and loss of functionality in shrub-steppes (Santos and Suárez, 2005; Íñigo et al., 2008). Finally, strict specialist steppe birds, giving their high habitat specificity (Knick and Rotenberry, 1995), could be lastly affected by crops, not only at the landscape scale by direct loss of optimal habitat, but also by increasing the land-use intensity at crop scale, and thus altering the habitat quality in the surroundings of the crops. The effect of increasing land-use intensity on vegetation structure, arthropods biomass and true steppe birds beyond the crops has, to our knowledge, not been adressed in Iberian shrub-steppes, as in other agroecosystems (Guerrero et al., 2011). Moreover, we have found no studies providing information about distance of impact from the edge of the crop to the shrub-steppe.

Hence, the first goal of this study was to evaluate the effect of the edge between crops and the natural landscape matrix on habitat quality for insectivorous birds in terms of vegetation structure and food availability (arthropod biomass). Since the presence of agrarian inputs (herbicides, pesticides and even nutrients) has been detected in water, air and food (IARC, 2015), it seems reasonable that negative effects of crops and their associated practices on habitat quality may extend and be detected beyond the area strictly under cultivation. Thus, we predict that: 1) crops will have an effect on plant structure and food availability not only within the cultivated area but also beyond its limits, 2) these effects will decrease as the distance to the crop increases, and 3) the effect of crops on vegetation structure and food availability will change along the year due to seasonal variation (Arnaldos et al., 2010; McLaughlin and Mineau, 1995). The second goal is to disentangle the edge effect of crops and habitat quality on the use of space by steppe birds, using the threatened Dupont's lark (*Chersophilus duponti*) as a model species. The Dupont's lark is a strict shrub-steppe habitat specialist (Garza et al., 2005) with insectivorous habits (Cramp and Perrins, 1994) that may be affected by changes in its preferred habitat beyond the limits of the crops. We predict that the Dupont's lark will avoid crops if they reduce habitat quality, that is, a vegetation structure different from that expected in a natural shrub-steppe and lower food availability in terms of arthropod biomass. Thus, we expect an increase on the use of space by Dupont's lark associated with the distance to crops. These results may have relevant consequences on conservation strategies for this and other threatened coexistent steppe bird species.

2. Materials and methods

2.1. Study species

We selected the Dupont's lark as our study species because it is a threatened passerine (Gómez-Catasús et al., 2018) catalogued as Vulnerable at a world level (BirdLife International, 2020) and distributed over the Iberian Peninsula and Northern Africa in small and declining fragmented populations (García-Antón et al., 2019; Gómez-Catasús et al., 2018; Suárez, 2010). This species has strict habitat requirements: it selects flat natural shrub-steppes (<40 cm) with a slope less than 15% (Garza et al., 2005; Gómez-Catasús et al., 2019; Pérez-Granados et al., 2017; Seoane et al., 2006). In these habitats, cereal fields are usually interspersed in the shrub-steppe matrix and it has been described that Dupont's lark can use cereal crops outside the reproductive period (stubbles, Garza et al., 2005; Suárez et al., 2008). This may be due to a greater availability of arthropods in stubbles when compared to shrub-steppes (Suárez et al., 2008), as the Dupont's lark has insectivorous habits (Cramp and Perrins, 1994; Herranz et al., 1993; Talabante et al., 2015). The species has a territorial behavior during the reproductive period throughout the year (Garza et al., 2005). Previous studies have shown important effects of habitat fragmentation on the communication system of the species by decreasing song sharing among non-neighbors because of the lack of interactions among individuals isolated by habitat barriers (Laiolo and Tella, 2005). Moreover, recent studies have found a low degree of song sharing and microdialects within a population related to habitat fragmentation due to the presence of crops within a single habitat patch (Pérez-Granados et al., 2016).

2.2. Study area

The study was carried out in the "Tierra de Medinaceli" region, Soria province (central Spain; 41° 11′ N, 2° 26′ W, c. 1150 m a.s.l.; Fig. 1) in a
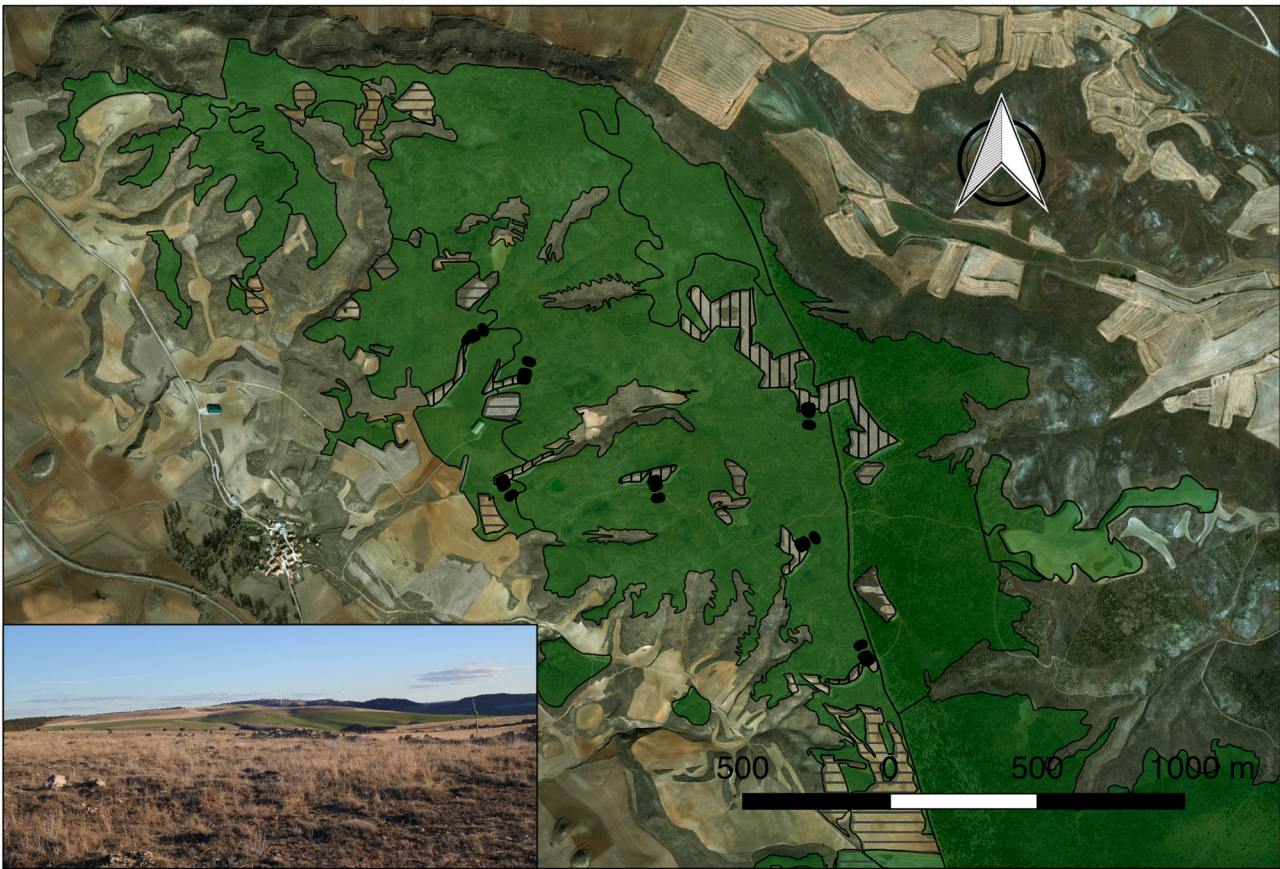
Fig. 1. Location of the study area. The map illustrates the studied patch with studied and active crop fields (vertical black lines polygons), non-active crop fields (horizontal black lines polygons) and Dupont's lark habitat (green). Black dots represent the sampling stations. A picture of the study area is shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

single large patch of Dupont's lark habitat of around 660 ha which holds around 60 males (own data, see below) located between the "Altos de Barahona" and "Páramo de Layna" Special Protection Areas (SPAs). This is a key patch to connect two of the most important areas for the Dupont's lark in Spain, holding some of the main European populations of the species (Suárez, 2010). Both this area and surrounding SPAs have suffered intense changes in the last decades, going from traditional extensive agriculture and livestock to both agrarian intensification and afforestation (Alados et al., 2004; Garza and Traba, 2016; Gómez-Catasús et al., 2016).

Climate is continental Mediterranean, with a mean temperature of 10.6 °C and a mean annual rainfall of 500 mm. Landscape is flat or gently undulated, dominated by a short shrub-steppe of *Genista pumila*, *G. scorpius*, *Thymus* spp. and *Linum* spp., and a scarce herbaceous cover of annual plants (Garza et al., 2005). There are cereal crops (approximately 7% of the area) interspersed in the shrub-steppe matrix, and ploughings and conifer afforestations receding the optimal habitat of Dupont's lark. A total of 27 crops are intermingled with natural shrub-steppe within this single habitat patch (Fig. 1) with a ranging size of 0.18–10.04 ha (mean ± SD = 1.23 ± 2.29 ha), and separated between 28.5 and 300 m. Some crops borders are low stone walls (15–30 cm) but mainly there are no physical borders. High land use-intensity associated with the use of machinery and agrochemicals as glyphosate has been reported in the area (Traba, 2020).

The study area holds an important steppe bird community, with the Little bustard *Tetrax tetrax*, Stone-curlew *Burhinus oedicnemus*, Great bustard *Otis tarda*, Pin-tailed sandgrouse *Pterocles alchata*, Montagu's harrier *Circus pygargus*, and Marsh harrier *Circus aeruginosus*, among others. During the breeding period the passerine bird community is mainly composed by the Dupont's lark *Chersophilus duponti*, Common

skylark *Alauda arvensis*, Thekla lark *Galerida theklae*, Calandra lark *Melanocorypha calandra*, Tawny pipit *Anthus campestris*, Western black-eared wheatear *Oenanthe hispanica* and Northern wheatear *Oenanthe oenanthe*, while during the non-breeding period only remain in the area the Dupont's lark, Rock sparrow *Petronia petronia* and some individuals of Thekla lark.

2.3. Locations of sampling stations

This study was carried out in and around seven crop fields, all included within the above-mentioned single Dupont's lark habitat patch. Crop fields (hereafter referred as crops) were selected according to three pre-assumptions: i) presence of suitable habitat for the species in the surroundings of crops (shrub-steppe with slope < 15%, Garza et al., 2005; Seoane et al., 2006); ii) high probability of finding Dupont's lark territories based on previous information about the space use by the species during the period 2008–2015 (Gómez-Catasús et al., 2019); and iii) minimum distance of 300 m between crop, according to the mean home range estimated for the species in the study area (8.1 ha, Garza et al., 2005). Sampling stations were located 10 m inside each crop and at increasing distances from the edge (1, 10 and 50 m; N = 28 sampling stations). Each sampling station consisted of three sampling points placed at 5 m intervals and located parallel to the crop edge (Supplementary Fig. 1). Studied crops size varied between 0.51 and 2.81 ha (mean ± SD = 0.95 ± 0.83 ha). Five of the active crops were planted with rye (*Secale cereale*) and two planted with barley (*Hordeum vulgare*) during the spring of 2016. They were harvested in the first fortnight of July 2016. Since this time, during autumn of 2016, winter of 2017 and spring of 2017, the crops remained in stubble and fallow, though no plant cover could be found due to the use of herbicides (see below).

We registered the use of agrochemicals in the crops by personal questioning to farmers. Crops were owned by two farmers but there were no differences in level of application of inputs between crops. Both farmers applied in the studied crops herbicide with glyphosate as active substance in a 1.5–2 L/ha dose twice a year (June and October), seed fertilizer NPK (Nitrogen-Phosphorus-Potassium) 8-24-8 or 15-15-15 in a 250 Kg/ha dose during November after direct sowing. These NPK complex are inorganic fertilizers with a high phosphorus content that has been shown to have a negative impact in bacterial community in long-term fertilization (Pan et al., 2014). Farmers also applied in the studied crops nitrogen at 32% in a single application of 200 Kg/ha during March-April and 2,4-D contact herbicide in 0.75 L/ha dose with MCPA (2-methyl-4-chlorophenoxyacetic acid) in 1 L/ha dose during April-May. Application of 2,4-D herbicide with MCPA reduces egg production in birds after remaining in treated crops during 14 days (Dobson, 1954) and is toxic to bees by the ingestion of nectar of the treated plants (Way, 1969).

2.4. Microhabitat variables sampling

In each sampling point, we measured vegetation structure and food availability while controlling the distance to the edge of the crop.

2.4.1. Vegetation structure

We conducted three vegetation samplings in spring and autumn 2016 and spring 2017. Autumn samples were used as an approach of vegetation structure during the winter due to the minimal variation between these periods (authors' own data). A set of vegetation variables were measured in 1×1 m (Supplementary Fig. 2). To determine horizontal plant structure, the covers of overall vegetation, shrub, herbaceous, detritus, rock, moss, lichen, and bare soil were visually estimated within each quadrat. Regarding the vertical plant complexity, we measured the maximum modal height (cm) and the number of contacts at 0–5 cm, 5–10 cm, 10–30 cm, and above 30 cm (see Morales et al. (2008) and Gómez-Catasús et al. (2019) for a similar approach).

2.4.2. Food availability

Arthropod biomass was measured in April, May, June and October 2016, and February, April, May and June 2017, thus completing a full annual cycle with two breeding seasons. In each sampling point a pitfall trap to collect epigeous community was placed next to the 1×1 m quadrats (i.e., three pitfall traps per sampling station). Pitfall traps were transparent plastic cups (220 ml; 70 mm diameter, 100 mm depth), with holes in the upper part to prevent flooding in case of heavy rain. Plastic cups were protected by a PVC cylinder to avoid trap collapse. They were filled with 120 ml of 40% ethylene glycol and a drop of liquid soap to reduce surface tension (Schmidt et al., 2006; Topping and Odderskaer, 2004). After a week, epigeous arthropods were collected in plastic tubs with 70% ethanol. At the moment of collecting pitfall traps, we used sweep nets along the longest distance between pitfall traps (10×2 m band) to sample flying arthropods and other species for which pitfall traps are not a suitable sampling method. This combined system has been proven as an effective method for the capture of a broad spectrum of epigeous and flying arthropods (Traba et al., 2007). At this moment, coprophagous arthropods were sampled with one pitfall trap per sampling station using 200 g of fresh sheep dung provided by local farmers as bait and they remained active 24 h. We only identify those arthropods considered as coprophagous: order *Coleoptera* family *Scarabaeidae* (*Gymnopleurus sp.*, *Onthophagus sp.* and *Scarabeus sp.*), and order *Diptera* suborder *Brachycera*. Finally, the biomass of hypogeous arthropods was measured in February, April, May and June 2017, in 20×20 cm and 2 cm depth soil samples next to pitfall traps. Samples were stored in plastic bags and sieved and identified before 48 h to avoid organic degradation. Oligochaetes were also identified because some studies highlight their importance in steppe birds' diet (Buchanan et al., 2006).

Arthropods were identified in the laboratory, taking as an Operational Taxonomic Unit (OTU) the order level for all taxa, except for *Coleoptera* order, which were identified to family or species level. Corporal length of specimens, excluding legs, antennae, and other appendices, was measured to obtain overall biomass for each group of arthropods applying the Hódar specific equations (Hódar, 1996). For oligochaetes, we applied the biomass equation proposed by Collins (1992). In each sampling period, biomass per OTU was calculated as the mean values per station, except in the case of coprophagous biomass since only one sampling point was located per station. Lastly, total biomass per OTU during the spring when three samples were taken (April, May and June) was estimated as the mean of the means of the three sampling periods. Again, see Morales et al. (2008) and Gómez-Catasús et al. (2019) for a similar approach.

2.5. Dupont's lark censuses

We carried out bird censuses by foot transects to determine bird abundance and spatial location during the breeding and non-breeding period (April, May, June and October 2016, and February, April, May and June 2017). We located three transects of 2 km length (Fig. 2A) crossing preferred areas for the species within a 500 m maximum detection band on each side. They were performed during its peak of activity (1 h before dawn) (Pérez-Granados et al., 2018) and spanned around 1 h. Singing males were mapped (Fig. 2A) by georeferencing with GPS (error ± 5 m) (see Pérez-Granados and López-Iborra (2017) for a detailed description). Each transect was repeated 4 times during the breeding season, alternating the starting point with the aim of registering the maximum singing activity in the species throughout the censuses (Pérez-Granados and López-Iborra, 2017). Autumn and winter transects were walked once. The number of breeding territories was estimated by mapping method, while winter and autumn observations refer to the number of recorded males in the single transect. Previous studies have demonstrated that a single transect is able to detect over 95% of the territories defined by the mapping method (Pérez-Granados and López-Iborra, 2017), and thus we consider that our data can be fairly compared.

2.6. Data treatment and analysis

Variables were log-transformed to achieve requirements of normality and homoscedasticity (Siegel and Morgan, 1996) and standardized (mean = 0, standard deviation = 1) to account for differences in the scale of measure. We incorporated to the analyses those arthropod groups with a mean contribution equal or higher than 4% of the total biomass collected in order to avoid overparameterizing the models with rare arthropods groups. Due to the high proportion of ants found in the samples, order *Hymenoptera* family *Formicidae* was considered as an independent group.

We carried out Principal Components Analyses (PCA) on vegetation variables in order to summarize them (see mean and SD of original variables in Supplementary Table 1), avoiding collinearity problems and enabling their interpretation in the form of ecological gradients (see Morales et al. (2008) and Reverter et al. (2019) for a similar approach). PCA was performed separately on horizontal and vertical plant structure variables (Supplementary Fig. 2), using a covariance matrix for horizontal structure as all variables were in the same units of measure, and a correlation matrix for vertical ones because the units of measure differed. In each PCA, the scores of the components with eigenvalue > 1 were retained. Then, scores retained were used as predictors in downstream analyses. PCA were fitted using SPSS Statistics 21 software (IMB Corp. Released, 2012).

Intensity of space use by the Dupont's lark was calculated by means of a Kernel Density Estimation (KDE). KDE was conducted for each sampling period employing the locations of Dupont's lark singing males for each period (50 males in spring 2016, 43 in autumn 2016, 17 in winter 2017 and 57 in spring 2017; Fig. 2A, see similar approach in
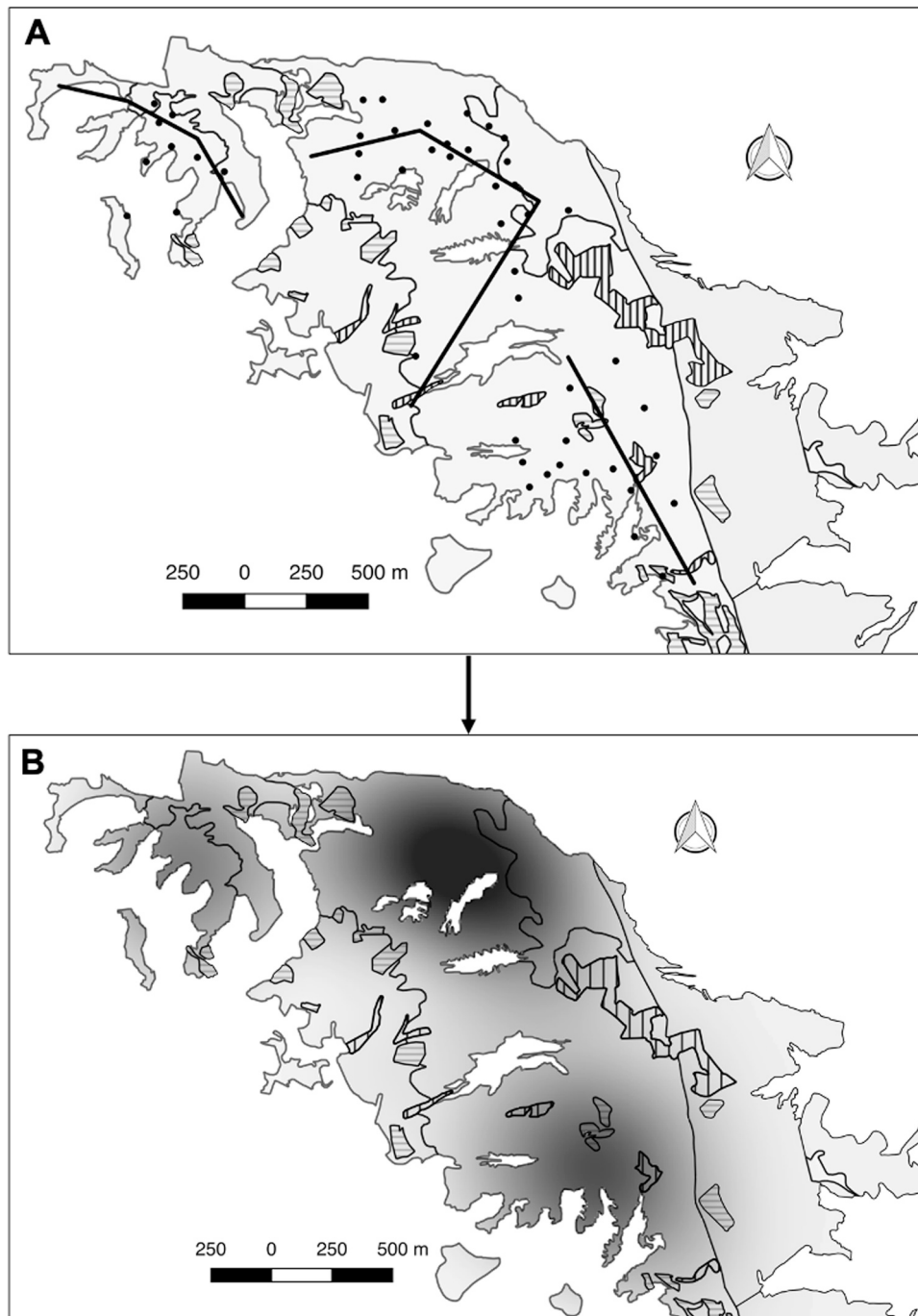
Fig. 2. Workflow to estimate intensity of space use by Dupont's lark: (A) black lines illustrate the three censuses transects, black dots represent Dupont's lark singing males mapped and (B) a gradient of the intensity of space use by Dupont's lark (greyscale) estimated by KDE for the spring of 2016 from high (dark grey) to low intensity of space use values or absences (white).

Gómez-Catasús et al. (2019)). KDE gives higher probability values to those areas with a greater number of territories, adjusting the assigned values depending on the smoothing parameter (Worton, 1989). We estimated a KDE for each season using the Kernel Density Estimation function of SAGA, in QGis 2.18 (QGis Development Team, 2017) with a smoothing factor of 600 m in accordance with Dupont's lark maximum home range (37.3 ha, Garza et al., 2005) and 10×10 m cell size in order to find differences in the intensity of space use at different distances to crops (i.e., 1, 10 and 50 m). After we calculated the KDE for each period, we extracted a value of intensity of space use (probability) for each sampling station (N = 28) in each period using the Point Sampling Tool implemented in QGis 2.18.28 (see for example KDE for

spring of 2016 in Fig. 2B). Finally, a single value of space use intensity per sampling station per sampled period was calculated as the mean probability value for its three sampling points.

Linear Mixed Models (LMMs hereafter) were adjusted to evaluate the effect of season and crop distance on habitat quality. We fitted one model for each habitat quality response variable: biomass of epigeous, coprophagous and hypogeous arthropods, and plant structure axis resulting from PCA.

Then, we built an LMM to disentangle the effects of both distance to crops and habitat quality on the intensity of space use by Dupont's lark, using as response variable the KDE values. Season and distance to crop and the interaction between both factors were included as predictors. In

order to avoid overparameterization, three LMMs were sequentially adjusted, one for each set of predictors with ecological sense (Table 1). Lastly, a final LMM was adjusted introducing only those significant variables in each partial model.

Best-fit models were selected attending to Akaike Information Criterion corrected for small samples (AICc). Akaike weights (w_i), representing the relative probability for model i to be the best among all considered models, were calculated for the subset of models having Δi (AICcbest - AICci) < 7 (Burnham et al., 2011). In those cases where several models were included in this interval, model averaging was employed to obtain for each predictor the weighted weight of its estimator (coefficient), the standard unconditional error according to the revised formula of Burnham and Anderson (2004) and its z and p-values, which allow us to identify significant effects (Burnham and Anderson, 2002). For this subset of models, the averaged estimators of the predictors were calculated (Burnham and Anderson, 2002). In the case where only one plausible model was found within the AICc interval, that single model with the significant variables was adjusted. Crop identity (seven levels) and sampling station (28 levels) were considered as random factors in all the analyses, the latter in order to take into account the design of repeated measures (Cayuela, 2015).

All the statistical analyses were performed using the *lme* function of the *nlme* package (Pinheiro et al., 2017) for fitting LMMs, and *dredge* and *model.avg* functions of the *MuMIn* package (Barton, 2011) to generate model set and perform model averaging in the free R software (v. 3.4.1; R Core Team, 2017).

3. Results

Five taxa of epigeous arthropods had a mean contribution biomass equal or higher than 4% (Supplementary Table 2). During the breeding season of 2016 and 2017, the mean biomass of epigeous arthropods was of 2593.33 mg/m^2 per day, compared to 1099.62 mg/m^2 per day collected during the non-breeding season, which means a food availability decrease of 57.59%. Hypogeous arthropod biomass showed a decrease of 50.89%: 5.03 mg/m^2 per day in the spring of 2017 compared to 2.47 mg/m^2 per day in the winter of 2017. The biomass of coprophagous arthropods showed a decline of 66.11.%: 248.90 mg/m^2 per day collected during the breading season compared to 84.35 mg/m^2 per day registered in the non-breading season.

3.1. PCA analysis - plant structure

The PCA on horizontal plant structure extracted two axes with eigenvalues > 1 (80.09% of total variance), explaining 62.55% and 17.54% respectively. The first axis VegHor-1 showed a gradient from sampling stations dominated by detritus (−0.963) to those with a high total plant (0.959) and shrub cover (0.654), and the second axis VegHor-

2 a gradient from shrub (−0.738) to herbaceous cover (0.775) (Supplementary Table 3, Supplementary Fig. 2). The PCA on vertical structure variables extracted two axes with eigenvalues > 1 (83.50% of total variance), which explained 50.44% and 30.06%, respectively. The first axis VegVer-1 indicated a gradient of high vertical complexity at intermediate heights, typical of shrub habitats, and the second axis VegVer-2 showed a vertical complexity gradient at maximum heights (Supplementary Table 4, Supplementary Fig. 2), typically represented by cereal crops.

3.2. Effect of sampling date and distance to crops on microhabitat quality

3.2.1. Plant structure

In relation with the LMMs built to test the effect of sampling date and distance to crops on plant structure, only one model was included in the 7 points AICc interval for VegHor-1 and two models were included for VegHor-2, VegVer-1 and VegVer-2 (Supplementary Table 5), so model averaging was applied. Sampling date had a significant effect on VegHor-1, VegHor-2, and VegVer-1. Differences between dates in these axes were associated to the presence of active crops in the spring of 2016, and therefore with a greater total plant and shrub cover (i.e., VegHor-1; Supplementary Fig. 3A) and vertical complexity at all heights (i.e., VegVer-1; Supplementary Fig. 3C). In the rest of sampling dates (autumn 2016, winter 2017 and spring 2017) crops were found in stubble and fallow and therefore with a greater detritus cover (i.e., VegHor-1; Supplementary Fig. 3A), lower herb cover (i.e., VegHor-2; Supplementary Fig. 3B) and vertical complexity (i.e., VegVer-1; Supplementary Fig. 3C). No differences were detected on vertical complexity at maximum heights (above 30 cm) between sampling dates (i.e., VegVer-2; Supplementary Fig. 3D). Distance to crop had a significant effect on both horizontal and vertical vegetation structure axis (Supplementary Fig. 4). VegHor-1 axis values were significantly lower (i.e. higher detritus cover) within the crop (i.e. distance 0 m) than outside (Supplementary Fig. 4A). VegHor-2 values were lower (i.e. higher shrub cover and lower herbaceous cover) far away from the crop (i.e. distance 10 and 50 m, Supplementary data. 4B). Therefore, a patchy structure of herbaceous and low scrub was found outside crops, with greater shrub cover and less herbaceous cover as the distance to crops increased (i.e. distance 50 m). Higher values of VegVer-1 (i.e. complexity at all heights) were observed at 1 m from crops than at the remaining distances (Supplementary Fig. 4C). VegVer-2 axis (i.e. complexity at maximum heights) showed a tendency to be lower outside crops (i.e. distances of 1, 10 and 50 m, Supplementary data. 4D), because natural steppes surrounding crops are dominated by low shrubs.

3.2.2. Food availability

The LMMs built to test the effect of sampling date and distance to crop on both epigeous and coprophagous arthropod biomass included only one model in the 7 points AICc interval for each analysis. Sampling date had a significant effect on the biomass of epigeous ($\chi2 = 237.52$; P < 0.001) and coprophagous arthropods ($\chi2 = 540.20$, P < 0.001). Epigeous arthropods were significantly lower in winter (t = −11.80; P < 0.001) and in autumn (t = −2.99; P < 0.001), when compared to spring (Fig. 3A). Coprophagous arthropods were lower in the winter of 2017 (t = −21.86; P < 0.001) and significantly higher in the spring of 2016 (t = −11.93; P < 0.001, Fig. 3B). However, the distance to crop did not have an effect on the biomass of epigeous and coprophagous arthropods.

Two models were within the AICc interval considered when analyzing the effect of sampling date and distance to crops on hypogeous arthropod biomass, so model averaging was applied (Supplementary Table 6). In this case, both sampling date and distance to crop had a significant effect on the biomass of hypogeous arthropods, being significantly higher in the spring of 2017 (Z = 5.94; P < 0.001, Fig. 3C) and at 50 m away from crops (Z = 2.64; P < 0.05, Fig. 4).

Table 1

Explanatory variables set incorporated in the partial LMMs in order to analyze the effects of habitat quality and crops on the use of space by the Dupont's lark.

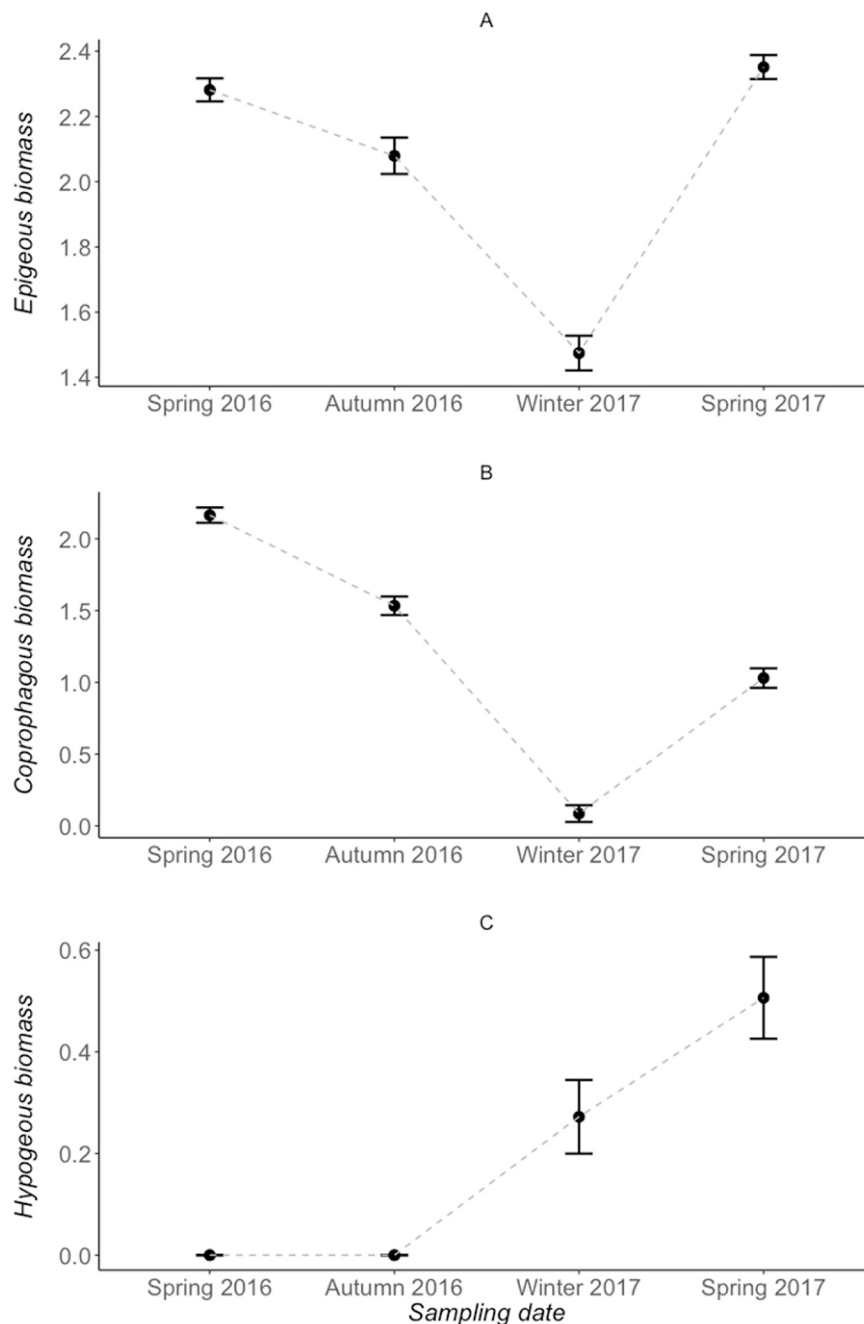| Set	Variables
Context	Sampling date (spring 2016, autumn 2016, winter 2017, spring 2017)
	Distance to crops (0 m, 1 m, 10 m, 50 m)
Vegetation structure	Horizontal structure axis 1 – VegHor-1 (gradient from detritus cover to total plant and shrub cover)
	Horizontal structure axis 2 – VegHor-2 (gradient from shrub to herb cover)
	Vertical structure axis 1 – VegVer-1 (gradient of high vertical complexity at intermediate heights)
	Vertical structure axis 2 – VegVer-2 (gradient of vertical complexity at maximum heights)
Food availability	Epigeous biomass
	Hypogeous biomass
	Coprophagous biomass

Fig. 3. Graphic display of the LMMs showing the effect of sampling date on the biomass of: (A) epigeous, (B) coprophagous and (C) hypogeous arthropods. Mean ± standard error of these three arthropod groups is depicted.

3.3. Effects of crops and habitat quality on the space use of Dupont's lark

After fitting the three partial LMMs, significant variables were incorporated in the final model (i.e. sampling date, biomass of epigeous, hypogeous and coprophagous arthropods and VegHor-2; see Supplementary Table 7). Eight out of 64 models generated to evaluate the factors affecting the intensity of space use by Dupont's lark presented an ΔAICc < 7 (Supplementary Table 8). Intensity of space use by Dupont's lark was significantly higher in the spring of 2017 compared with the other seasons (Table 2, Fig. 5A) and significantly greater 50 m away from crops (Table 2, Fig. 5B). Intensity of space use was positive and significantly related to hypogeous arthropod biomass (Table 2).

4. Discussion

Our results suggest a negative effect of crops beyond its limits by modifications on vegetation structure and food availability (see summary outline in Fig. 6). This result is in line with previous studies that have detected negative effects of increases in land-use intensity on arthropods (Boatman et al., 2004; Botías and Sánchez-Bayo, 2018; Dubey et al., 2020; Sánchez-Bayo and Wyckhuys, 2019), which may lead to lower food resources for insectivorous birds. This edge effect on habitat quality affects habitat-use patterns by the Dupont's lark, as a lower intensity of space use was detected in crop surroundings (Fig. 6). These results agree with earlier research, which demonstrated effects of habitat fragmentation (Gómez-Catasús et al., 2019; Laiolo and Tella, 2005; Pérez-Granados et al., 2016) and habitat quality (Gómez-Catasús
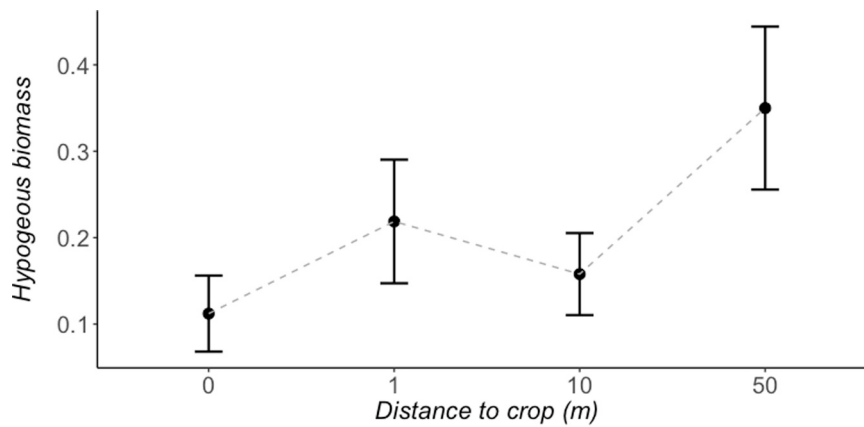
Fig. 4. Graphic display of the LMMs showing the effect of distance to crop fields on the biomass of hypogeous arthropods. Mean ± standard error is shown.

Table 2

Averaged coefficients of the eight selected mixed models (ΔAICc < 7) performed to evaluate the effect of distance to crop fields, sampling date and habitat quality variables on the intensity of space use by the Dupont's lark. Only variables (or levels within categorical variables) with significant effects are presented. Average regression coefficient (Value), standard error (SE), Z-statistic (Z), and p-value (p) are shown. Intercept correspond to spring 2016 and 0 m distance as reference level.

	Value	SE	Z	p
Intercept	0.33	0.31	1.06	0.29
Autumn 2016	-0.27	0.08	3.40	< 0.01
Winter 2017	-1.27	0.13	9.90	< 0.01
Spring 2017	0.39	0.11	3.51	< 0.01
Distance 50 m	0.24	0.07	3.35	< 0.01
Hypogeous arthropod biomass	0.09	0.03	2.77	0.01

et al., 2019) on the studied species, as well as on the space use by other larks (Bosco et al., 2020; Csikós and Szilassi, 2020).

4.1. Effects of seasonal variation on habitat quality and on Dupont's lark space use

As expected, seasonal variation affected arthropod biomass, vegetation structure, and the intensity of space use by the Dupont's lark. Changes in horizontal vegetation structure were exclusively associated to the presence of active crops in the spring of 2016 and to the presence of stubbles and fallows in the rest of sampling dates (autumn 2016, winter 2017, and spring 2017). In the case of arthropod biomass, however, a significant decrease was found during autumn and winter, which may be due to natural fluctuations caused by the ectothermic character of arthropods and their constraints to fulfil their physiological functions at low temperatures (Arnaldos et al., 2010). This decline in arthropod biomass may have important implications for community dynamics since changes in trophic resources may affect food web dynamics over time (Doblas-Miranda et al., 2007). Thus, a decrease in food availability during the winter could negatively affect survival, body condition, and future reproductive success (Buchanan et al., 2006) in species that remains in its breeding territories the whole year, such as the Dupont's lark (Gómez-Catasús et al., 2016). The decrease in food availability during the winter could be partially compensated by the reduction in the number of potential competitors for food resources, since most of the steppe species co-occurring with Dupont's lark during spring are migratory (de Juana and Suárez, 2020).

In the case of the intensity of space use by the Dupont's lark, our results showed a decrease during winter. This may be due to winter movements (Suárez et al., 2006) or due to a compromise between singing and energy limitations (Mathot et al., 2015). Apparently, vocal activity rate is linked to ambient factors (Vokurková et al., 2018) that in the study area could correspond with low temperatures; consequently, a lower vocal activity rate during winter could contribute to increase the long-term survival probability (Vokurková et al., 2018), but also providing a lower probability of detecting the species. Intensity of space use during autumn was similar to that estimated during the breeding season, which may be related to the similar vocal activity rate of the species during breeding and post breeding periods (Pérez-Granados et al., 2019).

4.2. Effects of crops on habitat quality

The present study reveals a relevant effect of crops on vegetation structure in its surroundings, as shrub cover decreases while herbaceous cover increases with the proximity to the crop. This edge effect of crops on vegetation structure is probably dependent on the intensity of agricultural practices (Sans et al., 2013) due to the use of herbicide and other agrarian inputs. Herbicides and other agrochemicals differentially affect shrubs and herbs (Boutin and Jobin, 1998), which may have promoted the last ones at close (1 m) distance from the crop.

The effects of crops on vegetation structure may have consequences on the arthropod composition and abundance. Indeed, crops had an effect on food availability (i.e. arthropod biomass), though their effects varied between arthropod groups. Epigeous and coprophagous arthropods were not affected by crops, while the biomass of hypogeous arthropods was lower in the crop surroundings. This may be due to the fact that epigeous and coprophagous arthropods have higher mobility than hypogeous (Simons et al., 2015). A higher mobility allows to avoid negative effects of crop intensification, as well as increases the potential for recolonization after disturbance (see e.g. Dziock et al. (2011)). Moreover, as coprophagous arthropods are attracted to the bait (see for instance Larsen and Forsyth (2005)), the effect of crops on this group is pretty difficult to evaluate.

On the other hand, hypogeous arthropods have lower mobility, so this group might be more sensitive and vulnerable to any agricultural disturbance activity on the crop and surroundings. Arthropod species can be affected by herbicide application due to the loss of their host plants (e.g. Sans, 2007; Sotherton, 1982; Taylor et al., 2006), to the elimination of their food sources (Wilson et al., 1999) or to a decrease in fertility (Chiverton and Sotherton, 1991). The extended application of glyphosate (Kolpin et al., 2006; Mañas et al., 2009) and other agrochemicals (Traba, 2020) despite the low productivity of yields in the study area, usually below 2000 kg/ha (Serra et al., 2014; authors' unpublished data), could be behind the negative impacts of crops detected on hypogeous arthropods, as it has been described for other groups of arthropods (Balbuena et al., 2015; Botías and Sánchez-Bayo, 2018).
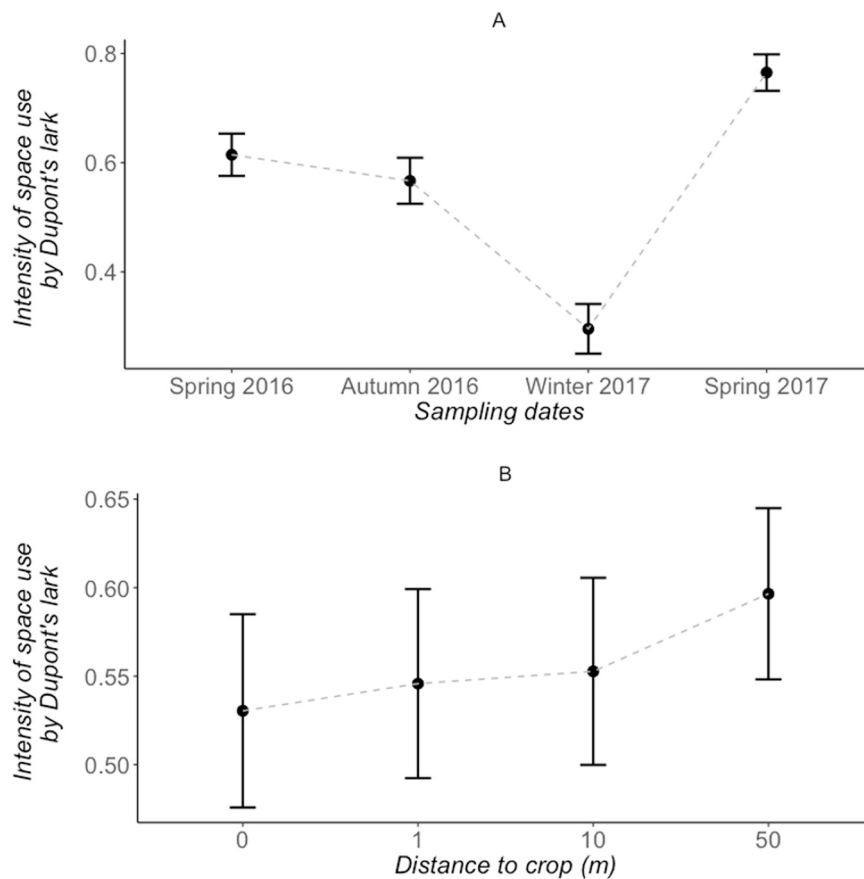
Fig. 5. Relationship between the intensity of space use by the Dupont's lark and (A) sampling date (season) and (B) distance to crop fields. Mean ± standard error is depicted.
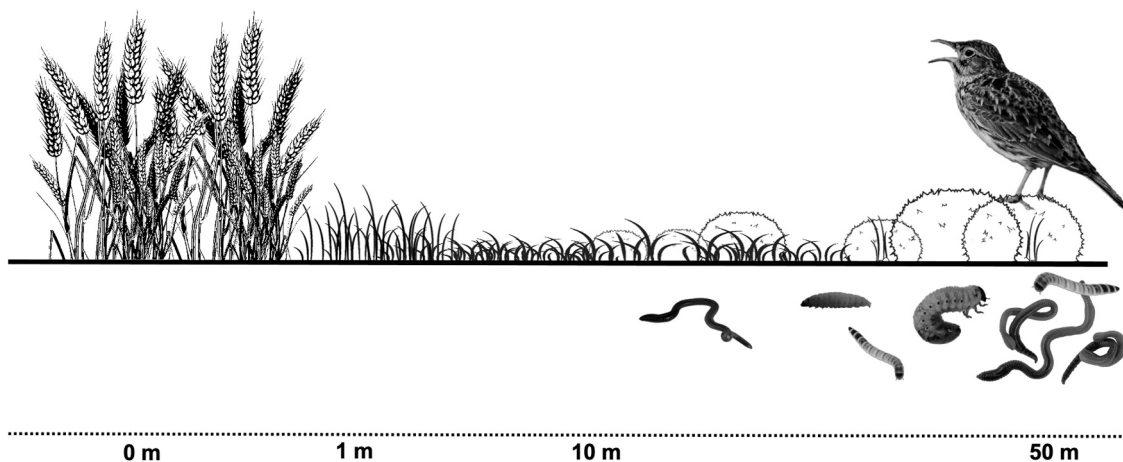

Fig. 6. Summary outline resulting from significant relations of the effects of crops on vegetation structure, hypogeous arthropod biomass and intensity of space use by Dupont's lark.

4.3. Effects of crops on Dupont's lark space use

Crops had a negative effect on the use of space by the Dupont's lark as the intensity of space use by the species increased with the distance to crops. The Dupont's lark is a habitat specialist species (Gómez-Catasús et al., 2019; Reverter et al., 2019) that requires a high percentage of shrub cover (see for example Garza et al. (2005), Seoane et al. (2006), Pérez-Granados et al. (2017)), so the direct avoidance of crops may partly explain this result. Edge effects generated by unsuitable habitats (Forman et al., 2003) have been previously associated with a decreased

habitat quality for habitat specialists (Burke and Nol, 1998; Mills, 1995), which finally diminish the effective area of suitable habitat. Thus, edges may negatively affect productivity and breeding success, decreasing population growth rate (Sheridan et al., 2020) and ultimately, space use in the surroundings of crop edges. Landscapes dominated by small or irregular patches with a large amount of edges are unlikely to provide suitable habitat for shrubland birds, and their effects pervade the entire landscape (Porensky and Young, 2013; Schlossberg and King, 2008). This leads to higher shrubland bird abundance in patch centers than along edges (Schlossberg and King, 2008). Lastly, the herbicide applied

in the studied crops can also have direct deleterious effects on birds due to the reported endocrine disrupting aspect of glyphosate (Gasnier et al., 2009; Rendón-Von Osten et al., 2005; Vyas et al., 2007), though more studies are needed in this regard.

4.4. Effects of habitat quality on Dupont's lark space use

The indirect effect of crops on the Dupont's lark through changes on habitat quality is reflected by the positive effect of food availability (i.e. hypogeous biomass) on the intensity of space use by Dupont's lark. Both the biomass of hypogeous arthropods (see above; Fig. 4) and the intensity of space use by the Dupont's lark (Fig. 5B) increased with the distance to crops, being significantly greater at 50 m from the crop edge. These results are in agreement with the pattern described for other birds (Boatman et al., 2004; Newton, 2004), which establish their breeding territories according to their quality (Muller et al., 1997) in terms of food availability and vegetation structure (Morales et al., 2008), Dupont's lark males could defend a territory with sufficient trophic resources, which in the case of hypogeous arthropods corresponds to distances greater than 10 m to crops. Moreover, *Oligochaeta* biomass has been described as part of moorland birds' diet (Buchanan et al., 2006), being significant and permanently higher than other invertebrates (Tucker, 1992). Thus, Dupont's lark could select areas with higher hypogeous biomass as a permanent trophic resource and therefore, this group of arthropods would be playing a key role in the maintenance of the species throughout the year. Future studies on the diet of the species should be addressed to solve these hypotheses.

Our findings predict a negative scenario for the species if an expansion on the cultivated area occurs. According to our results, the crop affection area is not limited to the cultivated extension, spreading an edge effect over at least 10–50 m away from crops that increase the habitat fragmentation. Thus, management and conservation measures must consider an affection area of, at least, those mentioned 10 m, and advisably, 50 m around crops in order to evaluate optimal habitat availability for the species (García-Antón et al., 2019). These results suggest that agricultural intensification, even at the field scale, may be one additional factor behind the decline of this threatened species, although further research is needed in order to estimate direct effects of crops on arthropods. Our results point to that increases in land-use intensity may affect steppe birds populations by reducing the optimal habitat, promoting within-patch erosion, and in consequence, increasing habitat fragmentation.

This is, to our knowledge, the first documented report about negative effects of crops on the natural matrix vegetation structure of shrub-steppes in the surroundings of the crops. Our results suggest the need for further research to find a balance between crop yield and the conservation of threatened species. Application of high-level doses of herbicides and other agrochemicals can have effects not only in the crop itself but also extend beyond their limits, affecting other ecosystem components different that the originally addressed. As shown by our results, this can be observed even in apparently extensified landscapes but with high land-use intensity at the field scale. Thus, the next generation of agrarian policies to be implemented under CAP after 2020 should encourage the decrease in agrochemicals inputs. Local scale processes have a critical importance in the total persistence of populations (Hanski et al., 1997) and thus conservation strategies of Dupont's lark and other threatened coexisting steppe birds should be aimed at improving the habitat quality in terms of vegetation structure and food availability within the patches, as also recommended by recent studies (Gómez-Catasús et al., 2019; Pérez-Granados et al., 2017), and specifically, undertake studies and action to increase hypogeous arthropods biomass, a key resource that seems to determine the occurrence of Dupont's lark.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107542.

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