



Spatial and seasonal variation in occupation and abundance of common vole burrows in highly disturbed agricultural ecosystems

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Abstract

Understanding how species respond to disturbance in human-modified ecosystems is critical for management and conservation of biodiversity in the Anthropocene. In agroecosystems, human disturbances severely modify the habitat of species, particularly for those that live in burrows. The common vole *Microtus arvalis* (Pallas, 1778) is a semi-fossorial microtine, which often exhibits large abundance fluctuations, becoming an agricultural pest in peak years. We evaluated how both agrarian disturbances (via types of crop and their management) and landscape heterogeneity influenced the abundance of common vole burrow systems along a yearly cycle, at the field and landscape scales. We seasonally recorded the number of burrows and their recent occupation in circular plots of 200-m radius including different types of crops in intensified agrarian landscapes in NW Spain. Our results showed a marked seasonal and spatial pattern in both total abundance and abundance of occupied burrows. After a population peak year, only 31% of burrows were occupied across the year (from 41% in spring–summer to 12% in autumn). The crop type and its management in relation to soil disturbance were the main factors driving seasonal and spatial dynamics of burrow abundance at the field and landscape scale. Alfalfa fields held the highest abundance of both total and occupied burrow systems across the year, while fields of traditional-tilled cereal retained the lowest. As a result, at the landscape scale, plots with a greater surface devoted to traditional cereal crops maintained a lower relative number of burrow systems. Regarding the landscape structural heterogeneity, plots with longer length of field margins and lower area of watercourses maintained higher abundance of burrow systems. An adequate landscape-scale planning of crop types, agricultural practices, and distribution of non-crop habitats could be a promising sustainable method to reduce the risk of crop-damaging vole plagues.

Keywords Agricultural pest · *Microtus arvalis* · Multi-scale approach · Small mammal · Soil perturbation

Introduction

Disturbances are one of the main drivers of spatial and temporal heterogeneity in ecosystems and landscapes (Turner 2010). Since disturbances change the availability of resources

and/or habitat structure, they affect the structure of populations, communities, and ecosystems (Sousa 1984; White and Pickett 1985). Disturbances, whether natural or anthropogenic, are rapidly increasing in intensity and frequency in ecosystems worldwide (Turner 2010), and thus the human-managed

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ecosystems may be causing an additional environmental stress to species and communities that thrive on them (Donald et al. 2001; Bonnet et al. 2013).

In highly dynamic ecosystems such as the agrarian ones, disturbances are regularly associated to crop management events, which affect vegetation cover and soil stability mostly through crop harvesting, application of herbicides, and plowing (Bradbury et al. 2001). Furthermore, agricultural systems are increasingly intensified, generating landscape homogenization, biodiversity loss, and, in turn, pest emergences due to alteration of a main ecosystem service of biodiversity in agrarian land, such as natural pest regulation (McLaughlin and Mineau 1995; Tilman 1999). Consequently, it is crucial to understand how disturbance regimes affect organisms in these increasingly common highly managed ecosystems, if we intend to improve our ability to predict the response of species to future changes in the environment and to promote pest management sustainability.

Semi-fossorial species that live in agricultural systems in which plowing is typically applied provide an ideal scenario to study how organisms respond to these highly dynamic ecosystems. In particular, semi-fossorial small mammals are good models to study this issue because of their high breeding rate and short life-span (Nowak 1999) and high sensitivity to structural and temporal changes in habitats (Fischer and Schröder 2014; Marques et al. 2015). They also are key species in ecological networks within agroecosystems, either as prey (Fargallo et al. 2009; Terraube et al. 2011) or as vectors/reservoirs of infectious diseases and parasites (Gratz 2018), and in some contexts, they can become agricultural pests causing significant crop losses (Singleton et al. 2010).

The common vole (*Microtus arvalis*, Pallas 1778) is one of the most abundant semi-fossorial rodents in the agrarian landscapes of the Palearctic (Jacob et al. 2014), which spend most of their lives in underground burrows (Mackin-Rogalska et al. 1986). The burrow systems of common vole are excavations formed by tunnels that converge in nests, food storage chambers, or dead ends. Aboveground, tunnel openings are communicated through visible paths (Fig. 1a and b; Brügger et al. 2010), which can be used as a reliable means to detect the presence and quantify the relative abundance of the species (Liro 1974; Mackin-Rogalska et al. 1986; Jareño et al. 2014). The abundance of common vole often exhibits marked temporal fluctuations, sometimes cyclical (Gaines et al. 1979; Delattre et al. 1992), ranging in optimal habitats from less than 10 voles/ha during low abundance years to more than 1000 voles/ha during peaks (Vidal et al. 2009; Rodríguez-Pastor et al. 2016; authors' unpublished data). Population peaks occur every 2–5 years (Luque-Larena et al. 2015) and are often associated with crop damage and outbreaks

of several infectious diseases (Jacob and Tkadlec 2010; Luque-Larena et al. 2015, 2017).

In agroecosystems, the spatiotemporal abundance of common voles may be severely affected by human disturbances, in particular to those related to crop management. For example, deep plowing is a traditional management technique that drastically destroys subterranean structures and removes the herbaceous cover, so this practice might reduce abundance of semi-fossorial species such as common voles (Jacob and Hempel 2003; Cavia et al. 2005). However, modern techniques like low-tilling, which does not turn the soil over and reduces soil degradation and greenhouse emissions (although it can involve more intensive herbicide use; McLaughlin and Mineau 1995), seem to favor the development of some rodent populations (Hygnstrom et al. 2000; Sterner et al. 2003; Witmer et al. 2007), including common voles (Eggert et al. 2011; Heroldová et al. 2018; Roos et al. 2019). Moreover, in croplands, the non-crop patches, such as linear habitats (i.e., hedgerows, field margins, irrigation, and road ditches), could be also disturbed by human management activities of different intensity (sowing, plowing, road maintenance works). The role of herbaceous linear habitats as a refuge for common vole is well known (Jareño et al. 2014; Briner et al. 2005), but their role as drivers or buffers of common vole abundance is debate matter (Jacob and Hempel 2003; Briner et al. 2005; Delattre et al. 2009; de Redon et al. 2010; Delattre et al. 1992). Therefore, given that both linear habitats and crops characteristics seem to be relevant for vole populations (Delattre et al. 1992; Rodríguez-Pastor et al. 2016), an approach considering the compositional and structural heterogeneity of agrarian landscapes is necessary to understand the spatiotemporal abundance of common voles.

The spatiotemporal patterns of abundance of small mammals have been the focus of numerous studies, which can be based either on direct (captures) or on indirect signs of presence (Bowman et al. 2001; Cavia et al. 2005; Brown et al. 2007; Sokolova et al. 2014). These studies have been based mainly on the use of a variable number of small sample units spread across a range of habitats or landscapes (Delattre et al. 1996; Millán de la Peña et al. 2003; Fischer and Schröder 2014), but intensive sampling over large areas remains unexplored. Here, we perform for the first time a study on the patterns of abundance and potential occupation of burrows by common voles at large-scale and over completely sampled areas (entire crop fields and landscape-scale plots) in a highly disturbed agroecosystem. At field scale, we assess how different types of crop and their management influence the seasonal abundance of common vole burrow systems. At the landscape scale, we examine the influence of habitat compositional and structural landscape heterogeneity on the abundance of burrow systems. This study provides a deep insight into the

Fig. 1 Photographs of common vole burrow systems (BS). **a** and **b** are images of occupied common vole burrow systems (OBS) with recent excavation signs on their burrow openings and runways visible. **c** and **d** show the common vole activity signs considered for this study: fresh droppings on a burrow opening (**c**) and vegetation cut and hoarded by the voles on a burrow opening (**d**)



spatial and seasonal variation patterns displayed by vole burrows in a regularly perturbed ecosystem at both the field and landscape level, while allowing the identification of some key information for pest management.

Materials and methods

Study area

We conducted the study in 2012 in the region of Castilla y León (NW Spain), in the Spanish northern plateau, which includes the Duero River basin, a central agricultural plain surrounded by mountains. This central plain is mainly dedicated to agriculture (ca. 3.7 million ha; 37.81% of the total area of Castilla y León; (MAGRAMA 2012)) configuring a landscape generally flat with few trees and subject to a moderate-to-high agricultural intensification (Oñate et al. 2003). The extensive cultivation of fields with a 2-year fallow-cereal (mainly wheat, *Triticum* spp. and barley *Hordeum vulgare*) rotation is the traditional crop production in the area. Recently, the introduction of different irrigation schemes (mainly alfalfa *Medicago sativa*, sugar beet *Beta vulgaris* var. *saccharifera*, maize *Zea mays*, and some winter cereals, mainly rye *Secale cereale* and oat *Avena sativa*) and the increasing change from conventional tillage to low-tilling agriculture (MAGRAMA 2015) have created a landscape in which different farming methods are mixed, with fallows progressively disappearing. The most important types of crop in terms of cultivated surface are winter cereals (barley, wheat, and oat), alfalfa, annual legumes (common sainfoin *Onobrychis viciifolia*, common vetch *Vicia sativa*), and sunflower (*Helianthus annuus*). Plowed fields are also common

in traditional dry-agriculture systems, particularly out of growing season (more details in Jareño et al. 2015), but low tilling is spreading in the region.

Recording spatial distribution of burrow systems

To study burrow systems, we selected eight circular plots of 200-m radius (ca. 12.5 ha each) with a mixture of crops. We located the center of each plot at the corner of four crops fields, of which at least one was alfalfa (considered the optimal crop for common voles; Jánová et al. 2008; Jareño et al. 2014; Jacob et al. 2014). This design guaranteed a balanced variety of crops with optimal habitat always present (Table S1 in Supplementary Material A). We distributed the eight plots among four localities affected by recent vole outbreaks (Luque-Larena et al. 2015) and separated from each other by at least 800 m (see Supplementary Material B).

Plots were completely sampled to count burrow systems (BS hereafter; see detailed information about BS in Supplementary Material C, section “Burrow systems”). At each plot, teams of 1–12 trained observers recorded by walking abreast along parallel transects all common vole signs of presence (burrow openings, runways, droppings, and feeding signs—fresh clippings and little mounds of green vegetation inside or near the burrow openings; Fig. 1c and d) within a 5-m wide strip on either side of each observer. These samplings were carried out when plant cover was low (during early spring, after harvest, and after seeding), guaranteeing the detection of all burrow systems within the 10-m observation belt. Care was taken to cover the whole surface of each field, avoiding both double counting and gaps between transects

by regularly marking the outer edges of transect strips. The approximate central position of each BS with multiple openings was mapped using a hand-held GPS receiver (± 4 -m error). We assumed that all sampled burrows were excavated by common voles (see justification in Supplementary Material C, the “Other rodents in the area” section).

When we located a BS, we examined the number of burrow openings with signals of recent occupation (presence of fresh cut vegetation inside burrow openings, fresh droppings near openings, or recent digging signals, Fig. 1c and b; (Liro 1974; Heroldová et al. 2004; Terraube et al. 2011; Jareño et al. 2014). Therefore, we characterized each BS as occupied (OBS hereafter) when fresh signals of occupation were found in at least one burrow opening. Otherwise, we characterized BS as unoccupied (UBS hereafter).

We sampled all fields within 12.5 ha of each plot. Nonetheless, due to logistic constraints, some fields (four in summer and five in autumn) could not be surveyed, and thus the total area surveyed slightly varied among plots (Table S1). Linear habitats were not sampled in this study because visual surveys are of limited use where thick vegetation obstructs detection of burrows and individual identification of burrow systems may be impossible when they are a continuum along a narrow strip (see Brügger et al. 2010; for long linear burrow systems).

Seasonal sampling

To determine how the number of BS changes over time, we repeated the monitoring described above in each sampling plot three times during 2012, in March (Spring, hereafter), July (Summer, hereafter), and November (Autumn, hereafter), corresponding with the growing, harvesting, and resting crop seasons in that region, respectively. These periods also coincide with moments in which common vole populations suffer important seasonal changes that may affect burrowing activity and occupation, such as local population growth caused by reproduction (from spring to summer), or local movements due to crop harvesting (from summer to autumn) or other management practices (e.g., plowing/sowing/herbicide application in autumn) (Mackin-Rogalska et al. 1986; Delattre et al. 1992; Jánová et al. 2011; Rodríguez-Pastor et al. 2016).

Study scales

We adopted a multilevel spatial approach considering two scales: field and landscape. At field scale, we evaluated how the type of crop influences the number of BS and OBS within the field. At the landscape scale, we evaluated the influence of compositional heterogeneity (crop mosaic composition) and structural heterogeneity (linear features such as field margins, roadside, and track ditches) on the number of BS, and OBS recorded in the whole plot.

Data analyses

Response variables

At the field scale, we modeled (i) the number of BS and (ii) the proportional abundance of OBS (OBS relative to UBS, see below) in each crop field.

At the landscape scale, we considered the following response variables: (v) density of BS (dBS_{plot} , hereafter) and (vi) density of OBS ($dOBS_{plot}$, hereafter) in each plot. We calculated these variables as the sum of all BS or OBS counted in a given plot (considering all crop fields within each plot), divided by the total area sampled in each plot (excluding the area occupied by watercourses, rural tracks, and unsampled fields). At this scale, we used density rather than burrow counts due to slight differences in the area sampled in each plot (see Table S1).

Predictor variables

Given the differences in seasonal patterns of vegetation cover and soil stability for different land uses, the type of crop is expected to influence burrow numbers at field scale. The crops considered were as follows: (i) dry alfalfa (multiannual evergreen crop, Alfalfa hereafter), (ii) low-till cereal (winter cereals sown on unplowed stubble, LTcereal hereafter), (iii) traditional cereal (winter cereals sown on previously plowed lands, TRcereal hereafter) and, (iv) low-till legumes (annual legumes sown on unplowed stubble, LTlegume hereafter). Further information about agronomic practices carried out in each type of crop is summarized in Table S2. Sunflower crops were very rare in the area (Table S1), so we excluded them from field scale analyses, as well as empty fields that remained uncultivated (and regularly plowed) during all three periods (UF-S, hereafter). Hence, a four-level factor (Alfalfa, LTcereal, TRcereal, and LTlegume) named *Type of crop* was used in the analyses. In autumn, no burrow systems showed signs of occupation in TRcereal (Table 1), so this level of the predictor was removed from analysis at that season due to problems with convergence in parameter estimation.

At the landscape scale, we characterized each plot by the total area (ha) covered by each of the four types of crop (Alfalfa, LTcereal, TRcereal, and LTlegume) and the area covered by uncultivated fields and sunflower (UF-S, pooled in a single category), the area of the plot occupied by watercourses, rural tracks, and the total length of field margins per plot (boundaries between two adjacent crop fields, in km; see Table S3). Moreover, we calculated a Shannon index of diversity (Shannon 1948) with the types and the states of the crops (Fischer and Schröder 2014) by including nine categories: Alfalfa, LTcereal, TRcereal, LTlegume, LTcereal stubble, TRcereal stubble, LTlegume stubble, UF-S. We calculated the index for each plot and season as $H = \sum_{i=1}^m (p_i \times \log p_i)$,

Table 1 Descriptive statistics of the number of burrow systems (BS), occupied burrow systems (OBS), and unoccupied burrow systems (UBS) measured at field scale in different types of crop and seasons

Season	Type of crop	Number of fields <i>N</i>	Number of BS				Number of OBS				Number of UBS			
			<i>N</i>	Mean ± SD	Min	Max	<i>N</i>	Mean ± SD	Min	Max	<i>N</i>	Mean ± SD	Min	Max
March		51	2046	40.12 ± 52.70	0	236	842	16.51 ± 27.30	0	118	1204	23.61 ± 30.67	0	121
	Alfalfa	26	1542	59.31 ± 63.82	0	236	676	26.00 ± 33.64	0	118	866	33.31 ± 36.65	0	121
	LTcereal	7	81	11.57 ± 13.41	0	36	12	1.71 ± 2.36	0	6	69	9.86 ± 11.42	0	32
	TRcereal	8	143	17.88 ± 31.79	0	86	36	4.50 ± 8.85	0	25	107	13.38 ± 26.72	0	77
	LTlegume	10	280	28.00 ± 30.10	2	96	118	11.80 ± 18.69	0	62	162	16.20 ± 16.75	0	51
July		46	4228	91.91 ± 107.34	0	432	1741	37.85 ± 61.28	0	301	2487	54.07 ± 57.84	0	249
	Alfalfa	25	3186	127.44 ± 124.64	2	432	1531	61.24 ± 75.20	0	301	1655	66.20 ± 59.08	0	207
	LTcereal	5	411	82.20 ± 116.04	5	285	86	17.20 ± 15.55	1	36	325	65.00 ± 103.75	0	249
	TRcereal	7	222	31.71 ± 37.77	0	93	68	9.71 ± 15.65	0	43	154	22.00 ± 24.49	0	50
	LTlegume	9	409	45.44 ± 28.18	6	97	56	6.22 ± 7.61	0	22	353	39.22 ± 28.85	0	93
November		45	3227	71.71 ± 94.71	0	432	403	8.96 ± 14.13	0	64	2824	62.76 ± 83.23	0	368
	Alfalfa	26	2693	103.58 ± 99.23	2	432	381	14.65 ± 1637.00	0	64	2312	88.92 ± 85.14	0	368
	LTcereal	3	86	28.67 ± 14.98	12	41	2	0.67 ± 0.58	0	1	84	28.00 ± 14.42	0	40
	TRcereal	6	11	1.83 ± 2.86	0	6	0	0.00 ± 0.00	0	0	11	1.83 ± 2.86	0	6
	LTlegume	10	437	43.70 ± 93.66	0	301	20	2.00 ± 2.62	0	8	417	41.70 ± 91.29	0	293
Total		142	9501	66.91 ± 89.06	0	432	2986	21.03 ± 40.88	0	301	6515	45.88 ± 62.09	0	368

where m is the number of “type*state” categories in the plot and p_i is the proportion of fields with each category in the plot.

We used digital maps from the Geographic Information System of Farming Land of Castilla y León Region (<https://datosabiertos.jcyl.es>) for the year 2012 and Qgis v2.8.1 (Quantum GIS Development Team 2015) to calculate all landscape metrics.

Statistical analyses

Field scale

First, we modeled changes in the abundance pattern of BS (number of BS per field as response variable) between types of crop and seasons using a generalized linear mixed model (GLMM) with a negative binomial error structure and log link function, after verifying that Poisson distribution models showed overdispersion (Zuur et al. 2009). Second, we modeled fluctuations in the potential occupation pattern of BS also between types of crop and seasons, using the proportional abundance of OBS per field as the response variable. We built a two-vector response variable (number of OBS and number of UBS) and fitted a GLMM using a binomial error distribution and a logit link function (Crawley 2007). In both models, we included the log-transformed size of field (ha) as an offset variable, due to significant correlations among the size of each field (ha) and our response variables (Sperman’s rank correlation between field size and number of BS per

field: $r = 0.45$, $p < 0.001$, number of OBS per field $r = 0.36$, $p < 0.001$, and number of UBS per field $r = 0.45$, $p < 0.001$, $N = 142$). We also included in both models the field identity (Id_field hereafter, 51 levels) nested within plot (Id_plot hereafter, 8 levels) as a random factor.

For both models, we tested the significance of the interaction between the factors *Type of crop* and *Season* using partial likelihood ratio tests or Wald tests (Fox and Weisberg 2011; Zuur et al. 2009). Because we were interested in differences on average response(s) between different types of crop within each season, and between seasons for each type of crop, the comparisons of interest were tested by pairwise comparison of means (*multcomp* package; Hothorn et al. 2008).

We excluded the two smallest crop fields (< 147 m²) without burrow system records (147 m² is the maximum size registered in a single burrow system in our study area; authors’ unpublished results). Moreover, from these analyses, agricultural fields with land uses that were occasional in our study area (sunflower crops, $N = 2$) or that remained vacant during all three periods (uncultivated and regularly plowed fields, $N = 5$) were not considered. Finally, five agricultural fields were not sampled in July due to a delay in harvest (summer survey in cereal crops requires that the fields to be sampled were already harvested to obtain the owner’s permit to work), and six agricultural fields were excluded from the November dataset because the land use changed throughout the temporal sampling, making impossible to assign the response variable to a particular type of

crop. Therefore, the total dataset used in this analysis consisted of 51 fields in spring, 46 fields in summer, and 45 fields in autumn (Table 1).

Landscape scale

To test whether the crop mosaic composition and structural heterogeneity influenced common vole burrow abundance, we first summarized the landscape environmental variation by means of a PCA with Varimax rotation, aimed to reduce the original set of 11 explanatory variables with high multicollinearity (Table S4). We included the spatial coordinates of each plot (longitude X and latitude Y) to account for geographic effects, since we expected that some variables at this scale would be spatially structured. The 24 observations (eight plots sampled in three seasons) were included in the PCA. We retained principal components (PCs) that had eigenvalues > 1 (four PCs, see the “Landscape scale” section within the “Results” section), which were used as independent predictors in subsequent analyses. We performed LMMs models for each response variable (dBS_{plot} and dOBS_{plot}), using the four landscape components generated by the PCA as predictors and season as a random factor, and assuming Gaussian error and identity link function. We also calculated beta standardized coefficients (Bring 1994) to estimate the relative contribution of each predictor on the response variable.

We evaluated all models using the dispersion parameters and graphical methods to identify violations of assumptions of homogeneity of variance, normality of residuals and independence of both explanatory variables and residuals. Because of the seasonal structure of our data, we tested the temporal autocorrelation in the residuals of the BS and OBS at field scale models (function *Acf* in *forecast* package; Hyndman and Khandakar 2008; Hyndman et al. 2018). We found only significant temporal autocorrelation in the OBS model, but with a low autocorrelation value ($r < 0.25$) at lag-1. Therefore, we did not account for this temporal autocorrelation in order to reduce the model complexity.

We considered a significance level of $\alpha = 0.05$ for all analyses, and we carried out all analyses with R 3.3.3 (R Core Team, 2017). The R packages used were *forecast* (Hyndman and Khandakar 2008; Hyndman et al. 2018), *lme4* (Bates et al. 2015a, b), *car* (Fox and Weisberg 2011), *multcomp* (Hothorn et al. 2008), and *psych* (Revelle 2016).

Results

Field scale

From a total of 9501 BS recorded during the three study seasons, 2046 (21.5% of total sample) were found in spring, 4228 (44.5%) in summer, and 3227 (34.0%) in autumn (Table 1).

We found that the *Type of crop* in each field had a significant effect on the number of BS through the interaction with *Season* (GLMM $\chi^2 = 18.88$; d.f. = 6; $p = 0.004$). The detailed results of multiple pairwise comparisons are shown in Table S5. There was a general trend of increase in the number of BS from spring to summer, although it was statistically significant only for Alfalfa and LTcereal (Fig. 2a, Table S5). We found a significant decline in the number of BS from summer to autumn in TRcereal, and no statistical significant differences occurred between these two periods for the other crop types (Fig. 2a, Table S5). If we consider the differences between crop types within season, the number of BS were more abundant in Alfalfa fields than in the other crop types in the three seasons, and differences were statistically significant in all comparisons but one (Alfalfa-LT cereal in autumn, Table S5). In autumn, the number of BS was significantly less abundant in TRcereal fields than any other crop (Table S5).

Only 31.4% (2987) of the total BS recorded during the three periods showed clear signs of recent occupation. In spring, we found 842 OBS (41.15% of the total BS in spring), 1741 in summer (41.18% of the total BS in summer), and 404 in autumn (12.42% of the total BS in autumn; Table 1). For this response variable, there was also a significant interaction between *Type of crop* and *Season* ($\chi^2 = 72.75$; d.f. = 6; $p < 0.001$). Three out of the four crop types showed proportionately more OBS in summer than in spring (see Fig. 2b and

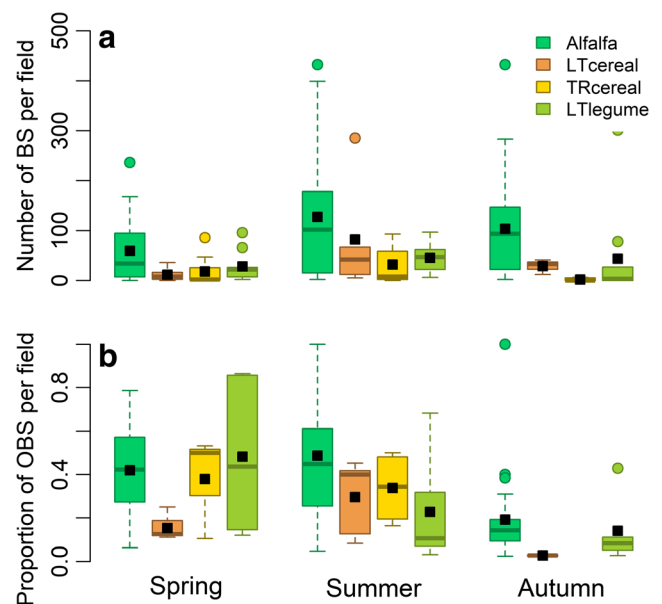


Fig. 2 Observed values of the number of BS per field (a) and proportion of OBS/BS per field (b) for each type of crop and season. The boxes show the interquartile range (IQR hereafter; the 25th and 75th percentiles). The bold line indicates the value of the median. The length of whiskers show: upper whisker = 75th percentile + $(1.5 \times \text{IQR})$, and lower whisker = 25th percentile - $(1.5 \times \text{IQR})$. Data beyond the end of the whiskers are outliers plotted as points. Black squares indicate estimated mean value of the variable. For abbreviations, see Fig. 1

Table S6) and a general declining trend from summer to autumn. The only exception was LTlegume fields, whose OBS proportion decreased continuously throughout the three study periods (Table S6). Considering differences between crop types within season, the proportional abundance of OBS in Alfalfa fields was overall higher than for all other crops in the three seasons, although the difference with LTlegume fields in spring did not reach statistical significance (Table S6).

Landscape scale

The PCA resulted in four PCs that retained 71.3% of total variance. The interpretation of each axis based on variable loadings is shown in Table 2; factor loadings, eigenvalues, and percentage of explained variance are available in Table S7.

The response variable dBS_{plot} was significantly and negatively correlated with PC1 and PC4 (Table 3). Therefore, more density of burrows was associated with increasing area covered by uncultivated plowed land-sunflower and total length of field margins in the plot, and with decreasing area covered by watercourses and lower values of latitude and longitude (the two landscape variables that loaded most heavily on PC1; Table 2 and Table S7, and Fig. 3). The negative effect of PC4 indicates that dBS_{plot} increases especially as the area covered by TRcereal in the plot decreases and, to a lesser extent, as the area occupied by legume crops increases, independently from geographic location (Table 2 and Fig. 3). Overall, the relative effect of PC4 on dBS_{plot} was greater than that of PC1 (beta standardized coefficients, Table 3).

The model examining $dOBS_{plot}$ produced similar results with respect to PC1 and PC4 to those found for dBS_{plot} (Table 3, Fig. 3), but PC3 also contributed significantly to this model. The third factor (PC3) correlated negatively with $dOBS_{plot}$ and, accordingly, density of occupied burrows in

each plot also increases as the LTcereal decreases (and legume crops increases, Table S7). The beta standardized coefficients of the predictors indicate that the effect of PC1 on the response variable dBS_{plot} was slightly lower than the effect of PC4, and both had a greater effect on $dOBS_{plot}$ than PC3 (Table 3).

Discussion

We found large spatial and seasonal variation in the patterns of burrow abundance and occupancy of a cyclic semi-fossorial small mammal thriving in intensified agricultural landscapes. The number and occupation of burrow systems across the annual cycle varied significantly between seasons and among sites at two spatial scales, suggesting that the patterns observed reflected both the species' population dynamics and the disturbances imposed by the agricultural environment.

Our multi-scale approach adds to the few studies performed hitherto on vole population dynamics considering simultaneously landscape and field scale (Delattre et al. 1996; Fischer et al. 2011; Fischer and Schröder 2014). Additionally, provided that processes and relationships at a large scale might be obscured by the variability that exists at smaller scales (Wiens 1989), our methodological approach, based on the whole count and occupation status of burrow systems in each field over large entire plot areas (i.e., 12.5 ha each), enables us to make reliable inferences about habitat and vole abundance relationships and how these ones vary seasonally. Therefore, our methodology is arguably more robust than other sampling methods, such as captures or burrow counts in small spatial subsamples, which are highly sensitive to small-scale spatiotemporal changes in vole distribution and abundance.

Table 2 Interpretation of PCs at the landscape scale, with variables retained based in loading values > |0.404|. For detailed information about variables, see the "Predictor variables" section

PC	Variables with loadings < -0.404	Variables with loadings > 0.404	Interpretation
PC1	Plot area covered by uncultivated plowed land-sunflower, total length of field margins	X coordinate, Y coordinate, plot area covered by watercourses	Gradient related to the geographic position of the plot (local effects, positive values towards SE plots), associated to higher presence of sunflower/uncultivated fields in NW plots (Table A3), and higher area covered with watercourses but lower length of field margins in SE plots (Table A3)
PC2	Total length of field margins	Plot area covered by uncultivated plowed land-sunflower, plot area covered by watercourses rural tracks	Gradient related to the landscape structural heterogeneity, defining a gradient from areas with large field margins length contrasting with areas with many tracks and uncultivated/sunflower fields
PC3	Plot area covered by LTlegume	Plot area covered by LTcereal	Gradient between both low-till crops: LTlegume and LTcereal.
PC4	Plot area covered by LTlegume	Plot area covered by TRcereal	Gradient between plots with large areas of LTlegume and plots with large areas of TRcereal

Table 3 Results from the linear mixed models (LMMs) for the density of burrow systems (dBS_{plot}) and occupied burrow systems (dOBS_{plot}) measured at the landscape scale. Selected principal components derived from the PCA (see Table 2 and Table S7) were included as predictors

	Density of burrow systems (dBS _{plot})				Density of occupied burrow systems (dOBS _{plot})					
	Estimate ± SE	χ ²	Degrees of freedom	P value	β standardized coefficients	Estimate ± SE	χ ²	Degrees of freedom	P value	β standardized coefficients
Intercept	38.25 ± 7.9	23.5	1	<0.001		12.4 ± 5.9	4.4	1	0.036	
PC1	-7.43 ± 3.4	4.66	1	0.031	-0.316	-4.7 ± 1.6	8.6	1	0.003	-0.387
PC2	-3.75 ± 3.4	1.19	1	0.276	-0.160	-0.2 ± 1.6	0	1	0.901	-0.016
PC3	-4.45 ± 3.7	1.43	1	0.232	-0.189	-3.48 ± 1.8	3.9	1	0.048	-0.286
PC4	-11.78 ± 3.4	11.7	1	0.001	-0.501	-3.94 ± 1.6	6	1	0.014	-0.324

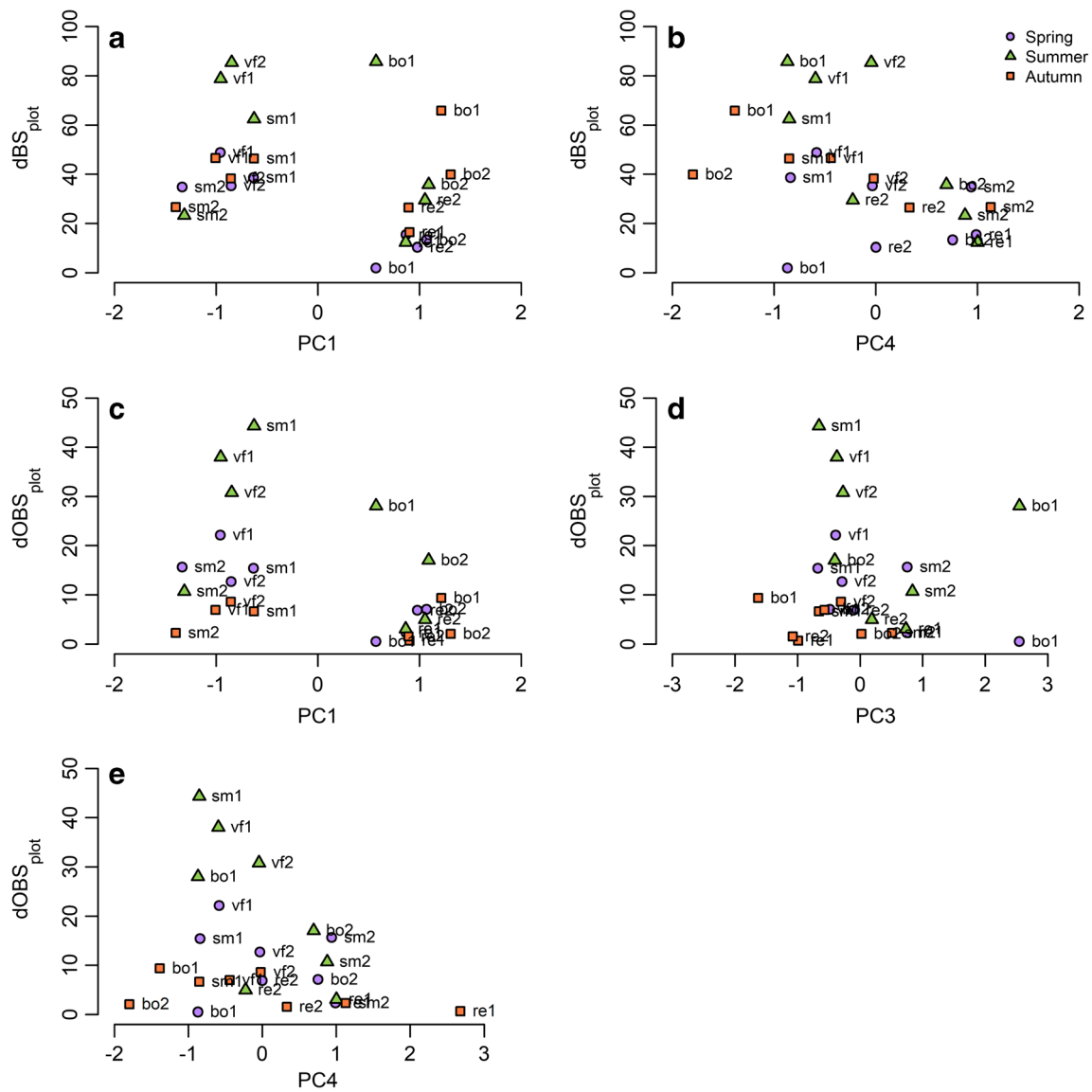


Fig. 3 Relationships between burrow systems at the landscape scale and axes extracted from principal component analyses (PCAs), summarizing variables at the landscape scale (Table S3). **a** and **b** show the density of BS (dBS_{plot}) against significant axes extracted from PCAs. **c**, **d**, and **e** show the density of OBS (dOBS_{plot}) against significant axes extracted

from PCAs. The eight plots studied are labeled with their corresponding Id_{plot} (bo1, bo2, re1, re2, sm1, sm2, vf1, vf2); purple, green, and orange circles indicate respectively spring, summer, and autumn observations. For abbreviations, see Fig. 1

Seasonal patterns of vole abundance and burrow occupation

The abundance of common vole exhibits marked between-year fluctuations (Delattre et al. 1992, 1996) that are reflected in the abundance of its burrows (Mackin-Rogalska et al. 1986; Delattre et al. 1990). Cyclic populations of this and other vole species exhibit phase-related changes in several demographic parameters and in different aspects of their ecology (Krebs 2013), which often leads to substantially different patterns between a peak and the next valley phase (Jánová et al. 2003; Pinot et al. 2014). Here, we present a thorough analysis of seasonal data collected during one valley demographic phase following a peak in previous summer-autumn abundance (Paz et al. 2013; Rodríguez-Pastor et al. 2016). Our design, therefore, allowed us to assess the occupation and fate of vole burrows after a vole peak, when their populations had already undergone a pronounced decline, thereby giving interesting insights about vole population dynamic, response to crop management, and spatial behavior.

We found a relatively small rate of occupied burrows during the study year (from 41% in spring-summer to 12% in autumn) that likely reflects the vole population decline in years following peak abundance. Indeed, the long-term persistence of a large number of vacant burrows after the peak year (Mackin-Rogalska et al. 1986) was further confirmed by the positive relationship found between abundance estimates obtained from vole trapping and density of occupied burrows rather than with the total density of burrows (whether occupied or unoccupied) (Table S8). Accordingly, the abundance of occupied burrow systems seems to better reflect the abundance of voles during the low phase than the simple count of burrow systems in the field without examining them for evidence of current occupation.

Trapping work carried out simultaneously and in the same areas of our study also confirmed a large population decline compared with the previous year. Vole density was overall low in the study year, with values of abundance similar to those reported in other “low vole years” in Spain (Fargallo et al. 2009; Paz et al. 2013; Rodríguez-Pastor et al. 2016), but with considerable differences between study plots (0.01–8.0 captures per 100 trap-nights; Fig. S1). This agrees with large differences between plots found in burrowing activity at both landscape and locality scale (see Fig. 3 and significant effect of PC1 in Table 3) probably reflecting differences in landscape composition and configuration (i.e., type, amount, and spatial arrangement of different land cover types, see below).

We found a clear seasonal pattern in the proportional abundance of occupied burrows, which showed a positive increase in abundance from spring to summer and a negative trend from summer to autumn (Table S6). This pattern is likely the result of the seasonal population dynamics of voles (differential survival and reproduction during favorable and unfavorable seasons in

a year). Seasonal fluctuations displayed by Mediterranean rodent populations, especially by primary consumers such as voles (Lantová and Lanta 2009), are characterized by a general spring-summer reproduction, and by a breeding stop during the drought season (end of summer) due to food shortage (Moreno and Kufner 1988; Rosário and Mathias 2004). The increase in total number of burrows and occupation found from spring to summer (Tables S5 and S6) suggests that voles built new burrows despite the existence of a large number of empty ones in the surroundings. Therefore, re-occupation of existing burrows does not seem to be a common behavior in the species, although such behavior would substantially save time and energy, and reduce risk of predation (Mackin-Rogalska et al. 1986; Reichman and Smith 1990). Once abandoned, burrow systems can remain in the ground for a long time (even for many months; Mackin-Rogalska 1979; author’s unpublished data), depending on soil features, agricultural perturbations, and weather conditions. It is possible that existing (vacant) burrows in our study no longer offer advantages in terms of food optimization (e.g., distance between foraging patches and home burrow), risk of predation (low protective vegetation cover or shelter in the surroundings of the burrow system), or burrow maintenance (low profitability of maintaining excessively complex systems). Reuse of burrows might also increase the risk of diseases and parasite infection (Epstein 1995; Leu et al. 2010), which might also select for constructing burrows anew.

Agrarian disturbances: crop type, soil stability, and vegetation cover

The number and occupation of burrows were largely explained by seasonal disturbances imposed by crop type at the field scale. Both occupied and total burrows were more abundant and showed less seasonal numerical fluctuations in alfalfa fields than in other crop types (Fig. 2). Our results support that multiannual crops provided a much more suitable habitat for voles than annual crops, as reported in more northern countries (Mackin-Rogalska et al. 1986; Jacob et al. 2014; Jánová and Heroldová 2016). In semi-fossorial species, the temporal stability of soil is a key factor for building and maintaining their burrows and thus essential for completing their life cycles (Reichman and Smith 1990; Laundré and Reynolds 1993; Kinlaw 1999). Our data reveal that patches of traditionally managed cereal crop hold both the lowest number of burrow systems and occupied burrows in autumn (Fig. 2). This is likely due to the traditional cropping system practiced by growers throughout this region, which is a tillage-based cultivation of winter cereals with deep plowing (30–40 cm underground), plus one or two cultivator passes (15 cm) before autumn sowing (Madejón et al. 2009). This kind of intensive agricultural practice strongly alters soil structure, thereby destroying vole burrows and tunnels (Jacob and Hempel 2003; Jacob 2003; Bonnet et al. 2013), which are usually excavated to a depth of 25 cm (Brügger et al. 2010). It is therefore

suggestive that traditionally managed cereal fields, the least-stable crop type in the area, might act as a sink habitat for voles, and that deep plowing can be a key crop management operation in reducing large-scale vole population growth and thus, the risk of pest development (Jacob 2003; Eggert et al. 2011; Jacob et al. 2014; Heroldová et al. 2018).

Overall, differences in burrow abundance found between low-till and traditionally managed cereal crops also suggest that crop management with reduced soil disturbance contributes to a more intense colonization of such habitats by voles (Heroldová et al. 2018; Roos et al. 2019). The increase in total burrows and the proportional abundance of occupied burrows in low-till cereal from spring to summer was greater than that in traditionally managed cereal fields, whereas in summer-to-autumn transition, the decrease was lower in low-till than in traditionally managed cereal fields (Fig. 2, Tables S5 and S6). Furthermore, the total abundance of burrows reached in autumn was significantly higher in cereal fields with low tillage than in traditionally managed ones (Tables S5 and S6). This suggests that, unlike traditionally managed, low-till cereal could maintain vole populations and burrows available to be reused during the winter following to a population peak, which could facilitate a faster recovery of the population after the crash.

However, cereal crop fields (even under low tillage) showed much lower burrow densities than low-till legume or alfalfa crops (Fig. 2). This is probably because of the lower preference of voles for nutrient-poor food such as cereals as compared with alfalfa and other legume crops (Heroldová et al. 2004, 2008; Lantová and Lanta 2009), and the low vegetation cover of cereal fields resulting from harvest and herbicide application, which limits available food for voles and shelter from predators (Jacob and Brown 2000). Hence, cereal crops under low-tillage practices can be considered a suboptimal habitat for voles. Nevertheless, this crop could be more susceptible to vole damage or to promoting the large-scale development of the vole pest than cereals under the traditional cultivation system (Hygnstrom et al. 2000; Sterner et al. 2003; Witmer et al. 2007; Heroldová et al. 2018).

Unlike previous studies, we focus on burrow systems, rather than on individuals, which provides a response to the disturbance with some delay with respect to individual responses or numerical variations (individuals disappear but burrows remain on the ground). Within our sampling design, the variable “occupied burrows” are expected to more accurately reflect the demographic response to a particular perturbation. As expected, there is a reduction in the proportion of occupied burrows in all crop types after harvesting (from summer to autumn, Fig. 2b), yet especially striking in cereal fields, which are the crops subject to the greatest disturbances through harvesting and plowing.

Landscape context and burrow systems occurrence

The relevance of soil stability promoting high vole burrow abundance at field scale is also corroborated at the landscape scale, where the amount of uncultivated (and regularly plowed) lands and the amount of traditionally managed cereal crops in the plot were the two single crop-related variables that defined each of the two gradients significantly related with burrow numbers and occupied burrow numbers (PC1 and PC4; Table 3). However, in the first case, the relationship with burrows indicates that the more area left uncultivated (regularly plowed), the more burrows the plot will have, what is counterintuitive. In our approach, this PC axis indicates a South-Eastern-North-Western gradient, with latitude and longitude being the main contributors to the axis. Therefore, the relationship is likely scale-dependent (Crowley 2007; p. 314), probably because the amount of uncultivated surface correlates to the geographic location of the plot (larger extent of this crop category in NW plots, see Table S3; Fig. 3). This type of land use is, indeed, the less abundant crop category in our study (Table S1), so the relationship observed could be unreal or meaningless.

However, the numerical response of burrows to the extent of traditionally managed cereal crops at the landscape scale is geographically independent and expressed a clear trend for highly perturbed cereal crop areas to achieve both less total burrows and occupied burrows, agreeing with the pattern found at field scale. The occupied burrows also showed a meaningful relationship with the type of low-till crop at the landscape scale (i.e., larger number of occupied burrows as the extent of low-till cereal crop decreases and the extent of low-till legume crop increases). Therefore, we suppose that growing low-till legume crops involves smaller disturbances to voles than low-till cereal crops, at least in our study areas. Although no direct evidence was available, the observed relationship could be related, however, with the quantity/quality of food provided by these two crops (Heroldová et al. 2008; Lantová and Lanta 2009), or with other variables not considered in the study, which make low-till legumes preferential by voles with respect to low-till cereals at the landscape scale.

Landscape structural heterogeneity—in terms of length of field margins and area of watercourses—emerges as other element affecting abundance and burrow occupation in the surrounding fields (Fischer et al. 2011; Fischer and Schröder 2014). In our study areas, the field margins are uncropped narrow strips (usually width < 1 m) between two adjacent crop fields, composed mainly by herbaceous species. Therefore, field margins can provide vegetation cover (shelter, food) during the most part of the year and undisturbed soil to construct stable burrows all year round. In contrast, watercourses are natural streams or irrigation ditches temporally flooded with well-developed vegetation (e.g., *Scirpoides holoschoenus*, *Typha* sp.), and generally wider (between 2 and 6 m) than field margins. We found that these linear structures participate in

PC1 (unless with the lowest contribution) and were both related with latitude, longitude, and the area cover by uncultivated plowed land (Table S7). When they are flooded (summer drought usually dries them in our study plots), they can act as physical barriers, hindering vole movements across them (Bohdal et al. 2016). However, they are also undisturbed and high-quality habitats relative to the surroundings (cropped areas). Therefore, this habitat has the potential to serve as wild refuges with larger capacity for voles and specialized predators (e.g., *Mustela nivalis* Linnaeus, 1766) than field margins, perhaps facilitating the reduction of vole density and occupancy in neighboring fields. This would support recent evidence showing that wide field margins may reduce vole colonization of adjacent crops (Briner et al. 2005; de Redon et al. 2010; Bohdal et al. 2016).

An intriguing result was the lack of any numerical response between burrows and the extent of alfalfa crops at the landscape scale. This may be because the variable including the total surface of alfalfa crops at the landscape scale showed little variation among plots (Fig. 3 and Table S1). Moreover, unfortunately, our sample size ($n = 8$ plots) is somewhat limited for generalizations at this scale, so future research should focus on the relative contribution of this particular habitat (in both extent and distribution) to the agrarian landscape and their potential influence in boosting vole numbers at large spatial scale. Previous studies have shown that increases in the production of alfalfa crops appear to be one of the main drivers explaining vole range expansion occurred in NW Spain (Jareño et al. 2015), but to date, no study has addressed the vole-alfalfa relationship from a landscape perspective.

Conclusions

Previous studies have shown that increased proportion of particular habitats in the landscape (e.g., wooden patches or field margins) limits the local abundance of voles (de Redon et al. 2010; Delattre et al. 2009). Our results further suggest that management of vole outbreaks should not only encourage the maintenance of particular habitats, but also the promotion of complex patterns of crop, non-crop habitat, and agricultural practices in the case of common voles. So far, agri-environmental schemes have mostly focused on the field scale (Jacob 2003; Jánová et al. 2011), including their margins (Rodríguez-Pastor et al. 2016). To be indeed effective, pest control actions need to be applied at larger scales, something that would require cooperation between farmers at a landscape scale. Consequently, an adequate landscape-scale planning of crop types, agricultural practices, and distribution of non-crop habitats could be a promising sustainable method to reduce the risk of crop-damaging vole plagues. However, we need to be careful when proposing management actions for similar future cycle phases on the basis of single-year studies, since yearly fluctuations in other factors (e.g.,

weather, predators, diseases) may alter the seasonal patterns that we have detected. Further research is needed, in different years and ecological contexts, to confirm the generality—or exceptional condition—of our findings.

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