

# “Living on the edge”: The role of field margins for common vole (*Microtus arvalis*) populations in recently colonised Mediterranean farmland



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## ABSTRACT

Small rodents are common inhabitants of farmlands where they play key ecosystem roles but can also be major pests when overabundant, causing crop damages and significant economic losses. Agricultural landscapes are characterised by high fragmentation with remnant semi-natural habitats being typically restricted to narrow field margins. These linear habitats are key to maintaining local biodiversity, but can also harbour “irruptive pest” species, such as voles. The common vole *Microtus arvalis*, is a main vertebrate pest in continental European farmlands, and recently invaded the inland Mediterranean agricultural landscapes of NW Spain, where regular crop-damaging outbreaks now occur. Knowing how reliant common voles are on field margins in Mediterranean agricultural landscapes would be an important step forward for more targeted management. Here we report on common vole habitat use in Mediterranean European farmland and compare them with those found in northern latitudes, thus seeking for both general patterns as well as geographical differences. We conducted seasonal trappings over 6-years in the main habitats (cereal and alfalfa crops, fallows, and their margins). We show a strong edge effect, in the form of an exponential decay in vole abundance from the margin towards the inside of fields, and vole abundances 2.3 times higher in margins than inside fields. The magnitude of this edge effect varied depending on crop type, season and vole abundance (density-dependence). Cereal crops were characterised by a stronger edge effect than alfalfas or fallows (with abundance 8–10 times higher in margins than in fields during spring and autumn). Cereals appeared as the least optimal habitat for common voles, with important spill-over of voles inside the fields in summer when densities increased. Field margins, where vegetation characteristics hardly change seasonally, provide a limited (5% of the agricultural surface) but stable habitat and key refuge for common voles in Mediterranean farmlands. Our results suggest that targeting management actions in the field margins of cereal crops during spring and autumn and inside alfalfa fields during population increases should be considered in integrated control schemes of crop-damaging common vole outbreaks.

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## 1. Introduction

Current agricultural landscapes result from the removal, fragmentation and reduction of original natural habitats, leading

to heterogeneous mosaics made up of large expanses of monoculture with scattered uncultivated areas of varying sizes and shapes (i.e., semi-natural habitats). In intensive agricultural landscapes, these semi-natural habitats are often reduced to linear features, such as hedges, field margins or grassy strips along watercourses, woods or roads (Tattersall et al., 2002) and non-linear habitats, such as set-asides, stubbles or fallows. Wild animals typically inhabit these uncultivated areas such that their conservation is crucial for maintaining habitat heterogeneity and biodiversity (Benton et al., 2003; Tschardt et al., 2005). In

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general, wildlife in farmlands is reliant on remnants of natural or semi-natural habitats for persistence (Benton et al., 2003). Semi-natural habitats also act as dispersal corridors, which favour connectivity between patches, colonization and population maintenance (Duelli and Obrist, 2003; Fischer and Lindenmayer, 2007). Moreover, these habitats are considered as refuges for burrowing herbivores, such as *Microtus* voles, which play a keystone functional role within communities, but when irruptive, can also become an agricultural pest causing crop damage, economic losses and disease spill-over (Delibes-Mateos et al., 2015; Jacob, 2003; Renwick and Lambin, 2013).

The common vole (*Microtus arvalis*) is the most abundant burrowing herbivore in open agricultural European landscapes where grasslands, meadows, set-asides, wildflower strips, grassy field margins or alfalfa crops occur (Bonnet et al., 2013; Delattre et al., 1996; Fischer et al., 2011; Janova et al., 2011; Janova et al., 2008). Common vole population dynamics are characterized by multi-annual cyclic fluctuations, with population peaks occurring every 2–5 years (Tkadlec and Stenseth, 2001; Lambin et al., 2006; Luque-Larena et al., 2013). Due to its ability to adapt to intensively cultivated areas, its irruptive population dynamics, and the damages to crops during outbreaks, this species is considered as a major rodent pest in many parts of its range (Jacob and Tkadlec, 2010; Jacob et al., 2014).

In NW Spain, the common vole recently invaded ca. 5 million ha of agricultural landscapes where the species was hitherto absent until the surface area of irrigated herbaceous crops including alfalfa steeply increased (Jareño et al., 2015; Luque-Larena et al., 2013). Ever since the colonization of agricultural areas, common vole population outbreaks have regularly occurred, causing significant economic losses to agriculture, as well as environmental impacts associated with the use of rodenticides for controlling vole populations (i.e., secondary poisoning of non-target fauna) and zoonotic outbreaks of tularaemia in humans (Luque-Larena et al., 2015, 2013; Sánchez-Barbudo et al., 2012; Vidal et al., 2009).

Agricultural habitats are seasonally dynamic and continuously modified by farming practices and crop phenology. Mechanical work in crop fields, such as ploughing, harvesting and mowing temporarily alters habitat suitability for burrowing rodents (Bonnet et al., 2013). The periodic alteration of soils greatly impacts vole populations in the cultivated portions of farming landscapes through habitat destruction, increased mortality, altered spatial behaviour, or reduced food availability (Brügger et al., 2010; Jacob and Hempel, 2003; Jacob, 2003). Field margins and fallows are not exposed to such frequent agricultural practises, and hence harbour a higher floral diversity and non-crop plant biomass than cropped fields (Heroldová et al., 2007). As such, field margins are known to provide relatively undisturbed and stable refuges for common voles in farmland areas of temperate Europe, where vegetation growth is not severely limited by rainfall (Bonnet et al., 2013; Jacob and Hempel, 2003; Jacob, 2003). In NW Spain, the inland Mediterranean climate is characterised by a period of strong hydric deficit during summer (i.e., summer droughts of variable duration and severity), which is critical for plant growth (Chaves et al., 2002). This consequently affects the availability of food, which in turn affects the reproduction and survival of upper trophic levels (i.e., herbivores such as voles) (Fernández-Salvador et al., 2005). The common vole is primarily a grassland species, so we would expect the semi-natural margins and fallows to be primary habitats and to act as refuges and sources of individuals for less optimal habitats during periods of low density. Alfalfa crops have also been pointed out as primary habitats for common voles in many European regions, owing to their long-term stability and suitability for vole colony formation (alfalfas remain unploughed for 5–6 years) and provision of cover and high-quality food for voles (Jareño et al., 2015). By contrast, cereal crops represent the

least stable habitats, since they are subjected to more vole-damaging tillage regimes, and thus are expected to be the least optimal habitats and potential sinks for vole populations. A better understanding of when and where voles are more abundant in the agricultural landscape, and of how reliant they are on field margins, would be an important step forward for more targeted management.

We report here on common vole habitat use in a novel farming landscape for this species. We studied the spatial and temporal variations in the use of semi-natural habitats (field margins and fallows) and of agricultural habitats (cereal and alfalfa crops) by common vole populations in recently-colonised Mediterranean farmland areas in the NW of Spain. Understanding the habitat use patterns by common voles in such recently-colonised agricultural landscapes would help us to: (i) understand patterns of habitat use and compare them with those found in temperate European farmlands, and (ii) infer specific management measures at regional level. We first identify the habitats harbouring more common voles at different phases of their population dynamics (two outbreaks and crash phases) according to the crop phenology (and associated variations in vegetation characteristics) and seasonality. We predicted that fallows and field margins, which are not subjected to continuous farming practises, would act as refuges or source habitats, particularly during low-density phases and when availability of green vegetation is reduced (i.e., during summer drought periods). We thus expected to find an edge effect in the form of a decrease in vole abundance with increasing distance from the edge towards the inside of crop fields. We further expected this edge effect to vary depending on the habitat quality for voles inside fields (i.e., stronger edge effect in sub-optimal crops). Innovatively, we also investigated whether the proportional abundance of voles in margins (relative to fields) was density-dependent, expecting any spill-over of voles from the margins towards fields with increasing density (due to field margin saturation) being particularly marked in sub-optimal crops. Better understanding the links between crop colonisation and vole dynamics will allow for more timely and crop-specific management actions. Finally, we investigated whether the relative vole abundance in margins varied with vegetation characteristics in the margins and fields.

## 2. Materials and methods

### 2.1. Study areas

The study was carried out on a large intensive agricultural region of NW Spain (northern plateau, Tierra de Campos, Castilla-y-León region). Fieldwork was conducted in three study areas (40 km<sup>2</sup> each) located in the provinces of Palencia (42°01'N, 4°42'W), Valladolid (41°34'N, 5°14'W) and Zamora (41°50'N, 5°36'W) (see Jareño et al. (2014) for a map of the region and more details on study areas).

The climate of Castilla-y-León is defined as “continental Mediterranean with cold winters”, and is characterised by a wide seasonal temperature oscillation due to an elevated average altitude (regional mean: ca. 830 m.a.s.l.) and the limitation of Atlantic-buffering effects by peripheral mountain ranges that completely surround the region: summers are dry and hot with a variable drought period, while winters are cold and humid (Jareño et al., 2015; Rivas-Martínez and Loidi, 1999). Rainfall follows a Mediterranean pattern, with precipitation maximums during spring and autumn; the short spring and autumn seasons are thus critical periods for plant growth. Summer is the most stressful season for animals and plants due to the high evapotranspiration rates during this period and the little surface water available. Winter is relatively longer compared to coastal Mediterranean arid regions, and is characterized by frequent periods of frost (Blondel et al., 2010).

The farming landscapes of the study areas consist of a mosaic of crops dominated by non-irrigated cereals (mainly wheat and barley; ca. 48% of the agricultural surface), scattered with irrigated and non-irrigated alfalfa crops (ca. 10%) and other herbaceous crops, such as sunflower, sugar beet, peas and maize (Jareño et al., 2015). These agricultural landscapes also include fallows (small and dispersed patches of uncultivated land, pastures or meadows; ca. 21% of the agricultural area) and a network of field margins (principally grassy or wildflower strips, but also linear patches of hedges or scrubs along field boundaries, tracks or roads) covering less than 5% of the agrarian surface (based on the average edge width in this study, and the average field size reported in Jareño et al. (2015)).

## 2.2. Vole trappings and abundance estimates

The monitoring of the three vole populations was conducted every 4-months (in March, July and November, hereafter referred as “spring”, “summer” and “autumn trappings”, respectively) from July 2009 to November 2014 ( $n = 17$  seasonal trapping sessions). During each trapping session in a given season and study area, we sampled the three crop types that dominate the agrarian landscape: cereal, alfalfa (including irrigated and non-irrigated crops) and “fallows” (natural or semi-natural habitats, such as uncultivated lands, meadows, pastures or set-asides). For each seasonal trapping, we selected 12 fields (4 cereals, 4 alfalfas and 4 fallows) randomly within each area amongst all the available crops. Our trapping method was extractive, in order to collect samples and detailed information on vole condition and reproduction for other aspects of our research agenda. Removing voles from sampled fields could influence subsequent local vole abundance estimates through migration movements, but in order to avoid such effects we avoided repeated trappings at the same fields in consecutive seasons and always selected fields as further apart as possible from previously sampled ones within a given 40 km<sup>2</sup> study area. Within each field (hereafter “sampling unit”), we set-up a total of 35 live traps (8 cm × 9 cm × 23 cm; LFAHD Sherman©) spaced every 2 m and forming a “T”-shape (10 traps were placed along a 20-m transect line in the field margin, and 25 traps were placed along a 50-m transect line perpendicular to the field margin and going towards the field centre (Fig. 1)). Each trap was baited with apple or carrot, which provide both food and water for trapped individuals. When the temperatures were low (autumn), hydrophobic cotton was also provided inside traps to increase vole survival. Traps were set up in the morning, were inspected after 24 h and subsequently removed.

Trapped small mammals ( $n = 6053$ ) were identified and we recorded in which individual trap each capture occurred. Most captures were of common voles (49.31%), followed by wood mice *Apodemus sylvaticus* (26.43%), Algerian mice *Mus spretus* (16.41%),

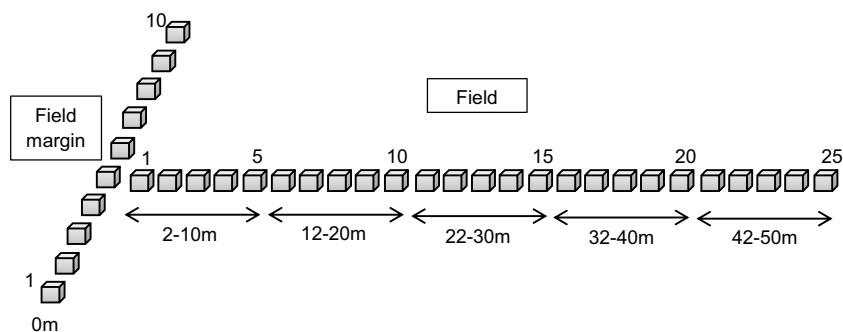
greater white-toothed shrews *Crocidura russula* (5.96%), least weasels *Mustela nivalis* (1.17%) and other species (0.71%).

For each sampling unit, we estimated: 1) the overall abundance of common vole as the number captured divided by the number of traps available for capture (the 35 set traps minus those that captured species other than common vole) and multiplied by 100 (hereafter “vole abundance”, in number of voles/100 traps/24 h). We similarly estimated: 2) vole abundance in the field margin (using the 10 traps set up in the margin, hereafter “field margin abundance”) and 3) vole abundance inside the field (using the 25 traps set up inside the field; hereafter “field abundance”).

In order to describe more precisely how vole abundance varied from the field margin towards the inside of fields, we also estimated within each sampling unit vole abundance for the following 6 distance categories (hereafter “distance to the field margin”): “0” = within the field margin ( $n = 10$  traps); “10” = traps located 2–10 m from the margin ( $n = 5$ ); “20” = the traps located 12–20 m from the margin ( $n = 5$ ); “30” = the traps located 22–30 meters from the margin ( $n = 5$ ); “40” = the traps located 32–40 m from the margin ( $n = 5$ ); and finally, “50” = the traps located 42–50 m from the margin ( $n = 5$ ) (Fig. 1). The variable “distance to the field margin” was subsequently used as a regressor, and trap groups (“0” to “50”) used as distance categories further improved convergence of capture probability models.

## 2.3. Vegetation characteristics of sampled fields and margins

We characterized the vegetation of the field and margins for 531 sampling units surveyed (due to field work constrains, not all vegetation characteristics were collected for all the sampled fields). We characterized: (1) the type of field margin, according to its topography (three categories: ditches,  $n = 290$ , flat margins,  $n = 100$ , and margins with slope > 45° (i.e., ridges),  $n = 141$ ); and (2) the margin width (in meters). Field margin topography may affect vole abundance in several ways. For instance, ditches may better retain water and tend to have denser and greener vegetation, whereas ridges could act as refuges when adjacent fields are flooded after heavy rainfall. We also characterized the following vegetation characteristics: (3) margin vegetation height (average height of the herbaceous vegetation and shrubs, in centimetres); (4) margin vegetation cover (percentage of ground covered by vegetation); (5) margin green vegetation cover (% of ground covered by green vegetation); (6) field vegetation height (average of height of the crop/fallow, in centimetres); (7) field vegetation cover (percentage of ground covered by crop/fallow) and (8) field green vegetation cover (% of ground covered by green crop/fallow). Vegetation variables were obtained by visual estimation and were indicative of the surface occupied by the line of traps (inside fields, a bandwidth of 1 m at both sides of the trapping line was considered to evaluate vegetation variables). The vegetation height



**Fig. 1.** Sampling unit (“T”-shaped trap matrix) consisting of 35 traps: 10 traps in the field margin and 25 traps inside the field. In the field, traps have been regrouped into 5 distance to the field margins categories (of 10 m each, traps being 2 meters apart).

is an estimated average between the tallest and the shortest herbaceous vegetation or shrubs.

#### 2.4. Statistical analyses

We used R v3.1.3 for all statistical analyses (R Core Team, 2015). We used Generalized Linear Mixed Models (GLMMs) and Tukey tests for post-hoc pairwise comparisons to test whether vegetation characteristics (height, cover, green cover) differed between habitats (considering four habitat types: field margin, cereal, alfalfa and fallow) by season (using separate models for spring, summer and autumn). The GLMMs included the variable “area-year” (unique combinations of study area- 3 levels- and years, 2009–2014) as random factor to account for the non-independence of abundance data collected in a given study area and year. We used GLMMs to test for differences in field margin characteristics according to season and crop type (cereal, alfalfa, fallow), including season, crop type and their interaction as explanatory variables. The variable “area-year” was used as random factor in all GLMMs performed in this study.

Differences in common vole abundance between habitats were tested by season using GLMMs and a post-hoc pairwise comparison. We also evaluated the temporal variations in vole abundance between habitats using a GLMM.

We modelled vole abundance (captures/100 traps/24 h) according to 6 distance categories to the field margin; (Fig. 1) included as a regressor using GLMMs that included the variables “sample unit” and “area-year” as random effects (to account for the non-independence of data from the same sampled unit and differences in abundance between study areas and years). The dependent variable was a two-vector response variable (number of traps that captured voles/number of traps that did not capture, for a given distance to the margin) fitted to models using a binomial error distribution and a logit link function (using the lme4 package in R; Bates et al., 2014). We analysed each crop type separately and compared three different models: (i) a null model (without the variable “distance to the margin”) that included only the explanatory variable Season; (ii) a model with a linear distance effect (abundance =  $a \times \text{Distance} + b$ ) that included the explanatory variables Distance (continuous), Season and the interaction Distance  $\times$  Season; and (iii) a model with an exponential decay distance effect (abundance =  $a \times \exp[-\text{Distance}] + b$ ) that included the explanatory variables  $\exp[-\text{Distance}]$ , Season and the interaction  $\exp[-\text{Distance}] \times$  Season. The best model(s) describing abundance variation was (were) chosen by the lowest value of Akaike’s Information Criterion (AIC). The strength of the “edge effect” (how and by how much the abundance decreases towards the inside of fields) is described by the type of model supported (from no effect – null model- to moderate effect –linear model- or strong effect –exponential decay model-) and, for a given type of model, by the values of the slope parameter estimates “a” (for a given crop type and season).

We investigated variation in the proportional abundance of voles in the field margin relative to the overall abundance in a given sampled unit using Generalized Linear Models (GLMs). The dependent variable was a two-vector response variable (abundance in the margin/overall abundance) and was fitted to GLMs using a quasi-binomial error distribution and a logit link function. For these analyses, we considered only sampled units with voles (i.e. overall abundance >0;  $n = 275$ ). Explanatory variables included vole abundance (voles/100 traps/24 h; Log-transformed), season (spring, summer autumn), crop type (alfalfa, cereal, fallow) and all the interactions between these variables. For these analyses, we were interested in identifying which variables best explained the relative use of field margins by voles, so we used a stepwise backward model selection approach. Non-significant variables (at

$P = 0.05$ ) were dropped sequentially starting with interactions following a  $F$ -test-based backward selection using the drop1 function in R.

We also investigated variation in the proportional abundance of voles in the field margin according to the margin and field characteristics using sampled units with voles (overall abundance >0) and for which we had data on all the margin and field characteristics (margin type and width, and vegetation height, cover and green cover of the margin and field). For these analyses, we considered only two crop types (alfalfa,  $n = 98$ ; and cereal,  $n = 65$ ) affected by agricultural practices and for which the field vegetation characteristics strongly varied between seasons (see results). Margin and field vegetation characteristics were weakly correlated (all  $r < 0.4$ ) and had variance inflation factors (VIF) below 1.5, so there was no issue of collinearity amongst these explanatory variables. Initial models included overall vole abundance, season, the interaction vole abundance  $\times$  season, and all the variables describing the margin and field characteristics. Non-significant variables were dropped sequentially following a manual  $F$ -test-based stepwise backward procedure removing the least significant variable at each step (using the drop1 function in R), with all terms with  $P(\chi^2) < 0.05$ .

### 3. Results

#### 3.1. Variations in common vole abundance according to habitat type and season

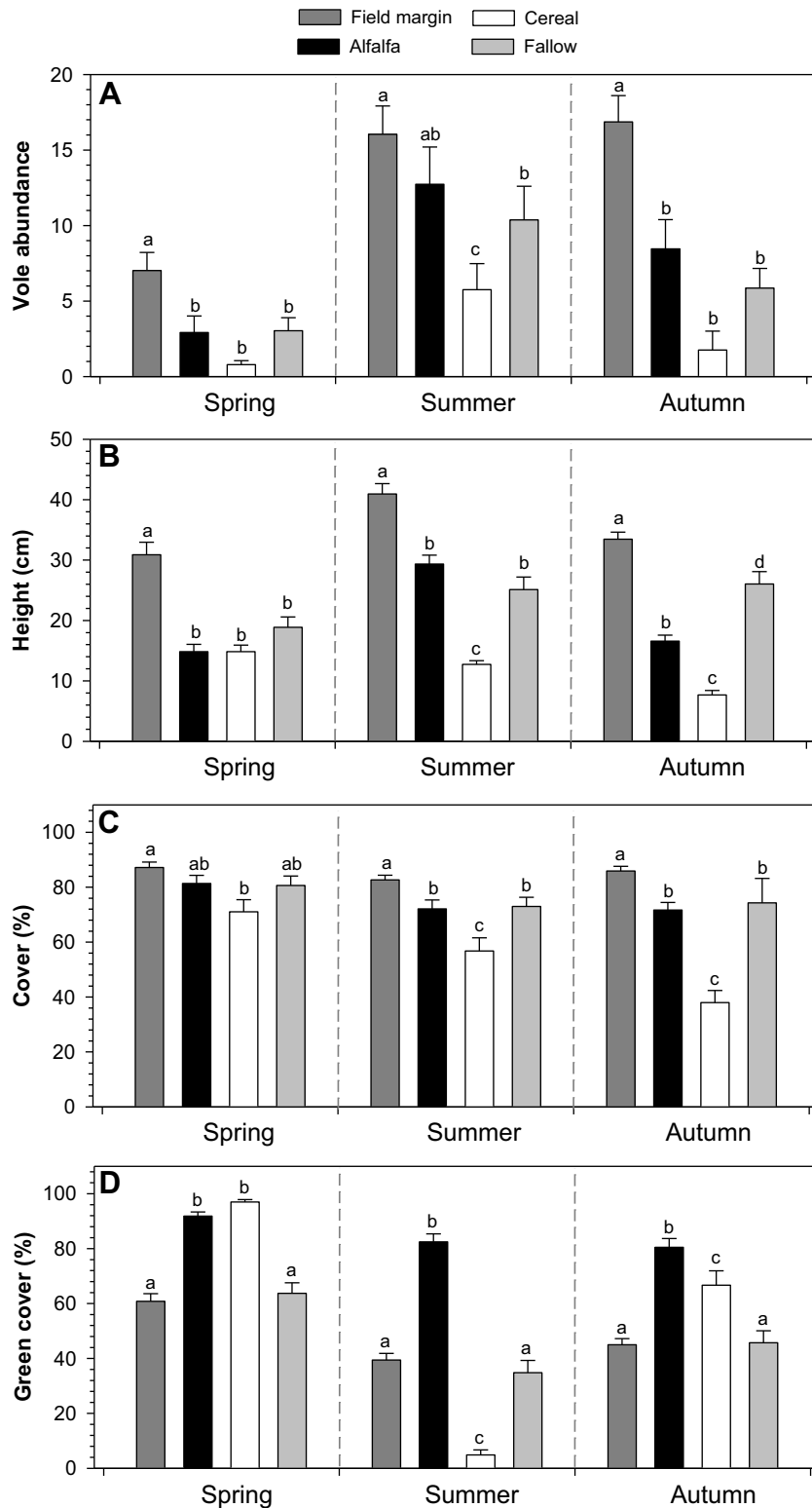
Seasonal changes in abundance consisted of lower numbers in spring followed by higher numbers in summer-autumn (Figs. 2 A; 3). Mean common vole abundance differed between habitats in all seasons (spring:  $F_{3,360} = 8.34$ ,  $P < 0.001$ ; summer:  $F_{3,432} = 15.57$ ,  $P < 0.001$ ; autumn:  $F_{3,432} = 24.00$ ,  $P < 0.001$ ; Fig. 2A) and was consistently higher in field margins than inside fields. Vole abundance was higher in field margins than in cereals in all seasons (45%, 23% and 46% higher in spring, summer and autumn, respectively). Vole abundance was also higher in field margins than in alfalfas during spring (30% higher) and autumn (26% higher), but not during summer (no significant difference). Finally, vole abundance was higher in margins than in fallows in all seasons (29, 13 and 33% higher in spring, summer and autumn, respectively).

#### 3.2. Temporal variations in common vole abundance by habitat type

When considering inter-annual seasonal variations in vole abundance, similar consistent differences among habitats were found ( $\chi^2 = 34.77$ , d.f. = 3,  $P < 0.001$ ; Fig. 3). During our study period, vole abundance peaked twice, in November 2011 and again in July 2014. Both peaks were characterized by greater vole abundances in field margins than in fields. This was particularly marked during 2011, when differences in abundance between field margins and other habitats were greatest for cereals (Tukey contrasts:  $+21.03 \pm 3.61$ ;  $P < 0.01$ ) and intermediate for alfalfas ( $+13.99 \pm 3.61$ ;  $P < 0.001$ ) and fallows ( $+12.27 \pm 3.61$ ;  $P < 0.001$ ). By contrast, during the pronounced 2014 outbreak, vole abundance increased in all habitats, including cereal crops. Again, differences were found between margins and other habitats (Tukey contrasts: Cereal crops:  $+24.87 \pm 3.45$ ;  $P < 0.001$ . Alfalfa crops:  $+12.20 \pm 3.45$ ;  $P < 0.01$ . Fallows:  $+16.83 \pm 3.45$ ;  $P < 0.001$ ).

#### 3.3. Vegetation characteristics of fields and margins

In our study areas, the width, vegetation height, cover and green cover of field margins averaged  $3.1 \pm 0.1$  m,  $35.7 \pm 1.0$  cm,  $85.2 \pm 1.0\%$  and  $47.2 \pm 1.5\%$ , respectively ( $n = 532$ ). As expected,



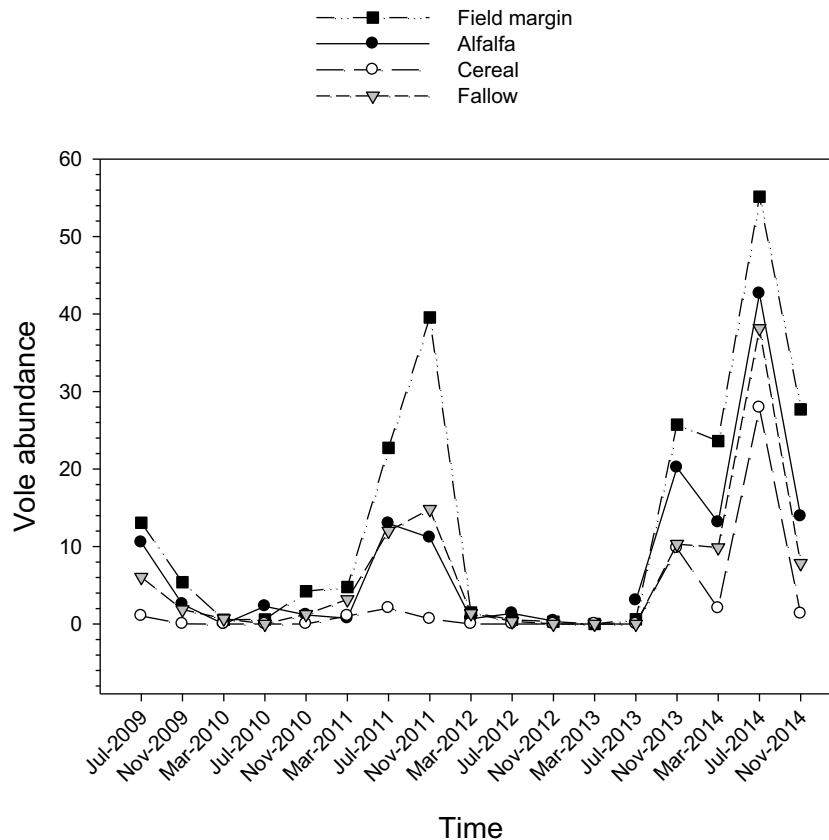
**Fig. 2.** Seasonal variations in vole abundance and vegetation characteristics according to habitat. (A) Common vole abundance (captures/100 traps/24 h), (B) vegetation height (cm), (C) vegetation cover (%), and (D) green vegetation cover (%).  $n = 531$  sampled fields. Habitat types: field margin = dark grey, alfalfa = black, cereal = white, and fallow = light grey field) and season. For pairwise comparisons within seasons, different letters indicate significant differences ( $P < 0.05$ ) between habitats (Tukey's tests) in a given season.

the seasonal variations in the vegetation characteristics of field margins were independent of the adjacent crop type (all crop type  $\times$  season interactions were non-significant), given that margins are not cultivated. Vegetation height, cover and green cover of study fields averaged  $18.7 \pm 0.6$  cm,  $68.1 \pm 1.4\%$  and

$61.5 \pm 1.7\%$ , respectively ( $n = 532$ ). However, unlike with margins, these field vegetation characteristics showed important seasonal variations, depending on crop type (Fig. 2B–D).

The vegetation characteristics of margins and fallows were overall very similar in all seasons (Fig. 2B–D), except for vegetation





**Fig. 3.** Temporal changes in common vole abundance (captures/100 traps/24 h) according to habitat type (margins=black squares; cereal=white circles; alfalfa=black circles; fallow=grey triangles) during the course of the study (July 2009 to November 2014). Abundance data are averaged for the three study areas and were collected every four months. Note the two population peaks (November 2011 and July 2014) when vole abundances were greater in field margins.

height, which was greater in margins than in fallows in all seasons (Fig. 2B). Cereal field characteristics were highly seasonal and characterised by a reduced vegetation height (Fig. 2B) and cover in all seasons (Fig. 2B), high levels of green cover in spring, but a lack of green cover in summer (Fig. 2D).

In terms of green vegetation cover, alfalfa crops had high values all year round, and were greener than other habitats in summer, that is, during the drier months (Fig. 2C), when voles were also abundant in this habitat (Fig. 2A).

#### 3.4. Spill-over: variation in vole abundance from field margins towards the inside of fields

We found that vole abundance declined exponentially with an increasing distance from the field margin towards the inside of fields. Such an edge effect was evident in all crop types (Table 1; Fig. 4) but its magnitude varied depending on crop types and seasons (see below). In all cases, the null models (no edge effect) or the linear models (linear decrease in abundance towards the interior of fields) were the least supported.

For cereal crops, the best model included the exponential decay, indicating a strong edge effect (Table 1). The Season  $\times$  exp[-distance] interaction was significant ( $\chi^2=30.22$ , d.f.=2,  $P < 0.001$ ), and slope parameter estimates comparisons among seasons indicated that the exponential decay in abundance with increasing distance to the margin was stronger in autumn (slope  $\pm$  se:  $2.161 \pm 0.439$ ) and summer ( $1.830 \pm 0.209$ ) than in spring ( $0.644 \pm 0.464$ ).

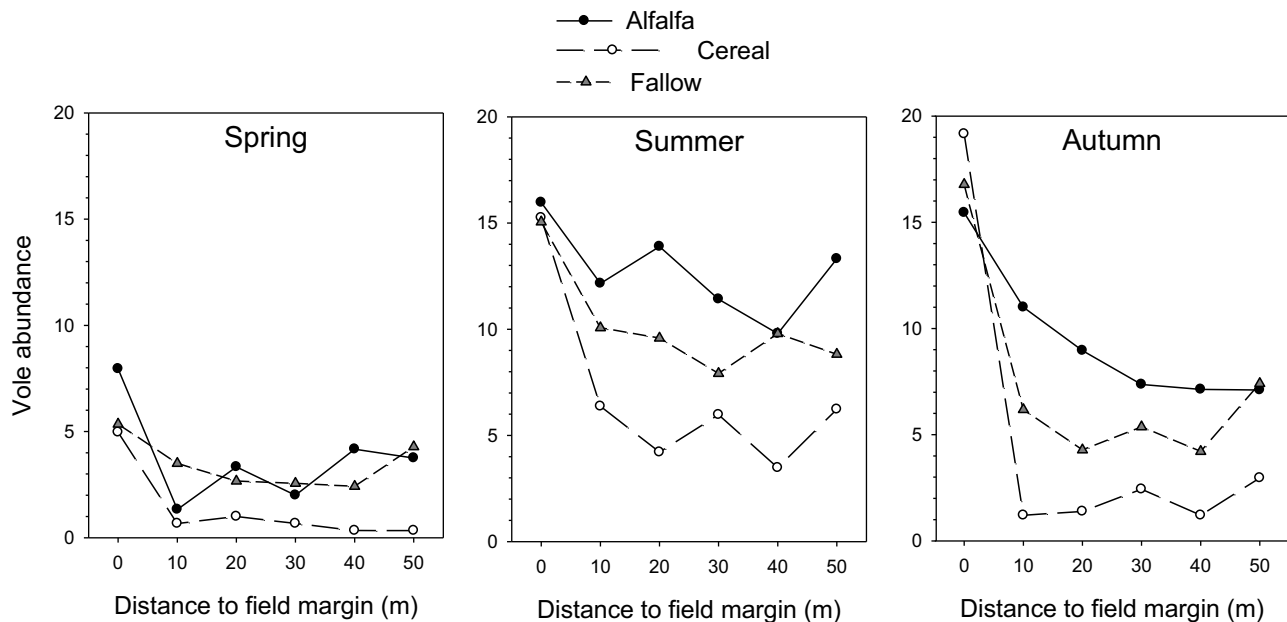
For fallows, the best model also included the exponential decay (Table 1) and the Season  $\times$  exp[-distance] interaction was significant ( $\chi^2=7.61$ , d.f.=2,  $P < 0.05$ ). The exponential decrease in abundance with increasing distance to the margin was stronger in autumn (slope  $\pm$  se:  $0.635 \pm 0.264$ ) and summer ( $0.814 \pm 0.176$ ) than in spring ( $-0.112 \pm 0.319$ ).

For alfalfa, the exponential decay model was also supported, with a significant Season  $\times$  exp[-distance] interaction ( $\chi^2=10.27$ , d.f.=2,  $P < 0.01$ ). The decrease in abundance with increasing distance to the margin was stronger in spring (slope  $\pm$  se:

**Table 1**

Results of Generalized Linear Mixed Models (GLMMs) describing how vole abundance varied with increasing distance to the field margin. The null model included Season as the only fixed effect. All other models included as fixed effects Season, Distance and the interaction Season  $\times$  Distance (see methods). The best models (lowest AICs) are highlighted in bold.

Crop type	Model	d.f.	AIC	$\Delta$ AIC
Alfalfa	Null	5	1685.84	62.88
	Linear	8	1643.17	20.21
	<b>Exp. decay</b>	8	1622.96	0.00
Cereal	Null	5	1188.62	319.80
	Linear	8	989.58	120.76
	<b>Exp. decay</b>	8	868.82	0.00
Fallow	Null	5	1440.26	76.26
	Linear	8	1400.76	36.76
	<b>Exp. decay</b>	8	1364.00	0.00



**Fig. 4.** Average common vole capture rate (captures/100 traps/24 h) according to the distance to the field margin (m), season and crop type (alfalfa: black dots-solid line; cereal: white dotted-long dashed line; fallow: grey triangles, short dashed line).

$0.843 \pm 0.301$ ) than summer ( $0.471 \pm 0.158$ ) or autumn ( $0.575 \pm 0.238$ ).

### 3.5. Proportional vole abundance in field margins according to overall abundance, crop type and season

The proportion of common voles captured in the margin as opposed to within the fields significantly varied with vole abundance depending on crop types and seasons (abundance  $\times$  crop type  $\times$  season interaction:  $\chi^2 = 14.16$ , d.f. = 4,  $P < 0.001$ ). We further explored these density-dependent patterns of margin use variation by season.

In spring, the proportional abundance of voles in margins depended on abundance and crop type (crop type  $\times$  abundance interaction:  $\chi^2 = 7.10$ , d.f. = 2,  $P < 0.05$ ; Fig. 4), with a positive relationship in cereal (estimate  $\pm$  se:  $4.042 \pm 2.113$ ,  $n = 65$ ), such that nearly all voles where in margin in spring at higher density, but there was no significant density-dependent relationships in alfalfa ( $0.036 \pm 0.448$ ,  $n = 65$ ) or in fallows ( $0.320 \pm 0.667$ ,  $n = 65$ ). When spring density increased, an increasing proportion of voles occupied the margins of cereal fields, but not of other crops (Fig. 5).

In summer, the proportion of common voles in field margins depended on vole abundance and crop type (significant interaction:  $\chi^2 = 5.08$ , d.f. = 2,  $P < 0.01$ ), with a negative relationship in cereal (estimate  $\pm$  se:  $-1.590 \pm 0.510$ ,  $n = 100$ ), but no significant relationship in fallows ( $-0.499 \pm 0.312$ ,  $n = 100$ ) and a positive trend in alfalfa fields ( $0.562 \pm 0.202$ ,  $n = 100$ ). When summer vole density increased, voles spilled over from the margins towards the inside of cereal fields, but no such density-dependent change occurred in fallow lands and alfalfa crops (Fig. 5).

In autumn, the proportion of common voles in margins also depended on vole abundance and crop type (significant interaction:  $\chi^2 = 3.78$ , d.f. = 2,  $P < 0.05$ ), with a negative relationship in cereal (estimate  $\pm$  se:  $-1.779 \pm 0.789$ ,  $n = 110$ ), and no relationship in alfalfa ( $0.274 \pm 0.258$ ,  $n = 110$ ) or in fallows ( $0.063 \pm 0.417$ ,  $n = 110$ ). As during summer, when autumn density increased, a decreasing proportion of voles occupied the margin of cereal fields, but no such density-dependent change occurred in alfalfa crops or fallows (Fig. 5).

### 3.6. Proportional vole abundance in the field margin according to vegetation characteristics

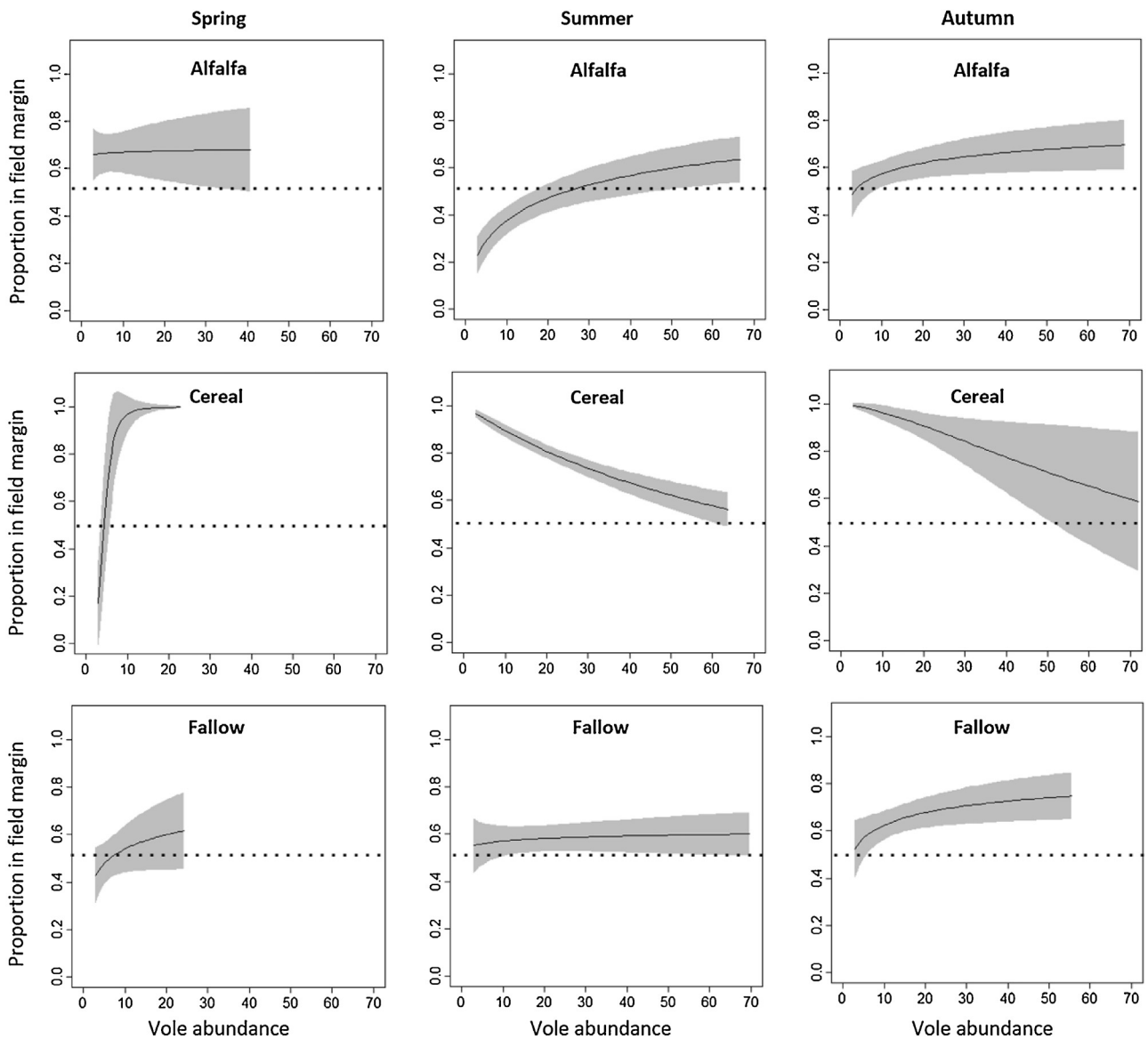
Using vole sampling occasions for which we measured vegetation characteristics (margin type and width, and vegetation height, cover and green cover of the margin and field), we further investigated whether these influenced patterns of margin use by voles in the two studied crops (alfalfa and cereal).

In alfalfa crops, the proportion of common vole in field margins varied significantly with vole abundance depending on season (abundance  $\times$  season interaction:  $\chi^2 = 71.70$ , d.f. = 3,  $P < 0.05$ ) and with crop height ( $\chi^2 = 70.90$ , d.f. = 1,  $P < 0.01$ ), but not with other vegetation characteristics of the crops or margins. The proportional abundance of voles in the margins increased with decreasing vegetation height in the alfalfa field (estimate  $\pm$  se:  $-0.0040 \pm 0.0160$ ,  $n = 98$ ; Fig. 6).

In cereal crops, the proportion of voles in field margins depended on vole abundance and season (significant abundance  $\times$  season interaction:  $\chi^2 = 22.26$ , d.f. = 3,  $P < 0.05$ ), and was also explained by crop height ( $\chi^2 = 23.35$ , d.f. = 1,  $P < 0.001$ ), margin type ( $\chi^2 = 22.22$ , d.f. = 2,  $P < 0.01$ ), margin height ( $\chi^2 = 18.69$ , d.f. = 1,  $P < 0.05$ ) and margin cover ( $\chi^2 = 19.12$ , d.f. = 1,  $P < 0.05$ ). The proportion of common voles in field margins increased with increasing margin vegetation cover ( $0.0381 \pm 0.0181$ ,  $n = 65$ ) and with decreasing vegetation height in the margins ( $-0.0332 \pm 0.0176$ ,  $n = 65$ ) and cropped field ( $-0.1316 \pm 0.0411$ ,  $n = 65$ ). Regarding differences between margin types, the proportional abundance in the margins was lower in ditches ( $0.76 \pm 0.35$ ,  $n = 35$ ) than in flat margins ( $0.89 \pm 0.13$ ,  $n = 9$ ) or in sloped margins ( $0.94 \pm 0.12$ ,  $n = 21$ ).

## 4. Discussion

Field margins represent a key habitat for common voles in the Mediterranean agricultural landscapes of southern Europe. This is in agreement with other studies conducted in northern and eastern regions of Europe, where conditions are less arid and semi-natural habitats are also optimal habitats for voles (Briner et al., 2005; Butet et al., 2006; de Redon et al., 2010; Delattre et al., 2009).



**Fig. 5.** Proportional abundance of common vole in the field margins according to season, crop type and overall vole abundance (captures/100 traps/24 h). Grey shades denote 95% confidence intervals of the predicted curves. The horizontal dotted line indicates a proportion of 0.5 (equal abundance in the margin and in the field).

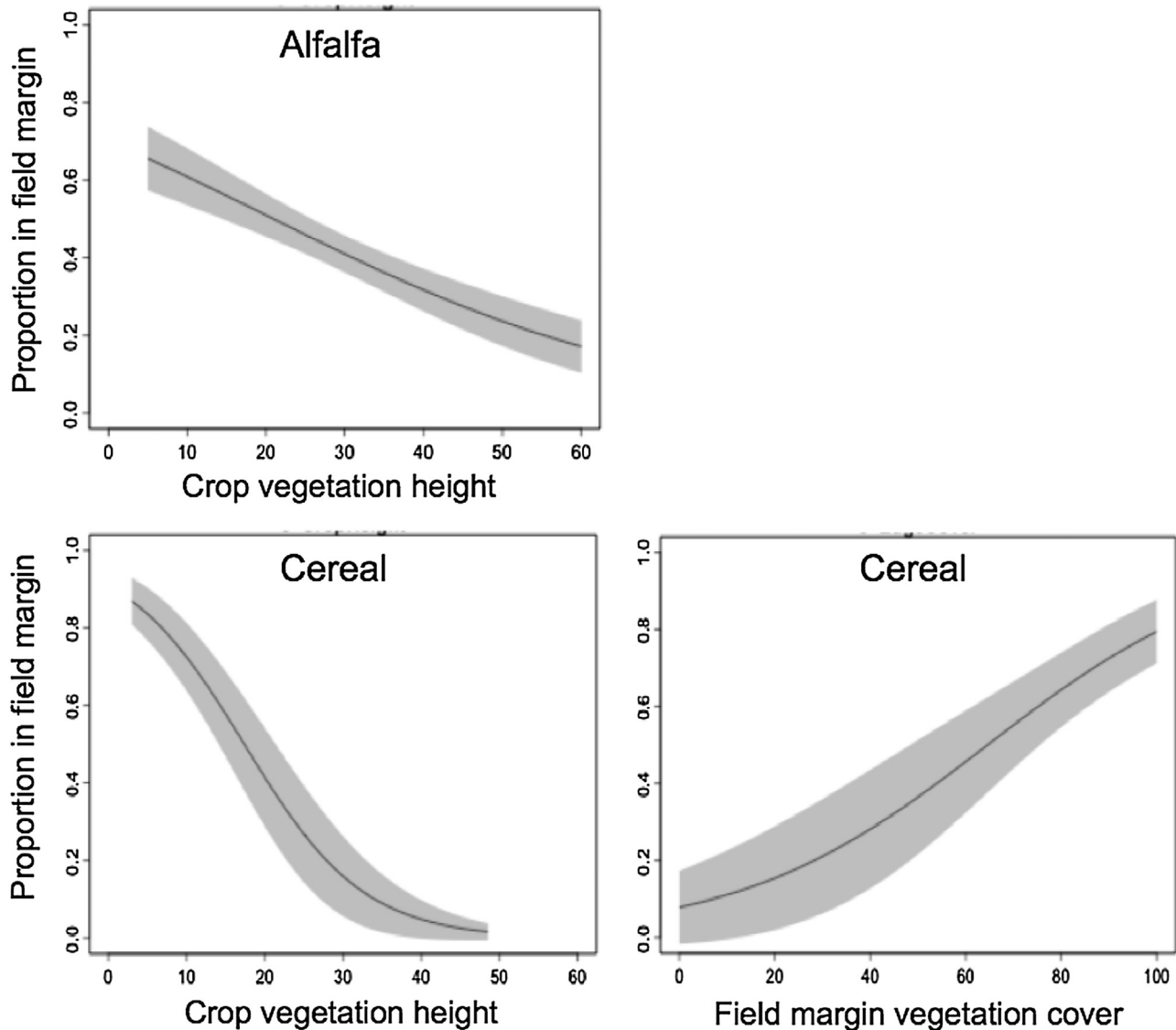
Our study is the first to highlight and quantify the use of field margins by *Microtus arvalis* in semi-arid Mediterranean farmland, where climatic conditions likely generate seasonal “bottleneck” periods, in particular the summer droughts that represent a major constraint for voles in terms of food availability and vegetation cover.

In intensive Mediterranean agricultural landscapes of NW Spain field margins are a relatively scarce habitat (less than 5% of the total agrarian surface), which nevertheless host disproportionately large abundances of common voles: about 2.3 times higher on average than within fields. The use of margins by common voles is dynamic and varied depending on crop type, season, and vole abundance, as well as according to vegetation characteristics of the margins. Remarkably, vole abundance in the margins of cereal crops was 8–9 times higher than in fields during spring and autumn. Considering our estimated vole abundances in margins vs. fields, and an estimated 5% of the agrarian surface corresponding to field margins (vs. 95% for fields), we could infer that margins host about 11% of the overall vole population in agricultural landscapes,

although this varied depending on vole density (9–15%) and crop types (Fig. 3). In the case of the margins of cereals, the dominant crop in the region (48% of the landscape), those estimates would reach 30, 14 and 34% of the overall vole population of cereals in spring, summer and autumn, respectively. By contrast, the margins of alfalfa fields would host 12, 7 and 9% of the overall vole population of alfalfas in spring, summer and autumn, respectively. Considering inter-annual variations in vole density, we observed that the greatest use of margins was for cereal crops during the (moderate) population peak of 2011, when margins hosted an estimated 53% of the overall cereal vole population. However, during the (large) population peak of July 2014, a much lower proportion of voles occupied the cereal field margins (c. 1%).

Common vole abundance in field margins varied seasonally and was low in spring (7.02 voles/100 traps/24 h), but still twice that found in the other habitats during that season. Abundance indices doubled by the beginning of summer (16.04 voles/100 traps/24 h) and reached the highest values in autumn (16.87 voles/100 traps/24 h). Such differences between margins and fields were observed





**Fig. 6.** Proportional common vole abundance in the field margins according to the characteristics of the cropped fields (vegetation height, in cm) and of margins (vegetation cover, in%). Grey shades denote 95% confidence intervals of the predicted curves.

in all habitats and have been also reported in central Europe (Janova et al., 2011), where vole abundance was always greater in field margins than in the other habitats, irrespective of the season. Field margins are key refuges in spring and, possibly, source habitats in summer and autumn, when voles move inside fields as density increases. This is particularly important for cereal crops that dominate the agrarian landscape and are particularly impacted in terms of crop damage during outbreaks. Seasonal cereal crops were found to be the least suitable habitat for common voles, with lower abundances and greater seasonal and density-dependent variations in abundance than in other habitats. The increase in vole abundance during summer and later in autumn was associated with a decrease in the proportion of common vole in margins. Again, this pattern suggests a source-sink dynamic between temporary and permanent habitats (Butet and Leroux, 2001).

A spill-over of common voles from margins towards the inside of fields was well modelled as an exponential decay in abundance with increasing distance from the margin (edge effect). This confirms a marked edge effect (Fig. 4), despite the possibility of

vole movements from the margin to a distance of 50 m inside the field (dispersing voles can move 10–100 m per day; Boyce and Boyce, 1988). Importantly, the strength of this edge effect depended on common vole density, type of adjacent field and season. In general, when maximum population density was reached, common voles spread from the margin to the adjacent field. The edge effect appeared to be weaker in alfalfa crops and fallows as compared with cereal crops, and was strongest in cereal crops in summer and autumn. This likely reflected the impact of cereal harvesting on voles at the end of summer, with the associated drastic reduction of vegetation height and cover within crops; this may also likely be associated with an increased predation risk. In addition, ploughing and sowing in autumn typically destroys vole burrows though it is known that the extent of damages to common vole population depends on the depth of ploughing (Jug et al., 2008). Thus, seasonal agricultural practices required in cereal crops (i.e., tillage) should limit vole populations to field margins (Bonnet et al., 2013). Contrary to previous observations in agricultural landscapes of central Europe, where the highest common vole abundances typically occur in cereals

during spring followed by a decrease after harvesting in summer (Bonnet et al., 2013; Gauffre et al., 2008; Janova et al., 2011), we found that vole abundances were lowest in spring and increased during summer. This may be related to the timing of the intensive ploughing activity that is recorded by the end of autumn, which destroys burrows and can literally eradicate common voles at local scale (Jacob, 2003).

With the exception of field margins, alfalfa crops harboured the highest vole abundances. Alfalfa is a multiannual perennial crop that, in our study area, remains at least five years without being ploughed and are subjected to repeated (up to 4 on average) mowing (cuts) during summer. Consequently, alfalfas provide voles with a stable habitat for underground breeding colonies and enough protective cover against avian predators, and older alfalfa fields typically harbour greater vole densities (Babinska-Werka, 1979; Heroldová et al., 2007, 2004; Jacob and Hempel, 2003). Edge effects are expected to be greater for younger alfalfa fields (more colonization from the margins) than for older ones (with already established colonies inside the field). Unfortunately, we did not know the age of sampled alfalfa fields, so we cannot exclude the possibility that we detected stronger edge effects in spring and autumn because we may have sampled a greater proportion of young alfalfa fields then. Alfalfas also offer higher quality food (high protein content) than fallows or cereal crops (Janova et al., 2008; Lantová and Lanta, 2009), which also contributes to greater vole abundances. Alfalfa crops were the habitat with the highest percentage of green vegetation cover (80–90%) from spring to autumn, providing voles with year-round green food. In field margins, fallows and cereal crops green cover ranged from 30% to 64%, with the exception of cereal in summer that had almost no green cover (c. 4%). This would imply that, in this Mediterranean landscape, fresh food availability and soil stability of alfalfa crops are not only important in summer, but also in autumn. During both seasons, common vole abundance increases and, in some occasions, reaches outbreak situations (as in November 2011 and in July 2014 in our study areas). Fluctuations in abundance of common voles in alfalfa crops were greater than in fallows. This result is in accordance with those of Janova et al. (2008) who found that populations of common voles living in alfalfa crops reached higher abundances than populations in grasses or set-aside habitats.

Although fallows and field margins had similar vegetation characteristics, they had different seasonal vole abundances. Most of the studies conducted in European temperate farmlands suggest that the suitability of fallows' vegetation for wildlife is not as high as in margins, which generally hold greater plant biodiversity (Ernault et al., 2013). In our study, however, we do not have the relevant data to evaluate this assumption. In farmland from central and northern Europe, fallows are considered as a suboptimal habitat for voles (Janova et al., 2008). The relatively lower vole abundances that fallows harbour in comparison to alfalfa crops could be explained by differences in green vegetation cover, which is higher in alfalfa than in fallows, the preferences of voles for certain plants (annual or biannual plants from fallows versus protein-rich herbaceous perennial plants from alfalfa crops) and also, for some parts of the plant, such as green parts, buds and roots from alfalfa (Heroldová et al., 2005; Lantová and Lanta, 2009). Nevertheless, fallows also represented an attractive habitat for common vole (with abundances comparable to those of alfalfas at different vole densities; Fig. 3), particularly in spring when the vegetation height of the adjacent crops is lower and fallows remain un-mowed. Although fallows occur moderately within our study area (ca. 21% of the agricultural surface), they could act as reservoir habitats from winter to spring, in addition to field margins. Both of them provide variable scenarios of stable vegetation cover

(protection against predators and a permanent food supply) and soil stability.

We also found that some vegetation characteristics of crop field affected the use of margins by common voles. The use of margins was greater when the vegetation height of cereal and alfalfa fields was lower, and was greatest in margins of cereal fields with greater vegetation cover. Vegetation cover and height are key determinants of predation risk and these observed patterns suggest that margins can be important refuges to avoid predation (Jacob and Brown, 2000). In our study, margin width averaged 3 m and did not seem to affect vole abundance, contrary to findings by Renwick and Lambin (2011) that pointed thresholds of margins width below which the vole densities quickly decrease. Finally, the topography of field margins influenced their relative use by voles, with proportionally fewer individuals in ditches than in flat or slope margins. This difference may arise because ditches usually become flooded after rainfall, mainly in winter and spring, and thus negatively affecting the survival of common vole colonies.

#### 4.1. Management implications

The management of outbreaking common voles in farming landscapes implies understanding: (1) how their populations are numerically and spatially distributed across the landscape, (2) how such distribution changes seasonally and with density, and (3) how these changes are affected by vegetation characteristics. The integration of empirical knowledge about all these aspects should facilitate the development of more explicit and scientifically-informed vole management strategies in farmland ecosystems. Our results tentatively suggest that, if preventive vole outbreak management actions were to be implemented (e.g. chemical control, vegetation burning or removal by scrapping) in semi-natural habitats, these would be more effective if they targeted only the margins of cereal fields during early spring and autumn, thereby leaving fractions of semi-natural habitats unmanaged so that other important species can persist. Indeed, spring is the time when the relative use of this habitat by voles is greatest, so targeting margin cereals in advance may contribute to reduce vole spill-overs inside fields later in summer. In our study area, the control of common voles during early outbreaks was based on chemical control campaigns at large scales, primarily using anticoagulant rodenticides. As frequently described in ecological scenarios holding chemical wars against rodents, the region also recorded major adverse toxicological effects on non-target species, including the secondary poisoning of endangered species (Sánchez-Barbudo et al., 2012). Alternative ecologically-based management actions have subsequently been promoted, such as the provision of nest-boxes to increase avian predation pressure on voles (Paz et al., 2013), deep ploughing of fields to destroy burrows, local flooding (whose effectiveness depends on field soil characteristics) or management actions on the field margins such as controlled burning and mechanical removal of soil or vegetation clearing (Caminero Saldaña et al., 2015). Most of the latter traditional management actions totally destroy vegetation (and sometimes soil horizons), affecting not only vole populations, but also numerous non-target species and biological communities (including legally protected and small game species). Field margins play a key functional role in the conservation of biodiversity in agrarian landscapes because their inter-connected webs of semi-natural habitats directly contribute to diversify agricultural mosaic systems, also enhancing the natural control of crop pests (Marshall et al., 2003). So the potential benefits of management actions on field margins (especially those that consider their physical destruction), in terms of reduced vole abundance, must be traded-off against potential adverse and cascading effects on

other species also inhabiting these semi-natural habitats (and which may contribute to maintain vole numbers down).

## 5. Conclusions

The recent occurrence of common vole populations in Mediterranean agricultural landscapes of SW Europe, where severe water deficit periods could seasonally limit the species distribution comparing with northern European latitudes, implies understanding how the species is distributed and its population dynamics. Field margins, reduced to linear patches inter-connected inside agricultural landscapes, are key habitats for common vole distribution acting as source habitats. Their vegetation characteristics remain relatively constant along time, mainly as these habitats are not subjected to farming practises altering soils such as tillage. Consequently, at high vole densities, margins act as source habitats; on the other hand, cereal crops act as sink habitats, which in farming terms is important during summer when cereal crops are totally grown and mature. The role of alfalfas as key crop habitat for common vole populations is also confirmed in Mediterranean agricultural landscapes. Despite of being mowed several times per year alfalfas typically hold well-established vole colonies over long periods of time, indicating: (1) that voles are not limited by the seasonal mowing of above ground plant parts (i.e., soil stability is putatively most relevant), and (2) that this high-protein fodder crop can effectively act as a source habitat for common vole populations across European farmlands.

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