Factors associated with the colonization of agricultural areas by common voles *Microtus arvalis* in NW Spain

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Short title: climate, land uses and vole range expansion

Abstract.

The common vole, considered a rodent pest when overabundant in agricultural areas, was traditionally absent from the agricultural plains of Castilla-y-León, NW Spain. However, it rapidly invaded ca. 50.000 km^2 of agricultural land, where regular outbreaks have caused crop damages and conflict with farmers. To better understand the factors that triggered this massive invasion of previously unoccupied habitats, we studied the associations between the common vole range expansion and changes in climate and land uses in the region since the 1970s. We found long-term trends in climate, with some changes that could have helped the range expansion (increased fall precipitation and winter temperature) and other changes that may have impaired it (reduced precipitation and increased summer temperatures). Dramatic changes in land use also took place prior to and during the invasion period (marked increases in irrigated and green herbaceous crops such as alfalfa, which are amongst the most favourable habitats for voles). We found strong associations between changes in vole distribution and the extent of green crops (irrigated crops and alfalfa) at regional level. The probability of a given agrarian county to be colonized increased with the extent of green crops, particularly so when vole presence in neighbouring counties was lower, and tended to decrease with increasing livestock abundance. Land use changes, especially increases in irrigated crops and alfalfa, appear to be one of the main drivers behind the range expansion. We discuss these findings in relation to the social conflicts and management challenges that arose from the recent invasion of agricultural areas by crop-damaging common voles.

Introduction

Biological invasions refer to range expansions of species into new areas (Valéry *et al.*, 2008). Although the term "invasive species" is often applied to species that appear in areas beyond major geographic barriers from their original distribution areas (Richardson *et al*. 2000; Collautti and MacIsaac, 2004), native species can also be invasive when they colonize new habitats (Thompson *et al.*, 1995; Davis and Thompson, 2000), particularly if they have major ecological impacts in the newly colonized habitats (Davis and Thompson, 2002). Both natural causes and human-mediated factors may lead to the disappearance of dispersal constraints and to colonization of new areas. Major distribution changes have occurred as a consequence of global transport and species trade (van der Velde *et al.*, 2006; Westphal *et al.*, 2008), climate change (Chen *et al.*, 2011; Hockey *et al.*, 2011) or human-driven land use changes (Okes *et al.*, 2008; Hockey *et al.*, 2011).

In Europe, the common vole *Microtus arvalis* (Pallas, 1778) is found in a wide variety of open habitats (meadows, forest steppes or agricultural areas) from sea level and up to 2600 m of altitude. The common vole is herbivorous and prefers the green parts of grasses and herbaceous vegetation (Jacob *et al.*, 2013). It is considered a rodent pest in most of its distribution range because of significant crop damage and associated economic losses during population outbreaks (Babinska-Werka, 1979; Jacob and Tkadlec, 2010). Until recently, the common vole distribution range in the Iberian Peninsula was restricted to mountain areas in the northern half of Spain, where it occupied stable habitats with high herbaceous or shrub cover (Gonzalez-Esteban *et al.*, 1995). However, at the end of the 20th century, this species rapidly invaded the central plains of Castilla-y-León, a semi-arid agricultural area of ca. 50.000 km^2 located in north-central Spain (Luque-Larena *et al.*, 2013). Since the range expansion, common vole population outbreaks in farmland areas have occurred regularly, causing significant economic losses to agriculture, as well as environmental impacts associated with the use of rodenticides for controlling vole populations, or zoonotic outbreaks of Tularemia (Luque-Larena *et al.*, 2013). In farmland areas of northern Spain, the common vole fits the definition of an invasive species (Davis and Thompson, 2002), as it greatly extended its range into a previously unoccupied region where it now has strong environmental impacts.

This study focuses on the factors that triggered this recent and massive invasion of agricultural areas. It is well known that rodents have the potential to rapidly respond demographically to climate or land use changes, with documented cases of fast range expansion when conditions are favourable (Singleton *et al.*, 2010). Climate is known to influence common vole abundance in continental Europe (e.g. Straka and Gerasimov 1971; Tkadlec *et al.*, 2006; Esthera et al. 2014). All climate change scenarios for Spain predict a uniform increase in temperatures, particularly in summer, and a reduction in total annual precipitation, especially in spring and summer (Moreno, 2005). The recently invaded area is characterized by a climate that could be considered “a priori” as suboptimal for the species due to prolonged summer droughts, a major constrain for a rodent relying on green herbaceous vegetation. Models based on current climate change scenarios indeed predict a future shrinking of the common vole distribution range in Spain, which is expected to be increasingly restricted to the mountain ranges of the northern half of the Iberian Peninsula, or even just to the Cantabrian Mountains and the Pyrenees (Araujo *et al.*, 2011). Agricultural intensification has led to a homogenization of the agrarian landscape of Castilla-y-León, which has been proposed as a major factor promoting vole expansion (Gonzalez Esteban *et al.*, 1995). Simplified habitats, which usually have fewer predators (Delattre *et al.*, 1999), may be easier to invade by new species (Ligtvoet and van Wijngaarden, 1994). However, other changes have occurred in the agro-environment during the same period, like changes in cultivated crops, livestock densities, increased mechanization, use of improved pesticides and fertilizers, or the development of non-tillage techniques, which may have also affected the availability of suitability habitats for voles. In France, common vole abundance and damage to crops are associated with areas with abundant grassland or with a highly connected grassy network (Delattre *et al.*, 1992; Delattre *et al.*, 1996; Delattre *et al.*, 1999), while cereal is considered a sub-optimal agrarian habitat as compared to other crops, such as alfalfa (Delattre *et al.*, 1992; Jacob *et al.*, 2014). Land use changes potentially favourable to the common vole would be an increase of grassy multiannual crops, especially alfalfa, one of the preferred habitats of common voles (Janova *et al.*, 2011; Jareño *et al.*, 2014), as well as an increase in irrigation, which would promote green vegetation cover and thus food availability, particularly during the dry summers that characterize the climate of NW Spain. By contrast, a reduction of fallows would reduce areas with natural vegetation, being potentially negative for the species. Changes in free-ranging livestock abundance could also affect common voles, as increased grazing pressure may reduce food availability for voles and increase predation risk. Livestock presence could also hamper the burrowing activity of voles due to soil compacting. Several studies in Europe have associated increases in sheep grazing pressure with reduced vole abundances (Steen *et al.*, 2005; Evans *et al.*, 2006; Wheeler, 2008; Villar *et al.*, 2013), and this relationship has also been found in Spain between the common vole and cattle (Torre *et al.*, 2007).

In this study, we investigated the relative importance of both climate and land use changes as factors explaining the recent invasion of farmland areas by common voles in NW Spain (Luque-Larena *et al.*, 2013). We hypothesized that the rapid range expansion by *M. arvalis* may have been triggered primarily by large-scale land use changes that took place in the newly colonized areas. We tested for temporal trends in climate and land uses, expecting the range expansion to be associated with changes *a priori* more favourable for voles (increases in winter temperature, spring-summer precipitation or reductions in summer temperature; increases in alfalfa and irrigated crops, reductions in livestock abundance). We discuss the implications of our findings for management of out-breaking vole populations in the recently invaded farmland areas.

Material and Methods

Study area

We studied changes in common vole distribution in the autonomous region of Castilla-y-León, an area of 9.422.100 ha located in the northern plateau of the Iberian Peninsula (Fig. 1). This region is divided in 9 administrative provinces and 59 agrarian counties ("*comarcas agrarias*"), holds the entire upper catchment area of the Duero river and includes central plains dedicated to agriculture (ca. 3.7 million ha) surrounded by mountain ranges (Fig. 1). Land uses changed over years (see results and Fig. S1). Towards the end of the study period (in 2010) they included mostly agricultural crops (37 % of the regional surface, with higher percentages in the central plains: e.g. 70 % in the central province of Valladolid), forests (31 % of the regional surface; higher percentages in provinces with mountain ranges, e.g. 49 % in the León province), and pasture land (25 % of the regional surface; with higher percentages in provinces with mountain ranges, e.g. 41 % in the Avila province; source: "Anuario de Estadística" 2011, Spanish Ministry of agriculture).

Common vole distribution data

Scientific and technical information on vole distribution was reviewed for the whole region and consisted of presence-absence data at the agrarian county levels in the following years: 1973, 1978-79, 1988, 1993-1994, 2002 and 2007 (Luque-Larena *et al.*, 2013, and references therein). In the early 1970s, common voles were present in 35 of 59 agrarian counties. By 1993-94 most of the region was colonized, and colonization was complete by 2002 (Luque-Larena *et al.*, 2013). Based on the available information, we summarized common vole distribution data at two spatial levels: (1) at the regional level, by using the % of agrarian counties with common vole presence at a given time (hereafter referred as to "regional vole occupancy"); and (2) at the agrarian county level, using presence/absence data in each county at a given time. At this level, we focused for analyses on those counties where voles were originally absent and that were subsequently colonized in the time period 1973-1993 (Luque-Larena *et al.*, 2013). For each focal agrarian county, we estimated neighbouring vole occupancy prior to a potential colonization event, using the % of adjacent counties in which the common vole was already present (hereafter referred as to "neighbouring vole presence level"). We estimated colonization speed (km^2 colonized per year) at different time intervals (1973-1979; 1979-1988 and 1988-1994) as the surface area (in km^2) of newly colonized counties during each period, divided by the number of years of each interval. Because vole occupancy data at regional level were available at only six time intervals between 1973 and 2007, we modelled regional vole occupancy in order to obtain a continuous yearly time-series of vole occupancy (see results) for further analyses.

Comentario [FM1]: Podemos citar una fuente para las superficies de las comarcas??

Climate data

The climate of Castilla-y-León can be characterized as Mediterranean with continental influence. Annual precipitation in the central plains ranges from 350 to 550 mm, mostly concentrated during winter and spring. Winters are cold while summers are typically dry and hot. Summers are characterized by a long drought period with reduced natural green vegetation, which lasts longer in central plains than in the mountain areas originally occupied by common voles. We obtained climate data for the period 1962-2002 from 70 weather stations located across the whole Castilla-y-León region (source: AEMET, National Meteorological Agency; http://www.aemet.es/). These climate data were summarized as seasonal average temperature (°C) and precipitation data (mm of rain) for winter (January-March), spring (April-June), summer (July–September) and fall (October-December). We selected the year 1962 as the beginning of the time series as this was the first year for which we had complete information on land use data (see below). We wanted to include climate and land use data prior to the beginning of the colonization to test for possible lagged effects (e.g. changes taking place prior to the colonization that may have set a favourable context for colonization to occur). The final year was 2002, when the regional colonization process by common voles was completed (Luque-Larena et al. 2013).

Land use data

We obtained yearly land use data for the period 1962-2002 from the “Ministerio de Medio Ambiente y Medio Rural y Marino” of Spain (http://www.magrama.gob.es/), for each province and thus the whole region. This consisted of the surface area (in *ha*) of irrigated and non-irrigated crop types (alfalfa and cereal, ie. wheat or barley), of other herbaceous crops (mostly corn, sugarbeet, sunflower and potato, hereafter “others herbaceous crops”) and of non-irrigated fallow land. Land use composition changed during the course of the study period (see results and Fig. S1). By the end of the study period (2010), wheat and barley were the most common crops (e.g. 48 % of the entire agricultural surface). In most agricultural areas, fallows are the only habitat with natural grassy vegetation (21 % of the agricultural surface in 2010), along with field margins and other small and dispersed uncultivated patches. Permanent and semi-permanent grasslands are common in the original distribution area, but scarce or absent in the newly invaded area, limited to mainly small and dispersed patches. Other herbaceous crops represented 27% of the cultivated area in 2010, and woody crops 2.5 %.

Comentario [BAL2]: Podríamos eliminar esto, suena un poco repetitivo (aunque no lo es)

We also obtained yearly data on livestock abundance for the period 1962-2002, specifically cattle, sheep and goat numbers, from the "Ministerio de Medio Ambiente y Medio Rural y Marino" of Spain. For the land use PCA (see below), we combined sheep and goat numbers due to their similar corporal mass and the presence of mixed flocks in Spain (Garcia *et al.*, 2013).

Statistical analyses

We used the R (R Development Core Team, 2011) and PAST (Hammer *et al.*, 2001) softwares for statistical analyses. We first modelled the trends in regional vole occupancy across time to get yearly occupancy estimates, by fitting a 4 parameters sigmoid curve [y=y0 + a/(1+exp(-((x-x0)/b))] using non-linear regression fitting implemented in R to estimate the parameters (y0, a, x0 and b). This allowed us to estimate vole occupancy data each year and to obtain a continuous time series of annual vole occupancy data at the regional level ("vole occupancy"), which was used for subsequent cross-correlation analyses with climate and land use annual data.

To reduce the number of climate variables (average precipitation and temperature data for spring, summer fall and winter) and of land use variables (surface area for each crop type, livestock numbers), we conducted two separate Principal Component Analyses (PCA) for climate and land use variables, respectively. We considered Principal Components (PCs) that explained >10% of variance for subsequent analysis. We analysed trends in climate and land use data using linear regression models (to test for linear trends during the study period) and piecewise regressions (to test for possible changes in linear trends before and after a certain year or cut-off point). We present results of the model that best fitted the data. We tested for temporal associations between climate / land use variables and modelled annual vole occupancy data using cross-correlation analyses implemented with the PAST software (Hammer *et al.*, 2001).

Comentario [BAL3]: Algo asi tenemos que decir ya que luego solo presentamos uno de los dos como nos pedia el referee

At the agrarian county level, we tested whether the probability that a given county was colonized by common voles during a given time period depended on the “neighbouring vole presence level” (% of nearby agrarian counties already occupied by the common vole), the extent of agrarian habitats “a priori” most favourable to common voles (irrigated herbaceous crops and alfalfa, referred as to “green crops”, in % of the cultivated surface; Jareño et al. 2014), and livestock (cattle, sheep and goat) abundance prior to a potential colonization event (“a priori” unfavourable to common voles). For the latter two variables, we used data from the province where each agrarian county was located (because such information was not available at the agrarian county level). The dependent variable (colonization probability, coded as 0=not colonized, 1= colonized) was fitted to a mixed model using a binomial distribution of error and a logit link function, with the variable “county” included as a random factor. Initial models included “neighbouring vole presence level”, “green crop extent”, “livestock abundance” and all the two-way interactions between these variables. Non-significant variables were dropped sequentially starting with interactions following a stepwise backward procedure (using the drop1 function in R). This function compares models with and without variables/interactions with LR chi^2 tests on AIC variations of those models.

Comentario [BAL4]: No sé si merece la pena poner esto, pero puede que sí.

Results

Vole range expansion

At the regional level, the vole range expansion started in the second half of the 1970s and was almost completed by the mid-1990s. Colonization speed between 1973 and 1994 averaged 2050 km^2/year, and was faster at the beginning of that period that at the end (2866 km^2/year during 1973-1979; 2175 km^2/year during 1979-1988 and 1097 km^2/year during 1979-1994). Changes in vole occupancy fitted well a sigmoid growth pattern ($F=812.4$, $P<0.0001$; $R^2=0.99$; Fig. 2), allowing us to model annual vole occupancy for the whole study period [Occupancy=0.435±0.006 + 0.572±0.008/(1+exp(-((Year-1978.520±0.194)/6.126±0.169)]. For subsequent analyses, we used these modelled vole occupancy data.

Climate trends at the regional level

The PCA conducted on seasonal climate data for 1962-2002 provided four climate Principal Components explaining more than 10% of variance (Table 1). Climate PC1 explained 25.6% of the variance and contrasted warmer winters and autumns and wetter autumns (positive loadings) with dryer winters (negative loading). Climate PC2 explained a further 20.5% of variance, and contrasted warmer springs and summers (positive loadings), with dryer springs (negative loading). PC3 explained a further

16.2% of variance, and contrasted wetter summers (positive loading) with colder winters and summers (negative loadings). Finally, PC4 contrasted wetter winters and autumns with dryer summers (Table 1).

We found significant temporal trends for climate PC1 and climate PC3, but not for climate PC2 or PC4 (Table 2). For climate PC1, a linear regression model indicated a significant positive trend for 1962-2002 (Table 2; slope ± se = +0.07 ± 0.02; Fig. 3a). For climate PC3, no significant linear trend was found for 1962-2002, but the piecewise regression identified two trends with a cut-off point in 1978, with a positive trend for 1962-1978 (slope= 0.08 ± 0.09), followed by a drop in 1978 and a lesser positive trend (slope= 0.04 ± 0.04 for 1978-2002; Table 2; Fig. 3b). In terms of climate trends, we therefore had evidence for a change in 1962-2002 towards relatively warmer winters and autumns, wetter autumns, and dryer winters, particularly after 1981. We also had evidence for a shift in climate PC3 after 1978, with relatively warmer winters and warmer and wetter summers during 1978-2002 as compared with 1962-1978. These climate trends were however weak (slope parameters close to zero).

Comentario [BAL5]: Bueno, esto depende de las unidades usadas (si usaramos centésimas de grado no serian close to zero). Para comparar el strenght del pattern con los de land use tendríamos que usar datos estandarizados…

Land use trends at the regional level

Marked changes in land uses occurred during the study period. Cultivated areas with non-irrigated and irrigated alfalfa increased 3- and 6-fold, respectively, those with irrigated and non-irrigated cereal increased ca. 1.5-fold, and those with other irrigated herbaceous crops increased 2-fold increase until the end of the 1980s (supplementary material, Fig. S1). By contrast, areas cultivated with non-irrigated herbaceous crops and fallows decreased (Fig. S1). In 1962-1992, the area occupied by non-irrigated cereals, irrigated cereals, and for other irrigated crops increased by 42%, 174% and 77%, respectively (Fig. S1). In 1962-1979, the surface area occupied by non-irrigated and irrigated alfalfa increased by 398% and 230% respectively (Fig. S1). Cattle numbers increased during the study period, while sheep and goat numbers decreased until 1980, and increased afterwards until the end of the 1990s (Fig. S2).

We summarized yearly land use data using a PCA (Table 3). The first PC (land use PC1) explained 59.8% and variance, positively correlated with the extent of irrigated and non-irrigated cereal, the extent of other herbaceous irrigated crops, except alfalfa, and cattle numbers, and negatively correlated with the extent of fallows and non-irrigated other crops (Table 3). Land use PC2 explained a further 25.8% of variance, positively correlated with the extent of irrigated and non-irrigated alfalfa, and negatively correlated with the extent of non-irrigated other crops, sheep-goat and cattle numbers (Table 3). Analyses of trends in land uses, as summarized by land use PC1 and PC2, indicated statistically significant temporal increases, which were best described by piecewise regressions rather than by linear regressions (Fig. 4; Table 2). Land use PC1 showed a marked increase in 1962-1992 (slope ± se = +0.27 ± 0.09), followed by a continued but lessened increase in 1992-2002 (slope = +0.20 ± 0.04). Land use PC2 showed a marked increase in 1962-1979 (slope = +0.22 ± 0.03) followed by a decrease in 1979-2002 (slope = -0.24 ± 0.01).

Temporal associations between vole occupancy and climate or land use

The cross correlation analyses between climate PC scores and regional vole occupancy data showed an association with climate PC1 only, with significant positive correlations for time lags between -8 to +2 years (correlation coefficients of 0.38-0.58; Fig. 5). The increase in vole occupancy appeared associated with a trend for increased winter and fall temperature, increased fall precipitation and reduced winter precipitations.

Comentario [FM6]: Indicate here the range of estimated correlation coefficients between climate PC1 and regional occupancy (approximately ≈0.4-0.6 ?)

The cross correlation between land use PC scores and regional vole occupancy data showed a strong positive association with land use PC1 for time lags between -16 to +2 years, and with land use PC2 scores for time lags between -16 to -9 years (all correlation coefficients > 0.86, Fig. 5). In other words, the vole expansion appeared to have followed the changes in land uses summarized by land use PC1 scores (increases in irrigated and non-irrigated cereals, and in other irrigated crops), as well as those described by land use PC2 scores (increases in non-irrigated and irrigated alfalfa), but with a greater time lag for the latter.

We further looked at the association between the changes in the extent of "green crops", i.e. those "*a priori*" most favourable to common voles (i.e. irrigated herbaceous crops and alfalfa, the crop types that had high positive loadings in the first two land use PCs; Table 3). At the regional level, the vole expansion appeared to have closely followed the increase in the extent of green crops (Fig. 4b), with positive cross-correlations for time lags between -15 to -1 years (all coefficients > 0. 87, all P < 0.01).

Vole colonization at the agrarian county level

The probability of colonization of a given agrarian county by common voles was significantly explained by its "neighbouring vole presence level" (χ^2=9.86; df = 1; p = 0.002) and by a significant interaction between the extent of green crops and the "neighbouring vole presence level" (green crops: χ^2= 3.68; df = 1; p = 0.055; interaction: χ^2= 3.79; df = 1; p = 0.045; Fig. 6). An association with livestock abundance was also marginally significant (χ^2= 2.84; df = 1; p = 0.092). For a given county to be colonized, common voles had to be already present in nearby adjacent county, and the greater the "neighbouring vole presence level", the greater the probability of colonization (Fig. 6a). In addition, colonization probability increased with the extent of green crops (Fig. 6b), particularly so when neighbouring vole presence levels was lower (Fig. 6d), and tended to decrease with increasing livestock abundance (Fig. 6c).

Discussion

Climate, land use and common vole range expansion

Our results support the hypothesis that the rapid range expansion and invasion of hitherto unoccupied farmland areas of Castilla-y-León by common voles was more closely associated with land use changes than with climate changes. The climate trends detected during the study period were overall weak, and the only observed climate trend that correlated with common vole occupancy data was a trend for increased winter and fall temperatures, increased fall precipitation and reduced winter precipitation (climate PC1). An increase in winter temperature and fall precipitation could increase vegetative growth during winter and thereby be favourable to common vole (Tkadlec *et al.*, 2006). Positive associations between common vole abundance and winter temperature have been found in the original distribution area (Fargallo et al., 2009), as well as an association between rainfall and vole abundance (Veiga, 1986; Fargallo *et al.*, 2009). Winter temperature is considered a crucial element in vole demography, and the upward recent trend reported for this meteorological variable at continental scale in Europe has been associated with large-scale synchronous changes in vole demography (Cornulier *et al.*, 2013). On the other hand, increased fall precipitation could be associated with more frequent flooding, detrimental to common voles (Jacob, 2003). Other climate temporal changes observed included a trend towards warmer and dryer summers during the expansion (as indicated by climate PC3 changes), which can be considered unfavourable for voles. Altogether, associations between climate changes and the vole expansion were weak and inconclusive, with some changes that could be favourable to voles as well as others that were most likely unfavourable. Therefore, climate trends alone do not appear to be sufficient to explain the fast vole expansion.

By contrast, we found significant and dramatic changes in land uses during the study period, which appeared more closely associated with the changes in vole occupancy. Most noticeably, a marked increase occurred in the surface areas used for cultivating “green crops” (alfalfa, irrigated cereal and other irrigated herbaceous crops), to the detriment of non-irrigated herbaceous crops and fallows, which could be the most important underlying cause of invasion of farmland areas by voles. The association between vole occupancy and green crop surface extent was apparent at regional and at agrarian county levels. Green crops could be particularly important for common voles during dry periods, particularly in summer, by providing them with food when it would be scarcest, either from the crop itself or from the improved green vegetation in irrigated field margins, which are a particularly important habitat for voles in this agricultural area (Jareño *et al.*, 2014). Moreover, alfalfa is one of the preferred habitats for the common vole in agricultural habitats in Europe (Janova *et al.*, 2011), as well as in the study region (Jareño *et al.*, 2014). Within alfalfa, voles find refuge, quality food and stability to build their colonies, since they are not ploughed during the 5-7 years production cycle. Green crops also include irrigated cereal fields, a suboptimal habitat because of recurrent disturbance by ploughing in summer after harvest (Jacob *et al.*, 2014). However, cereal could also be an important temporal habitat until harvest or in years of high abundance (Bonnet *et al.*, 2013). More research would be needed to better understand the importance of cereal fields for vole demography, and their role in the invasion of agricultural areas.

Other land use changes could also have facilitated vole expansion. For example, data from agrarian municipal censuses (carried out every 10 years, REF) show an increase in mean field size (Fig. S3), which suggests that the agrarian landscape became more homogeneous during the study period. Common voles are more abundant in homogeneous habitats (Fischer *et al.*, 2011). This may be because there are fewer refuges for predators and a reduced species richness overall (Benton *et al.*, 2003; Pereira *et al.*, 2010), which could facilitate vole expansion (Gonzalez Esteban *et al.*, 1995) or affect vole abundance fluctuations and thus colonization potential (Delattre *et al.*, 1999). On the other hand, increases in field size would imply a reduction of areas occupied by field margins, which are crucial for voles in the study area (Jareño *et al.*, 2014) as well as elsewhere (Delattre *et al.*, 1992; Delattre *et al.*, 1996; Delattre *et al.*, 1999). However, the reduction in the area occupied by field margins could have been compensated through the increase in the area occupied by irrigated fields improving habitat quality of remaining margins, a hypothesis that deserves further attention. Further studies on the effect of landscape scale changes in habitat structure (e.g. changes in field size and edges) that went along with the reported land use changes would also be useful to get a more precise idea of how predation may have interacted with land use changes in facilitating vole expansion (Kraehenbuehl *et al.*, 2010).

Finally, the reduction in sheep and goat numbers at the beginning of the study period, which mostly occurred in the northern and southern areas of Castilla-y-León (Fig. S2), i.e. in the original vole distribution areas, could have been favourable for the common vole expansion, as sheep grazing is known to reduce vole abundance (Steen *et* *al.*, 2005; Evans *et al.*, 2006; Wheeler, 2008). Indeed, colonization probability was marginally lower with higher livestock abundance. The reduction in sheep abundance could thus have contributed to vole population increases in the original distribution areas, facilitating colonization through dispersal. By contrast, the overall increase in cattle numbers throughout the time period would have been negative, as free-ranging cattle abundance negatively affects common vole abundance (Torre *et al.*, 2007). However, most of this increase in the study area was feedlot cattle (Domínguez-Martín, 2001; Garcia *et al.*, 2013), although the intensification was not so pronounced in the southern area (Milan *et al.*, 2006), where most of the overall increase occurred (Fig. S1 & S2).

Finally, other factors not contemplated in this study could also have favoured the colonization, like for instance changes in the distribution or abundance of vole predators. Unfortunately, the lack of information at the required spatial and temporal scales prevented investigating the relative importance of this driver in the range expansion.

Conclusions and implications:

Our results suggest that the common vole expansion in Castilla-y-León and the rapid invasion of hitherto unoccupied farmland areas was primarily associated with land use changes that took place prior to and during the colonization period, in particular increases in irrigated crops and alfalfa. Establishing such a link has implications for the management of voles and their outbreaks in farmland areas. As soon as the common vole colonized the agricultural plains of Castilla-y-León, regular crop damaging outbreaks have occurred (Luque-Larena *et al.*, 2013). This has created serious social unrest among farmers, who have urged governments to find solutions to the problem. This has prompted occasional large-scale and/or intensive vole control campaigns (Jacob and Tkadlec, 2010; Luque-Larena *et al.*, 2013), which have been criticized in other sectors of society: e.g. the chemical control campaigns have caused undesirable environmental impacts, through the poisoning of non-target species (Olea *et al.*, 2009; Sanchez-Barbudo *et al.*, 2012). Partly, the expectation of farmers has been to "get rid" of the invasive species that caused the problem. However, the land use changes promoted by farming have modified the landscape turning it beneficial for the common vole, and this is unlikely to change. This is because these changes are associated with a more economic approach to agriculture, higher revenues, and higher demands of certain crops (e.g. yields were c.175% greater for irrigated than for non-irrigated alfalfa in 2010). Therefore, current farming systems of Castilla-y-León are unavoidably concomitant with vole occurrence, and that these systems need to integrate long-term, sustainable, ecologically and economically viable ways of dealing with this species as part of the ecosystem. This study highlights that large-scale human-driven habitat changes may be key processes in driving biological invasions.

Comentario [FM7]: Ref. 1 asks to delete (speculative)

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Con formato: Español (alfab. internacional)

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Comentario [FM8]: To check against references cited in text

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Tables

Table 1. Results of the Principal Component Analysis of regional seasonal climate data (1962-2002). Climate PC5 explained only 8.5% of the variance and was not considered for subsequent analyses.

	Climate PC1	Climate PC2	Climate PC3	Climate PC4
Winter Temperature	**0.378**	0.166	**-0.457**	0.040
Spring Temperature	0.299	**0.592**	0.074	0.026
Summer Temperature	-0.016	**0.336**	**-0.66**	-0.138
Fall Temperature	**0.493**	-0.253	-0.115	0.311
Winter Precipitation	**-0.436**	0.167	0.08	**0.554**
Spring Precipitation	-0.004	**-0.600**	-0.284	-0.291
Summer Precipitation	0.299	0.159	**0.463**	**-0.537**
Fall Precipitation	**0.496**	-0.176	0.186	**0.449**
Variance explained				
-Proportion:	0.256	0.205	0.162	0.136
-Cumulative	0.256	0.461	0.623	0.759
Eigenvectors	2.044	1.64	1.299	1.092

Table 2. Results of the analyses exploring temporal trends in climate or land use variables (PC scores – see Tables 1 and 3) for the period 1962-2002 for the whole Castilla-y-Léon regions. We tested for linear trends using linear regressions, and for potential changes in linear trends before/after a certain year using piecewise regressions. Significant trends are highlighted in bold.

	Linear regression $F_{1.39}$	P	R^2	Piecewise regression $F_{3.37}$	P	R^2
Climate variables						
Climate PC1	**18.7**	**<0.001**	**32.41**			
Climate PC2	0.068	0.796		2.795	0.054	
Climate PC3				**3.122**	**0.037**	**20.20**
Climate PC4	0.249	0.620	-1.91	2.448	0.079	16.56
Land use variables						
Land use PC1				**346.3**	**<0.001**	**96.56**
Land use PC2				**216.1**	**<0.001**	**94.60**

Table 3. Results of the Principal Component Analysis of regional annual land use data (1962-2002). Land use PC3 explained only 6.9% of the variance and was not considered for subsequent analyses.

	Land use PC1	Land use PC2
Non-irrigated Cereal[1]	**0.392**	0.125
Irrigated Cereal[1]	**0.404**	-0.094
Non irrigated Other Crops[2]	**-0.362**	-0.258
Irrigated Others Crops[2]	**0.381**	-0.134
Non irrigated Alfalfa	0.296	**0.408**
Irrigated Alfalfa	0.196	**0.526**
Fallows	**-0.38**	0.272
Bovine cattle N.	**0.352**	**-0.335**
Sheep & Goat livestock N.	0.11	**-0.512**
Variance explained		
-Proportion	0.598	0.258
-Cumulative	0.598	0.856
Eigenvectors	5.39	2.32

[1] cereal= wheat or barley

[2] Includes maize, sugarbeet, sunflower, pea and oats.

Figure legends

Figure 1. Map of the study area (Castilla-y-Léon region, NW Spain) showing the boundaries (thickest black contour lines) and names of the 9 provinces, and the boundaries of agrarian counties (thinner black contour lines). The map also illustrates changes in vole occupancy at the agrarian county level for the period 1973-2002 (data from Luque-Larena et al. 2013).

Figure 2. Changes over time in vole occupancy (% of agrarian counties occupied by common voles) in the whole Castilla-y-Léon region. The dashed line shows modelled yearly vole occupancy data (see text).

Figure 3. Climate trends for the Castilla-y-Léon region in 1962-2002. The figure illustrates changes over time in climate PC scores for which significant trends were detected (PC1 and 3; see Table 2).

Figure 4. Changes over time in land uses within the Castilla-y-Léon region (a) as summarized by the first two land use PC scores (see Table 3); or (b) by the extent (surface area, in ha) of irrigated herbaceous crops and alfalfa ("green crops"). Modelled yearly vole occupancy data (% of agrarian counties occupied by common voles, thin dashed line; see Fig. 2) are also shown for comparison.

Figure 5. Results of the cross correlation analyses between the modelled annual vole occupancy data (% of agrarian counties occupied by common voles) and the annual climate data (top) or land use data (bottom). The significance of the correlations at different time lags is shown using bars of different colours (black: $P < 0.001$; grey: $0.001<P<0.05$; white: $P>0.05$).

Figure 6. Probability of colonization by common voles of an agrarian county according to (**a**) the neighbouring vole occupation level (the % of adjacent counties already occupied by voles) (**b**) the extent of "green crops" (irrigated herbaceous crops and alfalfa, in % of cultivated surface area), (**c**) the abundance of cattle and sheep within the province of the focal agrarian county, and (**d**) the interacting effects of neighbouring vole occupation level and of green crop extent. Grey shades denote SE at both sides of the predicted curves. In (a), (b) and (c), predicted probabilities

are plotted by varying one predictor while holding the other predictors constant at median values.

Fig. 1.

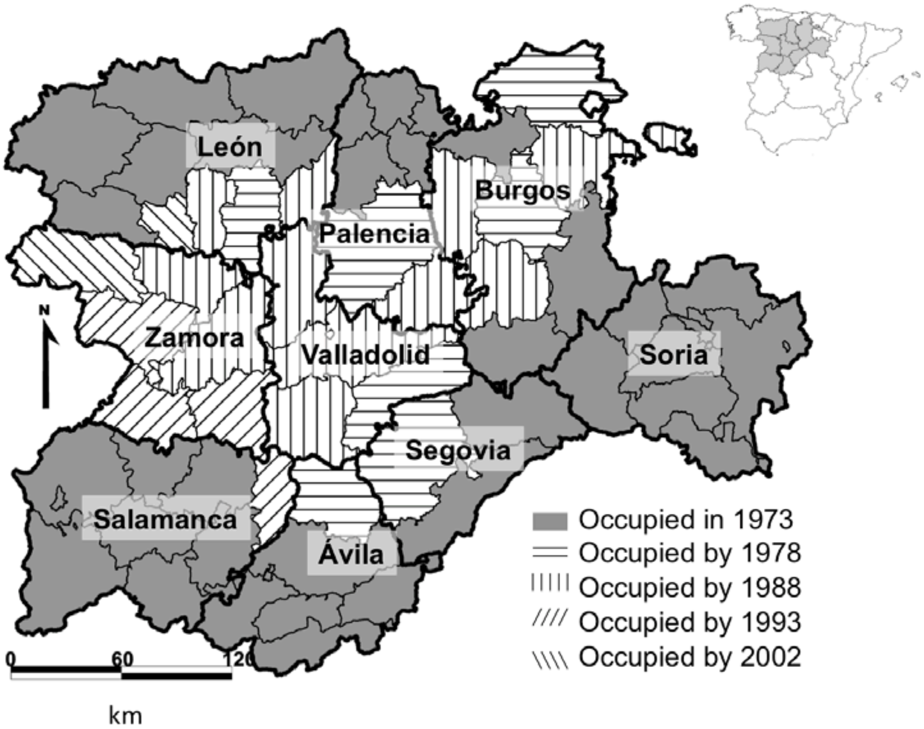

León
Burgos
Palencia
Zamora
Valladolid
Soria
Segovia
Salamanca
Ávila
N
Occupied in 1973
Occupied by 1978
Occupied by 1988
Occupied by 1993
Occupied by 2002
0
60
120
km

Figure 2.

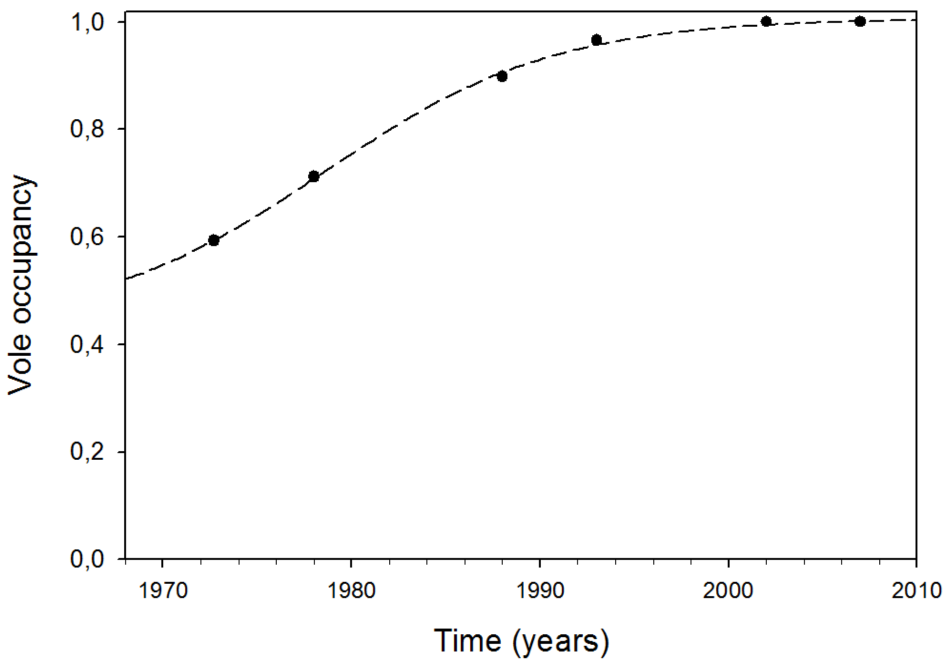
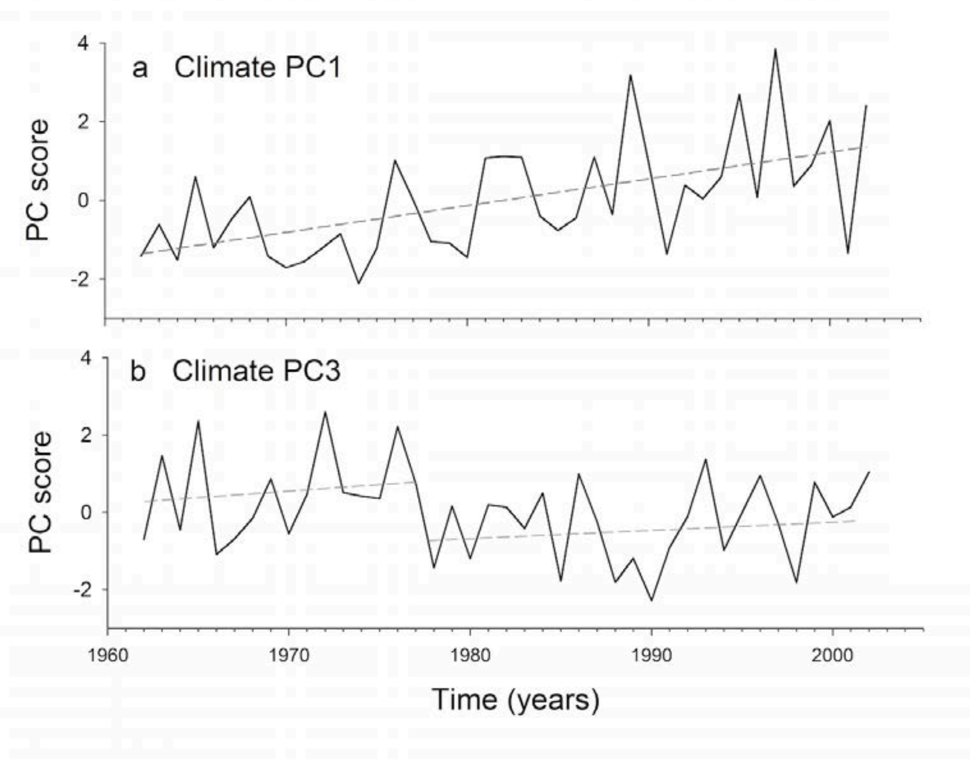
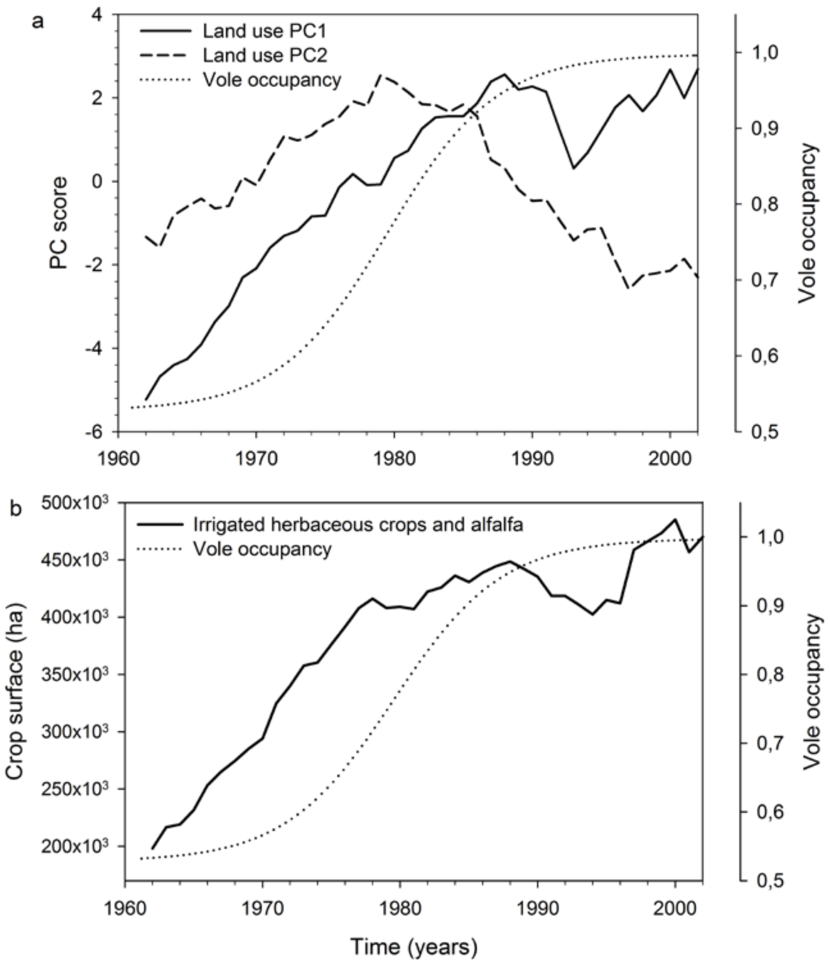

1,0
0,8
0,6
0,4
0,2
0,0
Vole occupancy
1970
1980
1990
2000
2010
Time (years)

Figure 3.


a Climate PC1
b Climate PC3
PC score
PC score
4
2
0
-2
4
2
0
-2
1960
1970
1980
1990
2000
Time (years)

656 **Figure 4.**



657
658

Figure 5.

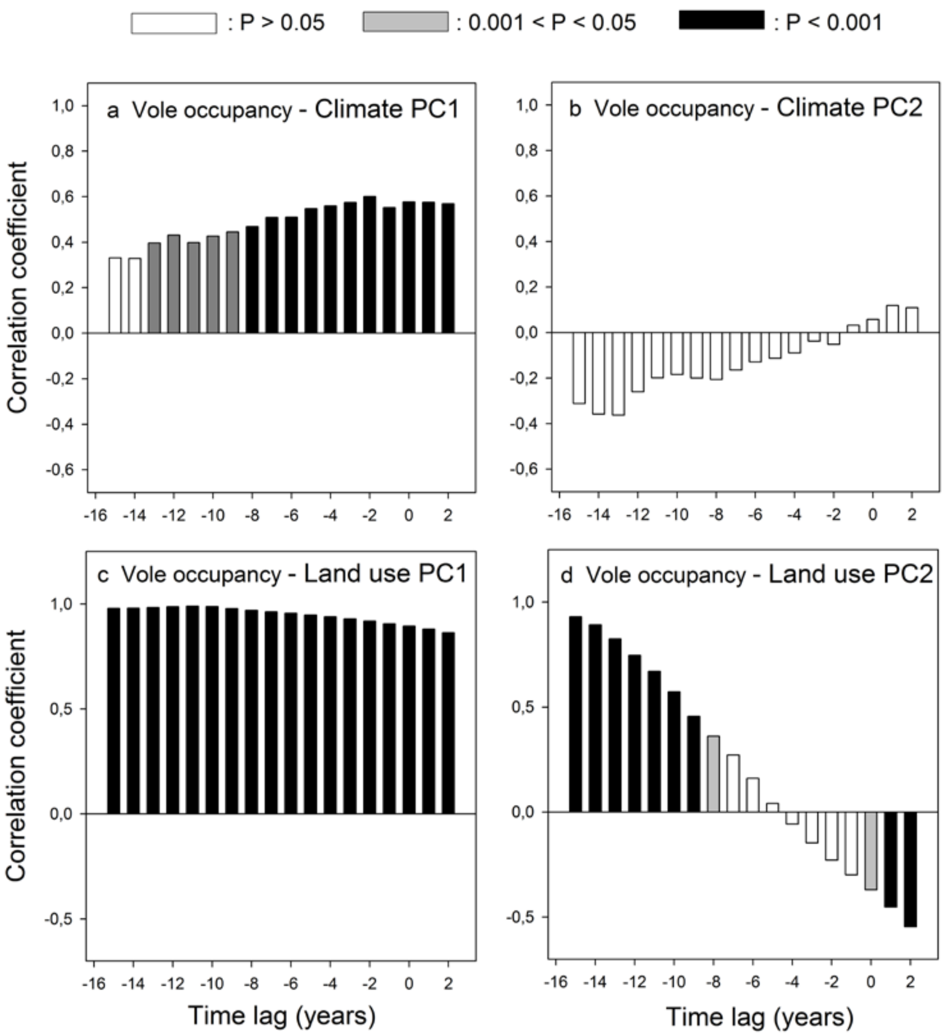
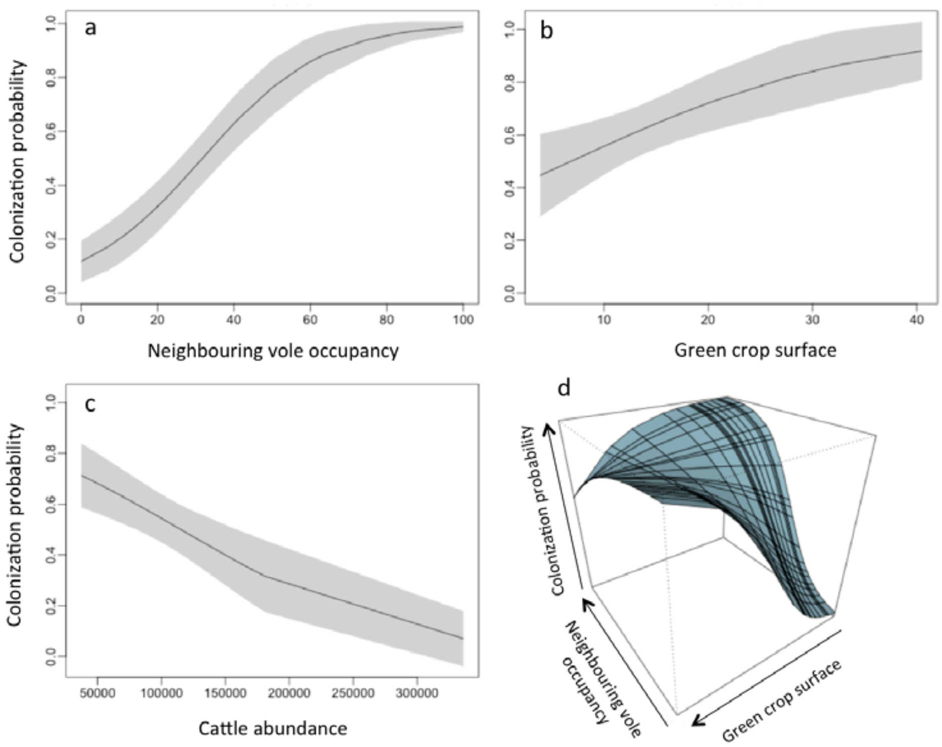

: P > 0.05
: 0.001 < P < 0.05
: P < 0.001
a Vole occupancy - Climate PC1
b Vole occupancy - Climate PC2
c Vole occupancy - Land use PC1
d Vole occupancy - Land use PC2
Correlation coefficient
Time lag (years)
1,0
0,8
0,6
0,4
0,2
0,0
-0,2
-0,4
-0,6
0,5
-0,5
-16
-14
-12
-10
-8
-6
-4
-2
0
2

Figure 6


a
b
c
d
Colonization probability
Neighbouring vole occupancy
Green crop surface
Cattle abundance
Neighbouring vole occupancy
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
10
20
30
40
50000
100000
150000
200000
250000
300000

Supplementary Material

Figure S1. Region-wide land use trends in Castilla-y-León and vole expansion. Modelled yearly vole occupancy data (% of agrarian counties occupied by common voles, thin dashed line; see Fig. 2) are also shown for comparison.

Figure S2. Trends in livestock numbers (a: cattle; b: sheep and goats) in Castilla-y-León by zone. North (black line, includes the provinces of León, Palencia and Burgos), Central (blue line, includes Valladolid y Zamora) and South (red line, includes Salamanca, Ávila, Segovia and Soria).

Figure S3. Trends in average field size (total agrarian surface in each farm divided by total number of fields in each farm) at the regional level (Castilla-y-León). Data source: "Censos Agrarios de España", Instituto Nacional de Estadistica (http://www.ine.es/) available for the years 1962, 1972, 1982, 1989 and 1999.

Figure S1.

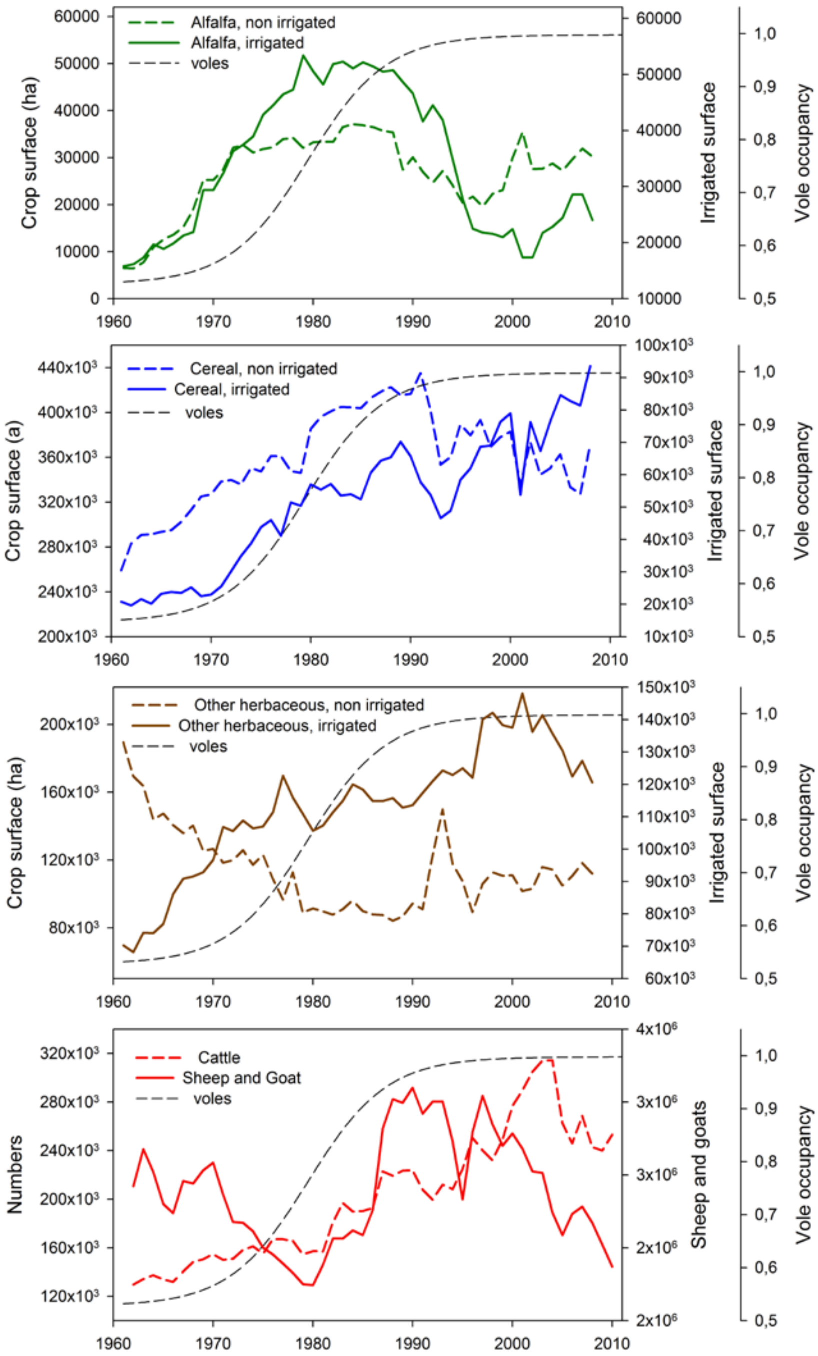
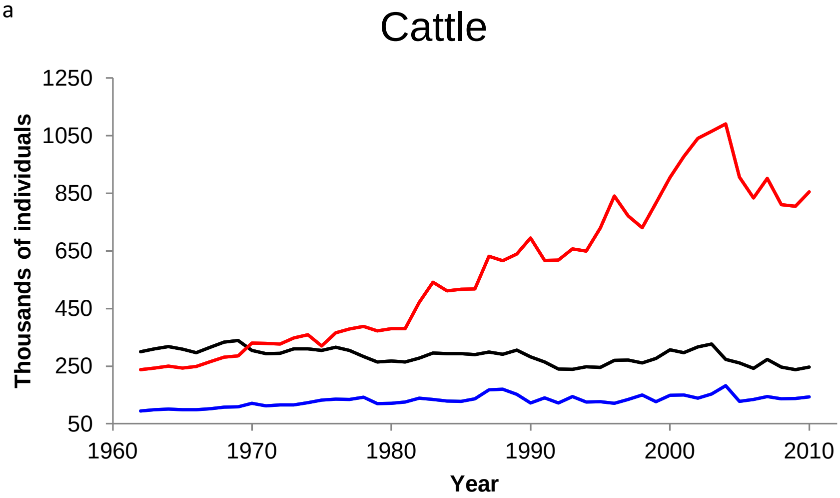
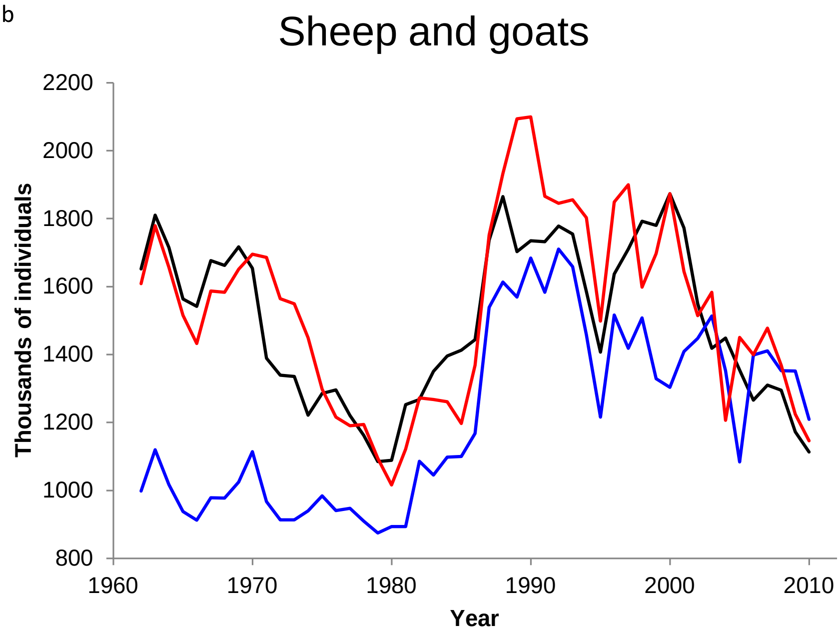

Alfalfa, non irrigated
Alfalfa, irrigated
voles
Crop surface (ha)
Irrigated surface
Vole occupancy
Cereal, non irrigated
Cereal, irrigated
voles
Crop surface (a)
Irrigated surface
Vole occupancy
Other herbaceous, non irrigated
Other herbaceous, irrigated
voles
Crop surface (ha)
Irrigated surface
Vole occupancy
Cattle
Sheep and Goat
voles
Numbers
Sheep and goats
Vole occupancy

Figure S2.

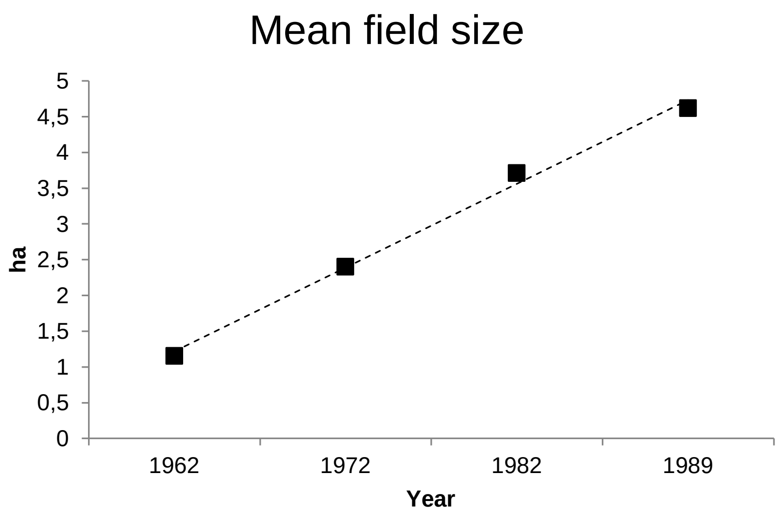
a


Cattle
Thousands of individuals
1250
1050
850
650
450
250
50
1960
1970
1980
1990
2000
2010
Year

b


Sheep and goats
Thousands of individuals
2200
2000
1800
1600
1400
1200
1000
800
1960
1970
1980
1990
2000
2010
Year

687 Figure S3.



688