# A large-scale assessment of European rabbit damage to agriculture in Spain

Running title: Agricultural damage by rabbits in Spain

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**Abstract**

BACKGROUND: Numerous small and medium-sized mammal pests cause widespread and economically significant damage to crops all over the globe. However, most research on pest species has focused on accounts of the level of damage. There are fewer studies concentrating on the description of crop damage caused by pests at large geographical scales, or on analysing the ecological and anthropogenic factors correlated with these observed patterns. We investigated the relationship between agricultural damage by the European rabbit (*Oryctolagus cuniculus*) and environmental and anthropogenic variables throughout Spain.

RESULTS: Rabbit damage was mainly concentrated within the central-southern regions of Spain. We found that rabbit damage has increased significantly between the early 2000s and 2013. Greater losses were typical of those areas where farming dominated and natural vegetation was scarce, where main railways and highways were present, and where environmental conditions were generally favourable for rabbit populations to proliferate.

CONCLUSIONS: From our analysis we suggest that roads and railway lines act as potential corridors along which rabbits can spread. The recent increase in Spain of such infrastructure may explain the rise in rabbit damage reported in this study. Our approach is valuable as a method for assessing drivers of wildlife pest damage at large spatial scales, and can be used to propose methods to reduce human-wildlife conflict.

**Keywords:** Google search; Human-wildlife conflict; Landscape change; *Oryctolagus cuniculus*; Pest species; Small mammals

## 1. INTRODUCTION

Negative impacts of wildlife on humans or their resources have occurred throughout prehistory and recorded history. Consequences of human-wildlife conflict can be both direct, including disease, injury and death from encounters with dangerous animals, and indirect, such as loss of crops and livestock and damaged infrastructure. Measures for preventing or reducing human-wildlife conflict are increasingly being developed.[1] Successful conflict resolution plans are often the result of the assimilation of proven methods of control or deterrence and their clear adaptation to the nature of the problem at hand.[2] The latter requires an accurate assessment of the human-wildlife conflict situation investigated, and a clear understanding of the efficacy, cost-effectiveness and social acceptability of the methods to be applied.

Although human-animal conflict involving large mammals is often highlighted in the media, human livelihoods are arguably much more impacted by small and medium-sized mammals.[3,4] These species often cause substantial damage to pastures as well as ground and tree crops through grazing or browsing. For example, outbreaks of rodents in apple growing areas in Germany can cause up to 25 million € per year of damage.[4] Close grazing by large numbers of the European rabbit (*Oryctolagus cuniculus*) can weaken or kill even persistent leafy crops, and scratching and burrowing can degrade pasture still further by encouraging the establishment of weeds.[5] In the UK, rabbit damage was recorded as being € 115 - € 150 million in 1986,[6] and around € 130 million per year in Australia.[7]

Country-wide assessments of the damage caused by rabbits in the UK and Australia[8,9] or coypu (*Myocastor coypus*) in Italy[10] have been undertaken. However, analyses of the spatial (where damage happens) and temporal (when damage occurs) factors determining the crop damage inflicted by a particular pest species have been largely missing from large-scale assessments. Such approaches allow for the application of understanding what variables may correlate with a species' propensity to cause damage and thus can permit managers to devise more effective measures of control especially since what may be successful at a smaller demonstration scale can fail when applied at the broader landscape level.[11]

Pest outbreaks can be linked to specific environmental conditions. In the case of the Douglas fir tussock moth (*Orgyia pseudotsugata*) eruptions correlated primarily with forest type and climate.[12] However, for some species, particularly insect pests, transport infrastructure (roads and railway lines) can also permit their dispersal and establishment.[13] There are few studies on the role of roads and railways as potential corridors along which pest species may disperse. An exception is a study of the brown marmorated stink bug (*Halyomorpha halys*) in the US, which showed that urban development and railroads facilitated the species' spread.[14] Given the ubiquity of transport infrastructure in many parts of the world, it is likely that pest species will reach remote areas as they establish themselves along roads or railway lines where they can become abundant, and from which they can proliferate.[15]

Assessing crop damage caused by indigenous small mammal pests, as well as increasing our understanding of what determines this, is important when the species in question also plays a key role in a native ecosystem. This is the case of the European rabbit in the Iberian Peninsula, its native range.[16] The control of the rabbit here needs to be effected in such a way that does not cause its unrestrained decline or extinction; this could produce cascading effects in the ecosystem.[16] Rabbits in Iberian Mediterranean ecosystems act as a multifunctional keystone species, not only because they are prey for over 30 predators, but also because of their role as an ecosystem engineer.[17] By contrast, rabbits cause substantial damage to agriculture in Spain and Portugal,[18,19,20] and are regarded as a severe pest species in some regions. Moreover, rabbits are one of the most important small-game species, hunted in their millions in the two Iberian countries. These multiple roles often lead to frequent conflicts between farmers, hunters and conservationists on how to manage the species.[18]

Knowing where and when rabbit damage occurs in Spain and which factors may drive it can help mitigate conflicts between the various stakeholders. In this study, we first describe rabbit damage throughout Spain, until now unrecorded, by: 1) documenting areas (i.e. municipalities) where rabbit damage has been reported to occur; 2) recording which crops are affected; and 3) evaluating the temporal evolution of rabbit damage in the country. Across multiple sites we then assess the probability of occurrence of crop damage caused by rabbits, and its relationship with local conditions and environmental factors, such as land use, natural vegetation or infrastructure. To do this, we employ large-scale databases of environmental and biotic variables, and use spatial modelling.[21] Our results are used to determine which areas are more prone to rabbit damage and assess which factors are correlated with this.

## 2. MATERIALS AND METHODS

### 2.1 Study area

Peninsular Spain covers 493,518 km$^2$ (nearly 85% of the Iberian Peninsula). The country is divided into 8,125 administrative municipalities (http://www.ine.es) the territorial units used in the current analyses. Climate varies widely throughout Spain, with precipitation decreasing eastwards and southwards, and temperature increasing southwards.[22] Mountains border the northern and Mediterranean coasts (max. alt. 3,478 m) but there are also east-west facing ranges in the centre of the Peninsula.

The natural vegetation in the mountains is pine and oak forests and scrubland, but lowlands are mostly dominated by herbaceous crops and river terraces, and hill slopes by woody crops such as olive. According to the 2010 European Union Farm Structure Survey

(FSS) the area under agriculture in Spain was 47% of the whole territory and involved around 9.8% of the economically active population of the country (http://ec.europa.eu/eurostat/web/agriculture/farm-structure). Arable land dominates over woody crops (~$12 \times 10^6$ ha *vs*. ~$5 \times 10^6$ ha). Cereal crops and olive trees represent just over 50% of arable land and woody crops, respectively. Fodder crops cover important area of arable land, while fruit trees and vineyards are common woody crops.[23]

## 2.2 Temporal and spatial characterisation of damage caused by rabbits

We used the Google search engine (www.google.es) and the search terms “pest” and “rabbit” (in Spanish: “plaga” and “conejo”, respectively) to identify websites containing information on areas affected by European rabbits in Spain.[24] We selected this word combination based on a previous study which showed that this permutation but also “rabbit” and “damage” worked better than “rabbit” and “crop”, and “rabbit” and “overpopulation”.[25] The first 600 consecutive sites resulting from our Google search were visited and their content evaluated by M. Delibes-Mateos.[24] Searches were performed between 18 May and 11 June 2015. Only websites unequivocally containing information on damage caused by the European rabbit in Spain were considered valid. These sites mostly included media reports on rabbit damage, discussion forums in hunters’ and farmers’ websites, and blogs. Websites that bore no relation to rabbit damage in Spain were discarded. Among those ruled out for analyses were websites dealing with pest rabbits in regions where the species is an invasive alien or advertisements for pet rabbits. We gathered information on the type of agricultural crop damaged by rabbits. As one of our main goals was to detect areas where rabbit damage occurred, we also documented those municipalities where such damage was reported. To assess the temporal evolution of the annual online information on rabbit damage in Spain we recorded the year that each website was uploaded. Because Internet usage has substantially increased in recent years thus affecting the availability of media reports on rabbit damage, we used the date function available in Google Advanced Search to conduct a search of the target keywords filtering by year for the period 2004-2014. The first 100 sites yielded by each search (i.e. for each specific year) were visited and those valid were selected to calculate a standardised index of available information on rabbit damage in each year; i.e. for each year, the number of valid websites / 100 websites visited. The temporal evolution of such index was compared with the evolution of the reports on rabbit damage obtained from the general search (see above).

### 2.3 Predictive model

To model the potential distribution of European rabbit damage throughout mainland Spain, we used the favourability function.[26] The favourability function assesses the extent to which environmental conditions change the probability of occurrence of an organism with respect to its overall prevalence in the study area.[27] Thus, compared to logistic regression, by using the favourability function we cancel out uneven proportions of presences and absences in the modelled data. Here, we use of this approach to model the relationship between European rabbit damage and environmental variables.

Firstly, a model of environmental favourability for the presence of the European rabbit in each UTM 10 x 10 km square of mainland Spain was constructed using the distribution map available in the Atlas of Terrestrial Spanish Mammals and Red Book.[28] We considered 35 predictor variables (Table S1). The ecological factors that could explain the environmental favourability of the European rabbit were based on climate and topography. Alongside these, we included descriptors of human land use and human activity to assess potential anthropogenic impacts.

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Overall, our model of European rabbit damage used a total of 136 predictor variables (Table S2). The favourability model for the presence of European rabbits included 79 ecosystem type descriptors based on natural vegetation structure, and 56 indicators of anthropogenic activity namely transport infrastructure (i.e. main railways and highways), agriculture and livestock. Spatial analyses to calculate the presence of transport infrastructure were performed using ArcGIS 10.0 (ESRI,

Redlands, California, USA).

We excluded nonlinear and interaction effects from the model to keep its mathematical formulation as simple as possible for explanatory purposes. To account for Type-I errors caused by the large number of variables considered, we controlled the False Discovery Rate (FDR).[29] Thus, using the presence/absence of European rabbit damage as the dependent variable, we ran a logistic regression on each of the 136 predictor variables, and only significant ($P < 0.05$) variables under an FDR of $q < 0.05$ were accepted as part of a multivariate environmental model. Multicollinearity was also minimised by excluding variables that were correlated with Spearman $r > 0.8$. Only then did we perform the favourability model using the following equation[26,27]:

$$F = [P/(1-P)]/[(n1/n0)+(P/[1-P])]$$

where $F$ is the favourability value in each municipality; $n1$ and $n0$ the number of municipalities with and without damage reported in websites, respectively; and $P$ the probability of rabbit damage presence in each municipality. $P$ was calculated with a multiple logistic regression, using the presence and absence of damage in each municipality according to the analysed websites as the dependent variable. A forward stepwise procedure was performed to avoid the inclusion of redundant variables in a model. The parameters in the models were fitted by iteratively maximizing the log-likelihood. (using IBM SPSS statistics 22).

### 2.4 Explanatory analysis of variables in the model

We employed a variation partitioning procedure to measure the relative participation of the four main factors described in Table S2 (favourability for the presence of European rabbit, transport infrastructure, natural vegetation and land uses) on the model explanation of favourability for damage occurrence.[30] In this way, we specified how much of the variation in favourability was accounted for by the pure effect of each factor (i.e., variation that is not affected by covariation with another factor), and what proportion was clearly attributable to more than one factor (i.e. shared effect).

The significance of the influence of all variables in the model was assessed using the univariate Wald test statistic.[31] Stepwise methods select variables acting on a larger scale in the first steps, and at subsequent steps only add variables that are significantly related to the residuals not accounted for by previously incorporated variables.[32] The regional relevance of every variable was, thus, analysed using two approaches. Firstly, we measured the correlation (Spearman *R*) of each variable with the favourability output, and compared the sign of *R* (which indicates global relationship within the study area) with the sign of the variable coefficient in the model equation (which indicates the sign of the variable contribution to explaining favourability). Secondly, we visualised the regional contribution of each variable to the model by mapping the difference between favourability values obtained in successive steps, along the stepwise variable selection.

## 3. RESULTS

### 3.1 Temporal and spatial characterisation of damage caused by rabbits

The general Google search yielded a total of 306 unique, valid websites containing information on damage caused by European rabbits in Spain. The first cases of rabbit damage were reported in 2004. There were few cases during 2004-2006, but these increased sharply until 2013, after which there was a sharp decline (Fig. 1). In 2014, we recorded the highest number of websites containing information on rabbit damage, reaching levels higher than in 2012. There was a strong significant correlation ($R$= 0.971, $p$<0.001) between the number of websites containing information on rabbit damage and year when we standardised our results using the Google search by date option. Nearly all analysed websites reported crop damage caused by rabbits (95.7%; n=301), with only a few documenting damage to infrastructure around railways or highways (10.3%; n=301), or human properties such as gardens or parks (9.6%; n=301). Most rabbit damage was reported for vineyards and cereal crops (66.1% and 53.3%, respectively; n=180), although it was also relatively frequent in olive groves and fruit orchards (28.3% and 21.7%, respectively; n=180). Green vegetables and other crops were less frequently mentioned in the websites (15.0% and 9.4%, respectively; n=180). Rabbit damage was reported in 437 (5.5%) municipalities across mainland Spain. These were mostly found in: 1) Guadalquivir and Ebro valleys in southern and north-eastern Spain, respectively; 2) Castilla-La Mancha and Castilla y León plateaus in central Spain; and 3) the coastal eastern regions, particularly the Comunidad Valenciana region (Fig. 2).

**3.2 Modelling favourability for European rabbit damage**

The favourability model for the presence of European rabbit damage included 18 different variables related to transport infrastructure, land use, natural vegetation and environmental variables (Table 1). The model showed that municipalities favouring the presence of European rabbit damage tended to be found near each other (Fig. 3), located mainly along the Guadalquivir and Ebro valleys, several areas of the Guadiana valley, North and South plateaus and some coastal areas of Southeast peninsular Spain.

Variables with the highest explanatory power within the model (Wald statistic > 25) were primarily transport infrastructure and land use descriptors (Table 1). Humanised habitats, such as croplands and infrastructure, and environmentally favourable areas for the presence of European rabbits were positively related to damage. In contrast, natural vegetation was negatively associated with rabbit damage. More specifically, highways and main railways, dry and irrigated olive crops, and dry and irrigated vineyards positively correlated with the occurrence of European rabbit damage, i.e. they showed identical signs within the model equation and in the variable correlations with the model, and their entry into the model produced an increase in favourability (Fig. 4). On the other hand, forests (specially mature oak forests), scrublands and pastures represented environmental constraints to the occurrence of European rabbit damage, i.e. both signs within the model equation and variable correlations within the model were negative, and their entry into the model produced a decrease in favourability (Fig. 4).

The greater proportion of the spatial variation in favourability was explained by habitat descriptors, represented by natural vegetation and land use factors. The sum of the pure and shared effects of these factors on favourability variation was 81.8% and 53.7%, respectively (Fig. 5). Transport infrastructure and environmental favourability for the presence of European rabbits only explained 8.4% and 10.6% of variation, respectively. We found shared effects between the different factors (meaning either cross or indistinguishable explanatory power). Land uses and infrastructure shared 90.3% of their influence, and land uses and natural vegetation shared 40.8%. The other shared effects between factors were considerably smaller. As a result, the pure effect of natural vegetation explained 39% of favourability for the presence of damage, whilst the pure effect of land uses, environmental favourability for the presence of European rabbits, and infrastructure explained only 10.0%, 3.0% and 2.3%, respectively.

## 4. DISCUSSION

We show that rabbit damage is more common in the central-southern regions of Spain, and in some northern areas (Fig. 2). We also demonstrate that the likelihood of damage by rabbits in an area depends on a combination of factors, which our model has clearly identified (Fig. 5). Most rabbit damage occurs in municipalities where farming dominates (and therefore natural vegetation is scarce), where main railways and highways are present and where environmental conditions for rabbit populations to succeed are generally good (Table S2). Using our approach we were able to highlight those areas potentially at greater risk of rabbit damage at a large national scale, which are likely to be missed using other means of verification. For example, our model clearly showed that areas such as Castilla y León region (north-western Spain) have relatively high favourability values even though the number of cases found in our Google search was low (Figs. 2 & 3).

Our study demonstrates that the modelling approach we use can be useful in determining the role of multiple factors at large spatial scales for explaining the damage caused by a pest species. In addition, we show that online media reports on pest damage can be an effective and relatively rapid option to understand the distribution of pest damage in a landscape as large as an entire country. However, a potential drawback of this information is that reports in the media on pest damage may only record the stakeholders' perceptions, but perceived and actual damage caused by wildlife may not be correlated.[33] Despite this, media reports have been successfully used previously to assess the impact of small mammal pests.[34] Thus, we argue that, even if there is some error involved, the information obtained in our study can help identify areas of potential stakeholder conflict regarding the management of pest species (farmers and hunters in our study model),[18,24] and can be used in the design of more realistic management plans.

According to the analysed websites in Spain, most rabbit damage occurred in crops. This is in line with the result of our model in which favourable areas for rabbit damage were positively correlated with several land uses related to agriculture; many different crop types were among the most important predictors of rabbit damage (Table 1). Our results suggest that, in Spain, the rabbit is a generalist agricultural pest since a variety of crops are damaged by this species (see also [20]). This contrasts with other Spanish small mammal pests that are linked to specific crop types; e.g. voles and herbaceous crops.[35] From the analysed websites, we showed that vineyards were the most frequently recorded crop type affected by rabbits, and both these and olive groves had significant effects on rabbit damage favourability in the model (Table 1). Notable reductions in woody crop yields from rabbit browsing have been reported in some Spanish agricultural regions.[21] Given that a vast proportion of agricultural land in some regions of Spain is devoted to these woody crops – e.g. >98% of the area in Montilla-Moriles Winegrowing Region in southern Spain[36] – losses caused by rabbits to olive oil and wine producers can be economically crippling.

Natural vegetation explained a large proportion of favourability for rabbit damage in our model (Table 1). The fact that most natural vegetation types were negatively associated with the potential occurrence of rabbit damage is not surprising, because the higher the proportion of land occupied by natural vegetation the lower the availability of crops to be grazed by rabbits. Furthermore, rabbits are found in low numbers in areas dominated by forests or dense scrublands,[37] thus decreasing the likelihood of damage to adjacent crops. Similarly, we observed that rabbit damage is most likely in areas environmentally favourable for the species (Table 1). In these areas high rabbit densities are possible in addition to being positively associated with the presence of woody crops,[38] typically damaged by rabbits.

Although the number of hunters in Spain has remained relatively constant (http://www.magrama.gob.es), rabbits hunted have increased alongside the spread of fast speed railways during the last decade (Fig.1, $R$=0.904, $p$<0,001). According to our model, one of the main predictors of rabbit damage was the presence of railways or motorways (Table 1; Fig. 4). The explanation is that rabbits can become more abundant close to these infrastructure,[39,40] particularly in areas within farmland regions where the availability of other suitable habitat for their successful establishment is scarce.[41] Verges and embankments along roads or railways (for fast-speed railways these are often chain-mesh security fenced) provide rabbits with refuge against predators and hunters, as predator abundance is lower and hunting often banned in these areas.[39,41] In addition, these verges and embankments offer ideal conditions for rabbit warren building,[40] essential to establish healthy social groups.[42,43] Similar reasons have been proposed to explain the high numbers of some small mammals found in areas with high road density[44] or the intensive use of areas adjacent to roads by juveniles of two lagomorph species.[45] In farmland areas, rabbits usually establish dense populations along the verges of roads and railway lines, where nearby crops are their only feeding source since natural vegetation has almost disappeared as a consequence of intensive agricultural practices.[36] This may also explain the high importance of human infrastructure explaining rabbit damage observed in the model.

Our Google searches uncovered very few sites containing information related to rabbit pests in Spain during the first half of the 2000s. This was a time when Spanish rabbit populations were at their lowest numbers in recorded history because most of them had not recovered from the huge impact of rabbit haemorrhagic disease (RHD), first detected in Spain in 1988.[46] The increase in the number of websites reporting damage between 2006 and 2012 matches the known recovery of some populations during that period,[47,48] particularly in some agricultural areas.[18] It also matches the increase in the number of rabbit control requests and the number of harvested rabbits recorded in Portugal[18] and in Spain (Fig. 1). These findings closely resemble the situation in Australia, where rabbit numbers were heavily suppressed by RHD between 1995 and 2002, but increased 5-10 fold between 2003 and 2010.[49] Our findings also show that in 2013 the available online information related to rabbit damage fell sharply, which seems to be only explicable by the population crash caused by a new variant of the RHD virus.[48,50,51] It is very likely that the decline in rabbits observed in agricultural areas resulted reduced rabbit damage, which was reflected in the lower number of websites addressing this issue. Interestingly, websites reporting rabbit damage increased considerably between 2013 and 2014 (Fig. 1), which suggests that rabbit populations might have recovered at least in some agricultural areas, although in natural areas rabbit numbers were still very low.[51]

Our findings indicate that the evolution of online reports on rabbit damage might be a good indicator of trends in rabbit population and their damage at a large scale in Spain, although such data have some potential limitations. For example, the relationship between rabbit abundance and their damage is complex, as damage to crops by rabbits has been also observed in areas with moderate rabbit abundance.[18] On the other hand, the considerable increase in the use of Internet over recent years might explain the growing availability of online information regarding almost any topic. However, the observed rise in rabbit damage reports when we controlled for sampling effort per year and the growing numbers of rabbits hunted and rabbit control permits requested[18,20] suggest that rabbit damage has in fact increased in recent years in Spain. In any case, we do recommend that online data be interpreted cautiously.

The presence of transport infrastructure was one of the main explanatory factors of rabbit damage in our model. Given the extensive development of fast-speed railways and highways that occurred in Spain in recent years, we suggest that such landscape modification may have been one of the main drivers in the rise in rabbit damage reported in our study. This seems to be supported by the significant overlap observed between the increase in the number of websites dealing with rabbit pests and increase in the length of fast-speed railways in Spain (Fig. 1; $R$= 0,869, $p$<0,001). Alternatively, the reduction of other food sources for rabbits has led to increased crop damage.[36] The role of humans in the expansion of small mammal pests and damage by these has been also observed in other farmland systems.[35]

Economic damage caused by mammal pest species can be high, particularly in farmland areas (e.g. [52]). This may be the source of conflict between stakeholders whose livelihood is affected by wildlife like farmers and other parties that make other uses of these species, such as hunters or environmentalists. Our case study is a good example, but there are others across the world.[16,53] We suggest that it is essential to assess what drives wildlife damage at large spatial scales as well as to identify areas where potential conflicts may emerge. The approach presented in this paper can be reproduced in other systems, to not only reduce wildlife pest damage, but also to work against smoothing out tensions between stakeholders regarding the management of wildlife.

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**Table 1.** Descriptor variables of the environmentally favourable areas for European rabbit damage according to the favourability model. Step: Order or entrance in the model; W: Univariate Wald test statistic quantifying variable significance in the model (all the variables shown were significant with $P < 0.05$); CfS: Sign of the variable coefficient in the model; CrS: Sign of the correlation (Spearman) between the variable and favourability values; AGI: Area of geographic influence of the variable in the model within the study area (SW = South-West, NE = North-East, E = East, SE = South-East). DRY_OLIV: Dry olive groves (% area); HIGHW_RAILW: Length of highway and fast-speed railway per municipality (m); IRR_OLIV: Irrigated olive groves (% area); DRY_VIN: Dry vineyards (% area); IRR_VIN: Irrigated vineyards (% area); F_WILDRABBIT: Favourability model for the presence of European rabbits, based on climate, topography and human activity (Table S1); ORG_CER: Organic cereal (% area); WOLIV_COP: Beech forest (% area); WOLIV_FOR: Wild olive tree forest (% area); P_UAA: Proportion of useful agricultural area (% area); NOAK_CLEFOR: Carob forest (% area); DEV_OAK: Development phase of oaks (Height); PAST: Pastures (% area); DIV_FOR: Diversity of forest uses and vegetation structure (Simpson diversity index); PINE_FOR: Birch forest (% area); GALL_FOR: Alignment (% area); OAK_CLEFOR: Boxwood forest (% area); PAST_SHRUB: Pastures and shrubs (% area).

| Variable | Step | W | CfS | CrS | AGI |
|---|---|---|---|---|---|

| | | | | | |
|---|---|---|---|---|---|
| Variables describing favourable areas for wild rabbit damages | | | | | |
| DRY_OLIV | 3 | 124.834 | + | + | |
| HIGHW_RAILW | 1 | 119.444 | + | + | |
| IRR_OLIV | 7 | 51.344 | + | + | |
| DRY_VIN | 8 | 43.624 | + | + | |
| IRR_VIN | 4 | 26.387 | + | + | |
| F_WILDRABBIT | 11 | 15.961 | + | + | |
| ORG_CER | 10 | 13.372 | + | + | |
| WOLIV_COP | 9 | 9.238 | + | + | |
| WOLIV_FOR | 13 | 7.006 | + | + | |
| P_UAA | 14 | 4.157 | + | + | |
| NOAK_CLEFOR | 6 | 9.686 | + | - | SW |
| Variables apparently outlining unfavourable areas for wild rabbit damages | | | | | |
| DEV_OAK | 5 | 32.730 | - | - | |
| PAST | 12 | 7.016 | - | - | |
| DIV_FOR | 2 | 6.276 | - | - | |
| PINE_FOR | 17 | 5.619 | - | - | |
| GALL_FOR | 16 | 5.294 | - | - | |
| OAK_CLEFOR | 18 | 4.075 | - | - | |
| PAST_SHRUB | 15 | 9.360 | - | + | SE, E, NE |

**FIGURE LEGENDS**

**Figure 1.** Evolution of the number of websites containing information about European rabbit damage according to a Google search (solid black line), the total length (km) of fast-speed railway in Spain (grey line; source: http://www.spanishrailwaysnews.com), and the millions of rabbits hunted in Spain (dotted line; source: http://www.magrama.gob.es and [46]).

**Figure 2.** Municipalities reporting European rabbit damage within the study area (in white) according to the analysed websites (see text for details).

**Figure 3.** Favourability model for European rabbit damage in each municipality of mainland Spain. The small map shows the environmental favourability for the presence of European rabbit in Spain, on UTM 10 x 10 km squares. Scale ranges from 0 (black) to 1 (white).

**Figure 4.** Mapped contribution of variables to the model of favourability for European rabbit damage along the stepwise variable selection. Step: Order or entrance in the model. Green: negative contribution to damage. Red: positive contribution to damage. HIGHW_RAILW: Length of highway and fast-speed railway per municipality (m); DIV_FOR: Diversity of forest uses and vegetation structure (Simpson diversity index); DRY_OLIV: Dry olive groves (% area); IRR_VIN: Irrigated vineyards (% area); DEV_OAK: Development phase of oaks (Height); NOAK_CLEFOR: Carob forest (% area); IRR_OLIV: Irrigated olive groves (% area); DRY_VIN: Dry vineyards (% area); WOLIV_COP: Beech forest (% area); ORG_CER: Organic cereal (% area); F_WILDRABBIT: Favourability model for the presence of European rabbits, based on climate, topography and human activity (Table S1); PAST: Pastures (% area); WOLIV_FOR: Wild olive tree forest (% area); P_UAA: Proportion of useful agricultural area (% area); PAST_SHRUB: Pastures and shrubs (% area); GALL_FOR: Alignment (% area); PINE_FOR: Birch forest (% area); OAK_CLEFOR: Boxwood forest (% area).

**Figure 5.** Variation partitioning of the final model. Values show the proportions of how much of the variation in environmental favourability for European rabbit damage occurrence is explained exclusively by infrastructure, environmental favourability for European rabbit presence, natural vegetation and land uses factors, and which proportion was attributable to their shared effects (intersections).

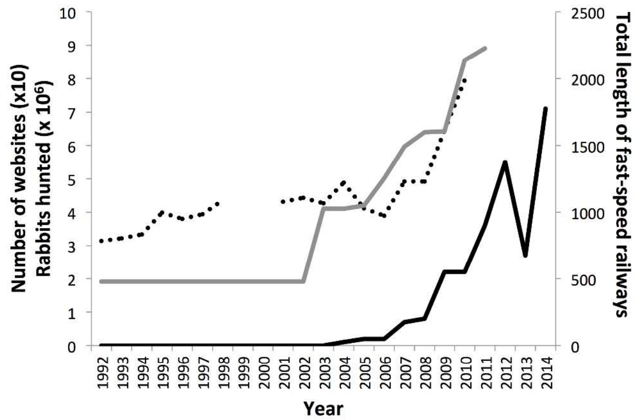
Number of websites (x10)
Rabbits hunted (x $10^6$)
Total length of fast-speed railways
Year
10
9
8
7
6
5
4
3
2
1
0
2500
2000
1500
1000
500
0
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014

Figure 1

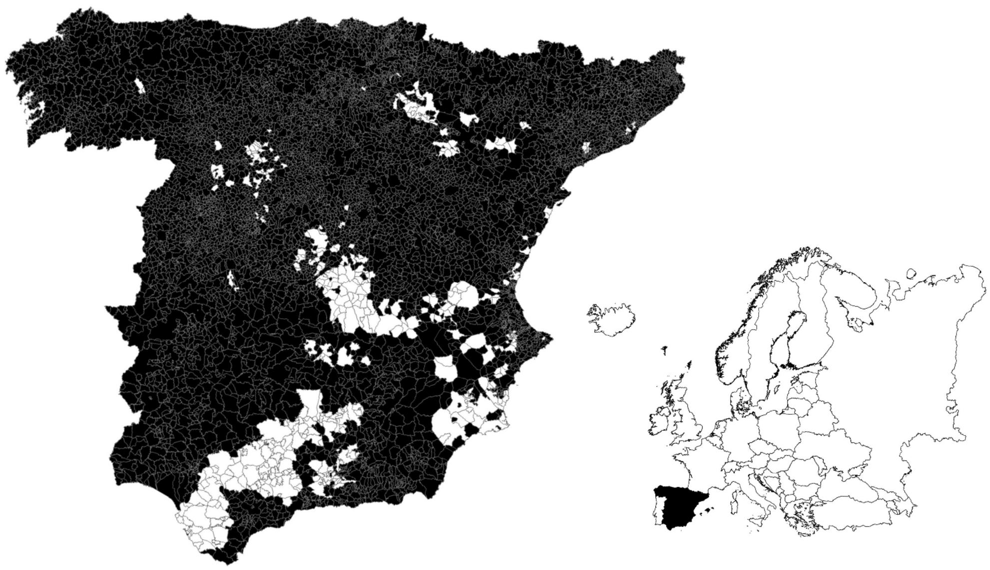

Figure 2

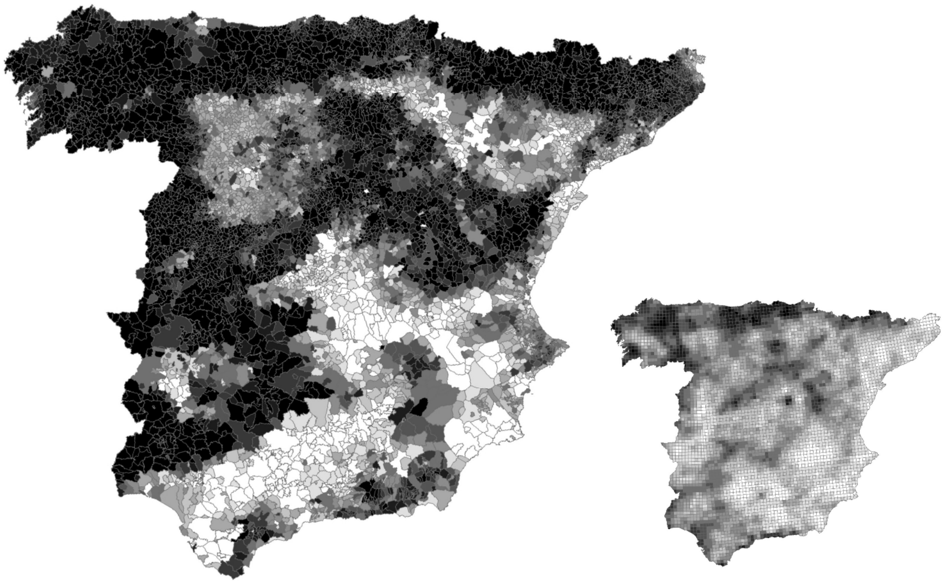

Figure 3

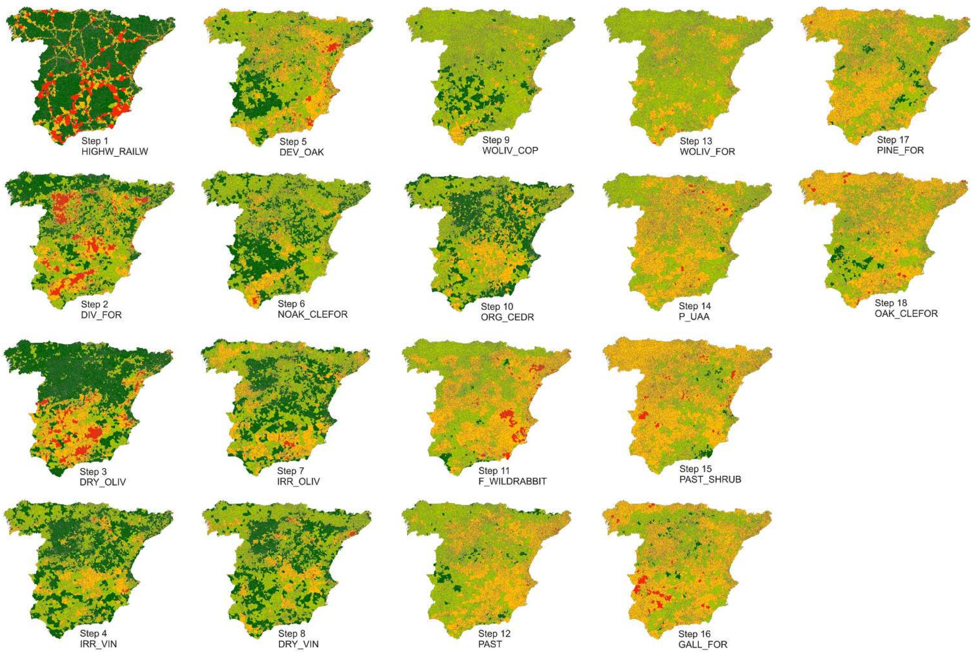
Step 1
HIGHW_RAILW
Step 5
DEV_OAK
Step 9
WOLIV_COP
Step 13
WOLIV_FOR
Step 17
PINE_FOR
Step 2
DIV_FOR
Step 6
NOAK_CLEFOR
Step 10
ORG_CEDR
Step 14
P_UAA
Step 18
OAK_CLEFOR
Step 3
DRY_OLIV
Step 7
IRR_OLIV
Step 11
F_WILDRABBIT
Step 15
PAST_SHRUB
Step 4
IRR_VIN
Step 8
DRY_VIN
Step 12
PAST
Step 16
GALL_FOR

Figure 4

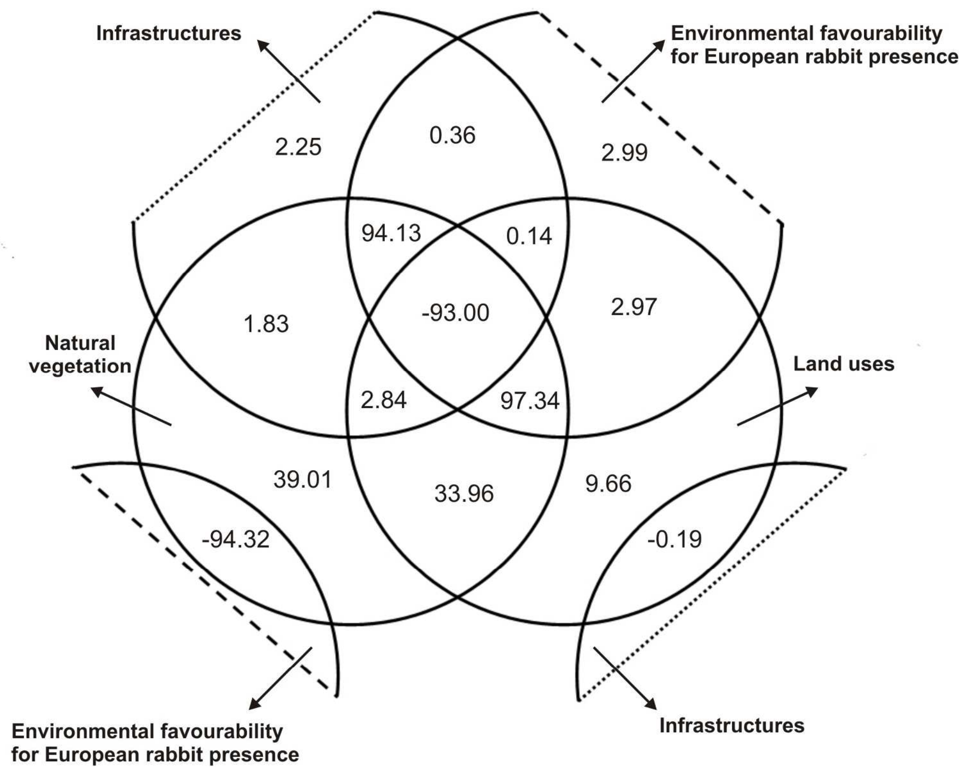
Infrastructures
Environmental favourability
for European rabbit presence
2.25
0.36
2.99
94.13
0.14
1.83
-93.00
2.97
Natural
vegetation
Land uses
2.84
97.34
39.01
33.96
9.66
-94.32
-0.19
Environmental favourability
for European rabbit presence
Infrastructures

Figure 5