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Modelling jay (*Garrulus glandarius*) abundance and distribution for oak regeneration assessment in Mediterranean landscapes

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ABSTRACT

Because natural regeneration of oak is strongly dependent on jay abundance and distribution, we need to understand the determinants of jay abundance and occurrence as a first step to assess oak regeneration. In this paper we modelled the jay population distribution and abundance in a Mediterranean landscape mosaic of the eastern Iberian Peninsula (Valencia, east Spain). The methodology was based on assessing landscape attributes (habitat composition and configuration variables) on seven 9-km^2 sites and registering jay fledgling locations. Using a stepwise regression model we determined the variables that best explained the jay density. The probability of occurrence of jay nests within each site was assessed by comparing the landscape attributes of jay and non-jay areas within each site. Results were validated by predicting each site on the basis of data from the remaining six sites and then calculating the deviation between the predicted and the observed values in the field. The results suggest that jay density correlates positively with forest cover and landscape heterogeneity variables, and negatively with shrubland cover. Validation of the results showed that the model is reasonably effective in predicting both jay abundance and distribution at the extent and resolution used.

1. Introduction

Oaks are frame trees in many ecosystems (McShea and Healy, 2002; Logan, 2005), including in many Mediterranean ones (Rodà et al., 1999; Aronson et al., in press). However, millennia of land overuse in the Mediterranean Basin have drastically reduced the abundance of oaks, mainly through agricultural expansion and charcoal and wood production. Currently, with the abandonment of many agricultural areas and the increase in disturbances (Pausas, 2004), oaks have become target species to be spread in oldfields (Pausas et al., 2004; Vallejo et al., 2006). This is not only because they were native to many landscapes, but also because of their high resilience capacity (Pausas, 1997; Rodà et al., 1999). However, both poor oak reforestation success (Mesón and Montoya, 1993; Vallejo et al., 2006) and reduced natural regeneration (Pulido and Díaz, 2005) have been pointed out as processes limiting the spread of oaks in Mediterranean conditions.

The regeneration process is a sequence of demographic stages; the collapse of any one of them will impede the overall regeneration (Schupp, 1990). For instance, the absence of the dispersal vector will limit regeneration even when other conditions are optimal, and thus variables defining the potential regeneration niche may not be sufficiently explicative of the absence of regeneration. Accordingly, the strong heterogeneity observed in natural oak regeneration (Pons and Pausas, 2006; Pausas et al., 2006) may be due to not only environmental conditions but also different dispersal vector abundances in the different areas. This means that for predicting oak distribution and spread, we need to be able to predict the presence and abundance of the main oak dispersal vector. This knowledge would allow us to better delimit the factors determining natural regeneration and thus reduce the sampling effort required for regeneration assessments of oak communities. Moreover, knowing the dispersal vector distribution is a first step in modelling the natural regeneration status of animal-dispersed plants in extensive zones (i.e., regional scale).

The European jay (*Garrulus glandarius* L.) is considered a key species in the dispersal and spread of *Quercus* species (Bossema, 1979; Mosandl and Kleinert, 1998; Pons and Pausas, 2007a,b). In autumn (the acorn production period), this corvid caches oak acorns in order to secure a steady food supply throughout the year. This food supply is especially required between May and July due to the high food demand by nestling and fledgling individuals (Bossema, 1979; Clayton et al., 1996). Acorns are the main food for

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jays, at least in autumn, spring and winter (Bossema, 1979; San Miguel, 1983). Oaks benefit from jays because of long-distance dispersal, the good conditions of the hoarding site, and the reduced predation of jay-dispersed acorns (Bossema, 1979; Pons and Pausas, 2007a,b).

Like other corvidae, jays seem to explore a wide food spectrum (Bossema, 1979; San Miguel, 1983). As a consequence they seem to prefer diverse and mixed habitats, which are presumed to have more varied and stable resources (Rolando et al., 1995). Because natural *Quercus* regeneration is strongly dependent on jay densities, it is important to be able to predict these densities from simple landscape units and thus be able to infer potential oak regeneration at landscape scale. However, little has been done to determine the habitat distribution factors of jay populations, especially in Mediterranean landscapes.

In this study we ask to what extent jay occurrence, density and spatial distribution are related to and predictable from landscape attributes. Our approach uses multiple regressions with basic landscape variables obtained from aerial photography and GIS tools (Martinez and Calvo, 2000; Sergio et al., 2004; Saïd and Servanty, 2005). The analysis is performed at two spatial scales: (1) at landscape scale, to assess the relation between landscape attributes (composition and configuration) and jay abundance; and (2) at nesting territory scale, to assess which parts of the landscape are selected by jay-pairs. The ultimate objective is to obtain a tool that can later be applied to larger extensions (e.g., a whole National Park).

2. Methods

2.1. Study area

The study area is located inside the Valencia region, which borders the Mediterranean coast in eastern Spain (Fig. 1). The climate is typically Mediterranean. The vegetation is the product of a long history of fire and land use, and many slopes were terraced and cultivated in the past, and then abandoned. In this region there are four main *Quercus suber* patches, from north to south: Desert de les Palmes (Castelló, lat = 40°01′, 10 ha), Espadà (Castelló, lat = 39°52′, ca. 70,000 ha), Calderona (València, lat = 39°44′, ca. 7000 ha) and Pinet (València, lat = 38°59′, ca. 70 ha). Soils in Desert de les Palmes, Calderona and Espadà are mainly acidic soils on sandstones. In Espadà soil pH ranges from 4.9 to 6.4 (mean: 5.7). In Pinet, cork oak occurs in non-carbonated soils on dolomites, with pH ranging from 5.5 to 7.5 (mean: 6.5; Pausas et al., 2006). Average annual rainfall in these cork patches ranges from 500 to 800 mm, with a clear seasonal pattern showing two peaks, in spring and autumn. Desert de les Palmes, Espadà and Calderona are currently Natural Parks and Pinet is a local Micro-Reserve.

Seven study areas (hereafter sites) of 9 km^2 each were selected (Fig. 1) to account for the Cork oak landscape variability in the eastern Iberian Peninsula. The sites were squares (3 km × 3 km, except site 6 which was irregular in shape but identical in size), they were located on the four different cork oak patches mentioned above and they showed similar conditions (medium height elevations, 300–1000 m.a.s.l. and rainfall between 600 and 800 mm); however, they presented different landscape structures and fire histories (see more details on the sites in Pons and Pausas, 2006).

2.2. Habitat composition

A vegetation map for each of the sites was elaborated on the basis of aerial photography with 1 m/pixel resolution and field validation. Then the vegetation composition was assessed by visiting the zone and setting the abundance of the main dominant species. The vegetation types obtained were aggregated according to their possible relevance in jay ecology and the possibility of their identification from available aerial photography. The final six landscape units (vegetation types) considered were: agricultural fields (in production or very recently abandoned), old fields (recently abandoned fields with high grass cover or incipient shrublands), shrublands (also including oldfields abandoned a long time ago with a well-developed shrub layer; tree cover <20%),

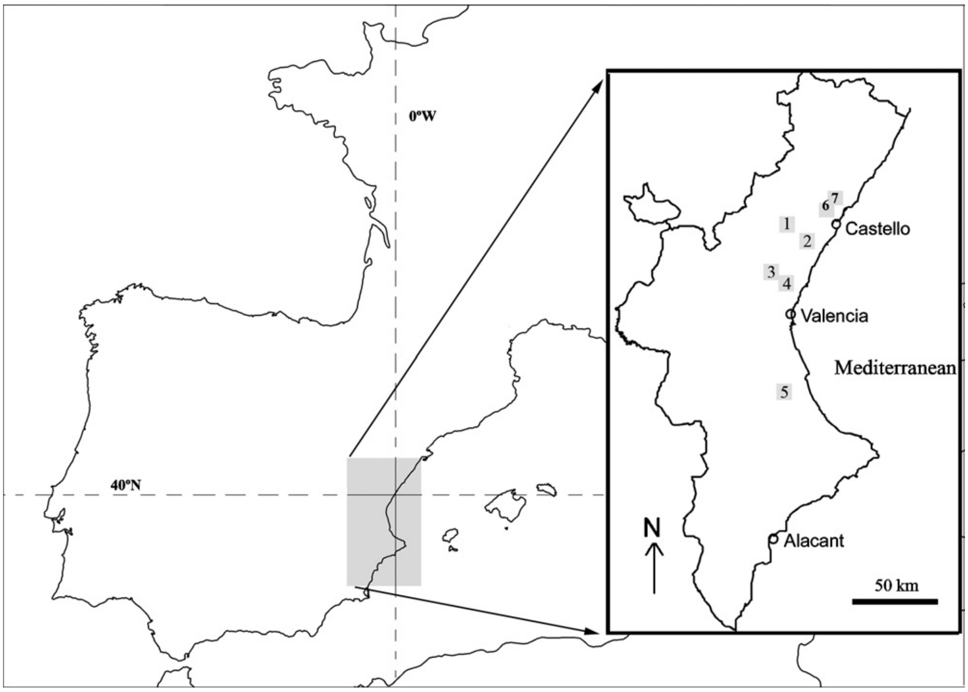

Fig. 1. Location of the seven study sites in the eastern Iberian Peninsula. Sites are located in the following areas (from north to south): Desert de les Palmes (sites 6 and 7), Serra Espadà (sites 1 and 2), Serra Calderona (sites 3 and 4), and Pinet (site 5).

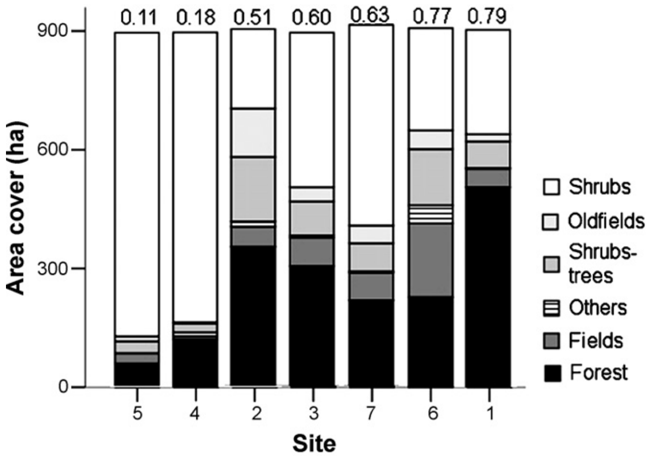

Fig. 2. Area covered by each vegetation type on the seven study sites ordered (from left to right) by increasing jay-pair density (indicated on top of each bar as the number of pairs/km^2).

Table 1
Bivariant Pearson correlation coefficient (r) of compositional and configuration variables with the jay pair density found on the seven study sites

Variable	r	
(a) Landscape composition		
Fields	0.648	ns
Oldfields	0.299	ns
Shrublands	−0.856	*
Tree–shrublands	0.591	ns
Forest	0.772	*
(b) Landscape configuration		
Mean patch size	−0.896	**
Patch size standard deviation	−0.921	**
Total edge	0.818	*
Mean patch edge	−0.797	*
Mean shape index	0.820	*
Habitat diversity	0.730	!

ns: non-significant; !: $p = 0.05$; *: $p < 0.05$, **: $p < 0.01$.

shrub–trees (shrublands and oldfields abandoned a long time ago with a well-developed shrub layer; tree cover of ca. 20–50%), Forests (tree cover ca. >50%), and others (other vegetation types, urban areas, ponds, etc.). The seven study sites showed different proportions of these vegetation types (Fig. 2). Sites 4 and 5 are dominated by shrublands (>80% cover), which are mainly the product of recent fires. Forest area on the other sites varies between 25.1% (site 6) and 56.1% (site 1). The main tree species in the area were pines (*Pinus halepensis* and *Pinus pinaster*) and oaks (*Quercus suber* and *Quercus ilex*).

2.3. Jay populations

On each site, jay abundance was quantified by assessing fledgling locations in June 2003. The methodology consisted of locating youngsters through their periodic feeding calls to adults (usually at 20–30 min intervals) in the few days after nest abandonment by means of a survey of the whole quadrat either by car, stopping every 500 m, or on foot through areas with no roads. The location obtained is a good estimation of nest position because young jays are unable to fly long distances during this period. For habitat selection analysis purposes we assumed jay-nesting territories as circles centred on the fledgling positions, with a radius equal to the mean half-distance of the five closest nest positions. To avoid jay nest territories overlapping and subsequent loss of independence, larger areas are not recommended. Jay pair numbers on each site were estimated as the sum of the jay pairs weighted by the proportion of jay nesting territory (as defined above) that falls inside the limits of the site. Otherwise stated, jay density is expressed as the number of jay-pairs/km^2.

2.4. Data analysis

2.4.1. Landscape level

On each 3 km × 3 km site, landscape composition (see above) and configuration variables (Table 1) were estimated using FRAGSTATS 3.3 (McGarigal et al., 2002). Configuration variables considered were: mean patch size (landscape area divided by total number of patches, expressed in ha), patch size standard deviation (PSSD) (the root mean square error in patch size), total edge (length of the edge, summed for all patches, expressed in km), mean patch edge (total edge divided by the number of patches, in m/patch), mean shape index (the mean of the shape index of each patch, which is the patch perimeter divided by the square root of the patch area) and habitat diversity (computed using the Shannon index and considering the proportional abundance of each habitat). The Pearson correlation coefficient was used to test both the correlations between landscape variables, and the relation of these variables to jay-pair density. Stepwise linear regression was used to determine the landscape variables that explain most of the variability in jay-pairs density. To assess the predictive error of the model, the regression was repeated seven times, each time excluding one of the sites and then comparing the predicted jay density for the excluded site with the actual jay density observed in the field for this site.

2.4.2. Nesting territory level

To determine the landscape characteristics of the nesting area selected by jays, we compared vegetation composition and landscape configuration between jay nesting territories and paired randomly generated circles of the same size (JAY vs. Non-JAY circles comparison; Martinez and Calvo, 2000; Lawler and Edwards, 2002). When generating random circles, all partially overlapping circles were discarded to avoid loss of independence. In order to minimise spatial variation, pairwise comparisons were made between the closest JAY/Non-JAY circles using a paired Wilcoxon test. Jay occurrence probability was estimated from the landscape variables on the seven studied sites using a binomial logistic regression, with a forward stepwise method for variable selection. This regression was then repeated seven times, excluding one site each time (i.e., removing a JAY/Non-JAY circle each time) from the analysis. The resulting regressions were used to predict jay occurrence for the excluded areas (validation exercise). To visually assess the predictive value of the model, significant variables were used to generate a probability-of-jay-occurrence image for one of the sites (site 7) using the FRAGSTATS 3.3 moving window option (McGarigal et al., 2002) and overlaying the observed nest locations.

3. Results

3.1. Landscape level

A total of 38 nesting positions were registered, but only 24 had more than 50% of their area inside the study sites. Densities ranged between 0.11 (site 5) and 0.79 (site 1) pairs/km^2, and were correlated positively with forest cover and negatively with shrubland cover (Table 1, Fig. 2). Jay densities were also positively correlated with several basic landscape configuration attributes

Table 2
Bivariant Pearson correlation coefficient (r) between landscape (composition and configuration) variables

Variable pair	r
Fields–total edge	0.766 *
Oldfields–tree–shrublands	0.872 *
Shrublands–tree–shrublands	−0.860 *
Shrublands–forest	−0.822 *
Shrublands–mean patch size	0.851 *
Shrublands–patch size standard deviation	0.910 **
Shrublands–total edge	−0.795 *
Shrublands–habitat diversity	−0.866 *
Tree–shrublands–mean patch size	−0.759 *
Tree–shrublands–patch size standard deviation	−0.807 *
Tree–shrublands–total edge	0.817 *
Tree–shrublands–habitat diversity	0.921 **
Mean patch size–patch size standard deviation	0.985 **
Mean patch size–total edge	−0.962 **
Mean patch size–mean patch edge	0.883 **
Mean patch size–habitat diversity	−0.822 *
Patch size standard deviation–total edge	−0.959 **
Patch size standard deviation–mean patch edge	0.821 *
Patch size standard deviation–habitat diversity	−0.865 *
Total edge–habitat diversity	0.898 **

Only significant correlations are shown (*$p < 0.05$, **$p < 0.01$).

such as the number of patches, the amount and density of edge, and the mean shape index, and they were negatively related to mean patch size and the standard deviation of patch size (Table 1). These relations between different variables are, in part, due to the high correlation between the compositional and configuration parameters (Table 2). All these attributes indicate that jays are more abundant in heterogeneous and diverse forested landscapes (with many small and size-variable patches).

Stepwise linear regression of jay density and site composition and configuration parameters for the seven study areas revealed PSSD as the best predictor of jay pair density at landscape scale ($F = 28.855$, adj. $R^2 = 0.823$, $p = 0.003$, jay density = 0.833–0.007 × PSSD); no further variable explained a significant variance when this variable was in the model.

Adjusted R^2 obtained from the seven regressions ranged from 0.674 (for site 5) to 0.941(for site 1) and all were significant at $p < 0.03$ (Table 3). The prediction error in jay density from actual (field observed) population density was high for site 2 (+32.6%) but less than 15% for the others (Table 3).

3.2. Nesting territory level

Closest inter-nesting position distances varied between 540 and 2841 m ($n = 25$). Mean half-distance of the five lower inter-nesting positions was 311.4 m (range 270–339 m). Vegetation composition and configuration were different between JAY ($n = 38$, total area = 1171 ha) and Non-JAY circles ($n = 38$, total area = 1148 ha): jays selected areas with higher proportions of forest, fields and oldfields and these areas were also more fragmented (i.e., higher number of patches, see Table 4). As at landscape level, jays preferentially used forested and heterogeneous portions of the area to locate their nesting position.

Table 4
Mean (and standard error of the mean) of landscape composition (%) and configuration metrics for paired jay (JAY) and non-jay (Non-JAY) circles ($n = 38 \times 2$)

Variable	Non-JAY	JAY	p
(a) Landscape composition			
Fields	5.0 (1.7)	11.6 (1.9)	0.002
Oldfields	3.2 (1.0)	8.0 (1.5)	0.003
Shrublands	54.6 (5.7)	27.4 (3.6)	<0.001
Tree–shrublands	8.6 (2.0)	10.7 (1.8)	ns
Forest	27.1 (4.7)	41.7 (4.0)	0.013
(a) Landscape configuration attributes			
Number of patches	7.8 (0.8)	13.6 (1.1)	<0.001
Mean patch size (ha)	6.8 (10.9)	2.9 (0.3)	<0.001
Patch size standard deviation (ha)	7.0 (0.7)	4.5 (0.4)	0.008
Total edge (km)	6.3 (0.5)	9.2 (0.5)	<0.001
Mean shape index	1.5361 (0.0450)	1.5953 (0.0221)	ns
Mean patch edge (m/patch)	982.6 (61.5)	758.2 (39.4)	0.002
Habitat diversity	0.9880 (0.0288)	1.3442(0.0396)	<0.001

Total area analysed was 1171 and 1148 ha, respectively. Mean differences were tested with the paired Wilcoxon signed-ranks test. Landscape composition variables (% of area) were arcsine-root transformed prior to analysis.

Table 5
Binomial logistic regression of composition and configuration variables of 38 pairs of circles (JAY–Non-JAY) with a radius of 311 m

	Constant	S.E.	W	Significant
Forest cover[a]	3.9606	1.1460	11.944	0.001
Total edge	0.00045	0.00014	10.663	0.001
Constant	−5.9010	1.6164	13.25	<0.001

Only the best model is shown. W = Wald regression statistics.

[a] Arcsine-root transformed.

Binomial logistic regression of JAY–Non-JAY with compositional and configuration variables (stepwise regression) reduced jay pair location prediction variables to total edge and forest cover (Table 5). The overall proportion of correct model predictions was 71.1% (Table 6). Correct predictions of jay occurrence on each site for the seven regressions ranged from 68.8 to 80.6%, and correct predictions of jay absence ranged from 62.5 to 76.7% (Table 6). In the validation exercise, jay absence was correctly predicted in 23 of

Table 3
Results of the regressions predicting jay density on each site from the other remaining six sites

Sites	Regression					Validation			
	Predictor	Adj. R^2	p	Constant	Coefficient	PSSD	Predicted	Observed	% Deviation
123456(7)	PSSD	0.848	0.009	0.830	−0.007	31.46	0.610	0.625	−2.4
12345(6)7	PSSD	0.780	0.012	0.832	−0.007	11.43	0.752	0.758	−0.8
1234(5)67	PSSD	0.674	0.028	0.834	−0.007	102.52	0.116	0.111	4.7
123(4)567	PSSD	0.741	0.017	0.829	−0.007	89.32	0.204	0.179	14.2
12(3)4567	PSSD	0.819	0.008	0.849	−0.007	25.34	0.672	0.608	10.4
1(2)34567	PSSD*	0.890	0.003	0.881	−0.008	25.35	0.678	0.511	32.6
(1)234567	PSSD*	0.941	0.001	0.783	−0.007	34.34	0.543	0.792	6.1
All	PSSD	0.823	0.003	0.835	−0.007	45.68	0.511	0.511	−0.2

The first column indicates the site # used as a predictors and the site used as a validation site (in brackets). The remaining columns are the regression results (Adj. R^2, p-value, constant, regression coefficients), the patch size standard deviation (PSSD) value of the site used as dependent, the jay density predicted from the regression, the actual jay density (observed in the field) and the deviation between the predicted and observed values. Jay densities in pairs/km^2. In the analysis using all sites (last row), the observed density is computed as the average of all sites. In all cases the predictor variable obtained with a stepwise method was PSSD except for sites 1 and 2 (*) where several other solutions (including PSSD as significant) were obtained; in these cases, and for simplicity, only PSSD was used.

Table 6
Percent of correct predictions of actual jay nesting positions using binomial regression, with forest cover and total edge as independent variables (all models were significant at $p < 0.005$)

Sites used	*N* pairs of circles	Correct predictions (%) in the regression			Validation	
		Non-JAY	JAY	Overall	Non-JAY correctly predicted/total	JAY correctly predicted/total
123456(7)	32	62.5	68.8	65.6	6/6	5/6
12345(6)7	37	64.9	73.0	68.9	1/1	1/1
1234(5)67	34	67.6	76.5	72.1	4/4	1/4
123(4)567	31	67.7	80.6	74.2	2/7	6/7
12(3)4567	33	63.6	75.8	69.7	2/5	5/5
1(2)34567	31	71.0	80.6	75.8	3/7	5/7
(1)234567	30	76.7	76.7	76.7	5/7	7/7
All	38	65.8	76.3	71.1	23/38	30/38

The first column indicates the sites used as predictors, with the site used for validation in brackets. The two validation columns refer to the number of Non-JAY circles and the number of JAY circles correctly predicted in the validation site using the equations from the remaining six sites (number of correctly predicted/total number of circles in the validation site). The cut point for Jay/Non-JAY validation was at 0.5 probability.

the 38 jay circles, and jay presence was correctly predicted in 30 of the 38 circles (Table 6). As an application exercise, the model was then applied to one of the sites (site 7) to obtain a probability surface of nest positions in the landscape and then compare the predictions with the observed data (Fig. 3).

4. Discussion

In our mediterranean landscape, jay distribution is clearly related to the amount of forested area. Jays select forested landscape and avoid shrublands (Fig. 1, Table 1(a)); however, jay selection is also related to areas with a high number of patches, i.e., heterogeneous portions of the landscape (Table 1(b)). The reason for this probably lies in the more diverse food spectrum in these areas (Rolando et al., 1995), which would translate into better reproductive success, as seems to be the case of the Steller's jay (Marzluff et al., 2004). In the Mediterranean region, the lower number of patches and larger variation in patch size (PSSD) are consequences of land abandonment and wildfires (Trabaud and Galtie, 1996; Lloret et al., 2002; Pausas, 2004). This complex landscape distribution might explain previous failures to relate individual breeding pairs to woodland fragment size alone (Hinsley et al., 1995). Contrary to our results, Brotons et al. (2004) found a tendency for jays to use continuous forest over isolated fragments of forest. We believe that this apparent discrepancy in jay preference is probably due to the fact that in the Brotons et al. study: (a) the forest fragments were too small to sustain a jay pair (mean size 10 ha); (b) the selected forest fragments were surrounded by homogeneous shrublands (avoided jay habitat); and (c) tree fruiting fields were not considered. That is, even though the jay requires heterogeneous landscapes, it seems to respond to a fragment suitability threshold.

Our spring jay densities were lower than those reported for European temperate landscapes (4.4–9.8 pairs/km^2, Grahn, 1990; Wilzak, 2005). This difference may be due to either the reduced forest area or the lower forest quality that jays find in Mediterranean landscapes as compared with temperate landscapes. Close examination indicates that both explanations seem to play a role. For example, the observed density on site 7 was 0.63 pairs/km^2, but since all the jays were located in 1/3 of the area (Fig. 3c) the density of the occupied area (minimum successfully reproductive pairs) was about 1.5 pairs/km^2, still lower than in temperate landscapes. Similar conclusions are extracted when analysing the other sites. We suggest that both the lower optimal habitat cover and the reduced capacity of the Mediterranean dry forest as compared with humid temperate counterparts contribute to lower jay densities.

Jay abundance was quantified by assessing fledgling positions. This method produces an underestimation of the real population since non-successful reproduction and floating jays may remain undetected (Grahn, 1990). However, it allowed us to optimise fieldwork while prospecting large areas because of the facility in locating fledglings from feeding calls. This contrasts with the difficulties in locating adults during the nesting period. Accuracy of the correspondence between fledgling and nest position depends on the time between location of the fledgling and nest abandonment (i.e., depends on the growth of the fledgling and the improvement in its flying skills). This is true not only because of the progressive separation from the nest but also because of the possibilities of confusion between neighbour pairs. Thus, the reduced effort required by this method must be carefully balanced by accurate fieldwork to obtain a realistic estimation of nest locations.

Jay-pairs nesting position probabilities maps (Fig. 3c), based on aerial photos, seem to be highly reliable as the configuration factors are easily quantified with standard GIS tools. However, we observed that some a priori suitable areas for jay breeding had no pairs at all (see Fig. 3c). Field observations suggest that competition and predation could be involved. For instance, ravens (in the southwest part of site 2) and magpies (southern part of site 5) seem to prevent jay nesting even in wooded and diverse habitat. The lower competitive ability of the jay with respect to other corvids (Rolando and Giachello, 1992), along with heavy nest predation by bigger corvids, squirrels, humans and sparrow hawks, has been reported (Goodwin, 1986). As a consequence, the pattern of nest predator distribution can modify jay-breeding positions in a way similar to that reported for the red-backed shrike (Roos and Part, 2004). The presence of goshawks on the study sites during spring was not observed; however, other predators like owls, hawks and genets may be involved in fine-scale jay-pair breeding positions, although this point needs further research.

At the scale analysed (9 km^2 extent, 1 m pixel for population density and jay-pair location, and 311-radius circles), both the jay-pairs density and distribution regressions provided reasonably good predictions (Tables 3 and 5, Fig. 3). Even with a certain grain aggregation (e.g., 5-m pixel) the resolution was sufficiently high to overcome changing grain problems. Moreover, total edge presented a consistent and robust scaling relation (Wu, 2004), enabling us to apply jay-pair position regression to regional areas.

Oak regeneration is strongly conditioned by jay acorn dispersal, especially at medium to high dispersal distances (Pons and Pausas, 2007b). As a consequence, studies analysing sapling densities (i.e., Pons and Pausas, 2006) need to consider jay presence in the sampling design; otherwise, seedling densities could be under-

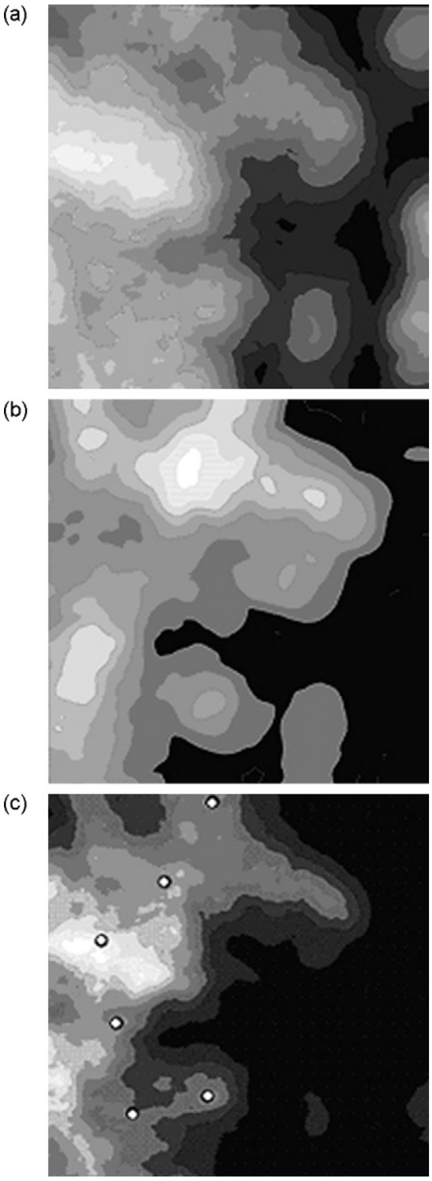

Fig. 3. Example of application of the model at landscape scale. In this example, jay-nesting locations on site 7 are predicted from data from sites 1 to 6 (first case in Table 6). Landscape attributes were obtained from aerial photography. Images were generated assuming a moving window of 311 m (fledging position buffer zones). (A) Total edge; (B) proportion of forests; and (C) spring jay nest position probability predicted from A and B; dots are the observed fledgling locations. Grey scale ranges from high (white) to low (black) values. Site dimensions are 3 km × 3 km.

estimated. As an example, very low densities of oak seedlings in dehesa-type ecosystems have been attributed to very low jay densities in these systems (Pulido and Díaz, 2005). In other words, to correctly separate the implications of each step in the oak regeneration, jay densities and distribution have to be implemented in the equation.

In summary, the results of this study suggest that jay-pair breeding locations: (a) are related to a mixture of landscape factors, including wooded area, complex landscape (diversity of food supply) and predators and competitors distribution pattern, and (b) can be accurately estimated from basic landscape attributes (woodland cover, fragmentation) using readily available tools (aerial photographs, GIS software). This methodology has also proved to be useful in modelling other vertebrates (Martinez and Calvo, 2000; Saïd and Servanty, 2005; Sergio et al., 2004). The implication for managers is that to favour natural oak regeneration they should take into account that jay populations are highly dependent on forest cover and landscape diversity. For instance, small agricultural fields inside forest areas increase jay populations thus favouring oak natural regeneration and colonization. Inversely, after fire, and especially when burned trees are removed (management activity often performed in the study area), shrub cover and landscape homogenisation increase. Our next step is to extend the model over wider areas (i.e., at regional level) and to integrate it in a landscape model for assessing oak regeneration.

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