



Research Article

Long-term colonization and extinction patterns of a forest-dependent rodent (*Muscardinus avellanarius*) in highly fragmented landscapes

Fabiola IANNARILLI^{1,3,*}, Ilaria MELCORE², Giulia SOZIO³, Davide ROVIANI⁴, Alessio MORTELLITI^{3,5}

¹Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, MN 55108, USA

²Museo di Storia Naturale del Salento, S.P. Calimera-Borgagne, 73021 Calimera (LE), Italy

³Department of Biology and Biotechnology “Charles Darwin”, Sapienza University of Rome, Viale dell'Università 32, 00185 Roma, Italy

⁴Via Santa Caterina 7, 33075 Cordovado (PN), Italy

⁵Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, 5755 Nutting Hall, Orono, ME 04469, USA

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Abstract

Colonization and extinction events play a major role in influencing long-term population dynamics, particularly in fragmented landscapes. Nevertheless, empirical knowledge on which factors drive these processes is still lacking for many mammals, likely due to difficulties in conducting long-term large-scale field studies. To determine which landscape features affect local colonization and extinction in *Muscardinus avellanarius* — a species highly sensitive to human landscape modifications — we collected detection/non-detection data in highly fragmented landscapes scattered through central Italy during a 7-year large-scale ($\approx 11000 \text{ km}^2$) study. We fitted multi-season occupancy models to our data; the results showed that both local colonization and extinction processes were driven by the level of connectivity in the landscape surrounding a patch. Specifically, the colonization probability of a patch increased with the number of patches within 1 km: the higher the number of surrounding patches, the higher the probability of colonization. Similarly, the extinction probability was positively affected by the mean edge distance to other patches within 1 km: the higher the mean edge distance — that is, surrounding patches at greater distance — the higher the probability of extinction of the local population. Our findings provide empirical evidence to support management actions aimed at conserving the hazel dormouse in areas where the populations are declining or threatened by habitat loss and fragmentation.

Introduction

Colonization and extinction dynamics drive the spatial and temporal distribution of species in fragmented landscapes (Hanski and Gaggiotti, 2004; Lindenmayer and Fischer, 2006). Hence, an understanding of the factors affecting local colonization and extinction is critical for managing species of conservation concern that often occur in small, spatially isolated populations (i.e. spatially structured populations). Nevertheless, a sound knowledge of the stochastic and deterministic factors determining species' distribution and long-term persistence in modified landscapes is still lacking.

Although several studies have directly linked colonization and extinction patterns to landscape features in fragmented landscapes, these focused on species characterized by short generation time and fast population turnover (e.g. butterflies: Hanski and Singer, 2001; birds: Gaston and Blackburn, 2002; amphibians: Peterman et al., 2013). Indeed the extinction and colonization parameters have not been studied extensively on mammals (but see Rodríguez and Delibes, 2003; Mortelliti and Boitani, 2007). This is likely a consequence of the great difficulties and resources needed to obtain the long-time series data over the relatively large spatial and temporal scale inhabited by mammals (Cagnacci et al., 2012). Most mammalian ecological studies are conducted for short time period (1–2 years) and/or in relatively small areas, consequently it is hard to reveal colonization and extinction patterns that, by nature, take place over a long time frame (i.e. more than 5 years; Elmhagen and Angerbjörn, 2001; Mortelliti et al., 2010a).

In this work, we analysed the effects of landscape structure on local colonization and extinction dynamics of the hazel dormouse (*Muscardinus avellanarius*). The hazel dormouse is a forest dependent arboreal rodent that mainly occurs in the early successional stages of deciduous or mixed deciduous-coniferous forests with a well-diversified understorey — these forest features assure cover and availability of food supply during the whole season of activity (Juškaitis, 2008; Bright and Morris, 1996). Compared to other rodents of the same size, this species is characterized by biological features that increase its sensitivity to human modifications of the landscapes, such as a relatively low potential of reproduction, large variation in annual reproduction success, low population densities, and relatively long lifespan (Bright and Morris, 1990; Bright et al., 1994; Juškaitis, 2008). In particular, habitat loss, habitat fragmentation and deforestation have been recognized as the major threats for this species by several legislations (see Bertolino et al., 2015).

Although this species is currently included in the IUCN Red List as Least Concern, some of the northern European populations have shown a declining trend, mainly due to habitat loss and fragmentation (Amori et al., 2008). As a result, the hazel dormouse is listed as a threatened species in different international conservation conventions, such as Appendix III of the Bern Convention and Annex IV of the EU Habitats and Species Directive, and different national Red Lists (Amori et al., 2008). Consequently, it is particularly important to understand the factors that affect the colonization and extinction dynamics over a long time frame as this will provide guidelines to develop evidence-based conservation strategies aiming at reversing the negative effects of habitat fragmentation in highly modified landscapes.

*Corresponding author

Email address: ianna014@umn.edu (Fabiola IANNARILLI)

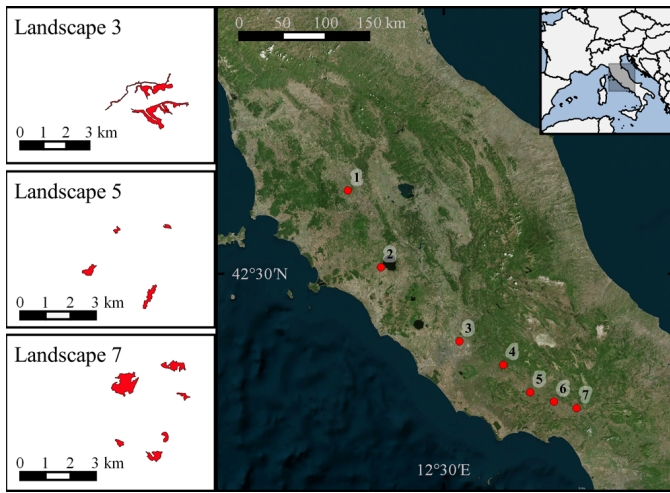


Figure 1 – On the right: study area. The red dots show the location of the seven 4×4 km landscapes sampled (numbered from 1 to 7). 1: Buonconvento, Siena Province (11 sites); 2: Capodimonte, Viterbo Province (5 sites); 3: Guidonia, Rome Province (2 sites); 4: Paliano (2 sites), 5: Arnara (4 sites), 6: Roccasecca (3 sites) and 7: Cassino (6 sites), Frosinone Province. On the left: as an example we provide details of the patches sampled in three different landscapes.

Previous studies conducted in highly fragmented landscapes have focused on the factors determining the occurrence (i.e. presence/absence) of this species. At the landscape level, the amount of residual forest cover (Mortelliti et al., 2011; Zapponi et al., 2013) and, to a lesser extent, the structural connectivity provided by networks of hedgerows (Capizzi et al., 2002; Mortelliti et al., 2011) affect the presence of the species. At the patch level, the occurrence of the hazel dormouse is influenced by the size of a habitat patch and by highly diversified undergrowth and high resource abundance (Bright and Morris, 1990; Capizzi et al., 2002; Mortelliti et al., 2011, 2014; Mortelliti, 2013). At this scale, this species is also influenced by forest management, that may alter the suitability of habitats by modifying the availability of food resources (Sozio et al., 2016).

Although factors affecting the occurrence of this species have been investigated in detail, we are not aware of any studies that have examined long-term colonization and extinction dynamics in the hazel dormouse. In a recent study, Mortelliti et al. (2014) examined the demographic mechanisms triggering short-term colonization and extinction events, making a first step towards understanding how long-term persistence could be maintained at the landscape-level. In this work, we aim at studying the long-term dynamics of this species, with a special focus on empirically evaluating the effects of patch size and connectivity on the probability of colonization and extinction. For this purpose, we followed several dormouse populations over a long time frame (7 years) and a large spatial scale ($\approx 11000 \text{ km}^2$), specifically aiming at testing the following two hypotheses:

Hp1: colonization probability in a given patch will increase with the number of hedgerows and/or the number of patches connected and will decrease with increasing level of isolation (distance from surrounding patches). Previous studies have highlighted the importance of connectivity (Capizzi et al., 2002; Mortelliti et al., 2011) and the amount of residual habitat in the landscape (Mortelliti et al., 2011; Zapponi et al., 2013) in determining the occurrence of the species. Therefore, we predict that these features influence the probability of colonization (or re-colonization) of a patch. Even if recent studies have shown that the species can cross open space (Büchner, 2008; Mortelliti et al., 2013), hedgerows are expected to be important at the landscape scale for the colonization of more distant patches.

Hp2: extinction probability is expected to decrease with increasing patch size and connectivity between patches. Larger patches are expected to support a larger number of individuals and this should lower extinction risk due to demographic and environmental stochasticity (Mortelliti et al., 2014). Similarly, increasing connectivity (i.e. connection or proximity among patches) should decrease extinction risk by

increasing the movement of individuals between patches (i.e. increase in immigration and, potentially, gene flow) and thus reducing the effects of the demographic and environmental stochasticity.

Materials and methods

Our study was conducted in central Italy, over a large area encompassing southern Tuscany and the whole Lazio region ($\approx 11000 \text{ km}^2$; $43^\circ 20' \text{ N } 11^\circ 20' \text{ E}$ to $41^\circ 27' \text{ N } 13^\circ 51' \text{ E}$; Fig. 1). The climate in this whole area is Mediterranean (temperate) with hot and dry summers and mild winters. Rainfall occurs mainly in spring and fall, with occasional snowfalls in the winter.

We selected 33 sites (sampling unit: patch) scattered in seven 4×4 km landscapes along the north-west south-east gradient of the study area (for more details about sampling design see Mortelliti et al., 2011). Each site consisted of a patch of deciduous oak woodland (*Quercus cerris* and/or *Quercus pubescens*), surrounded by a matrix of cultivated field, olives or vineyards. These features of our sampling design allowed to minimize possible differences in the internal structure of the selected patches. We chose to sample in landscapes in which the previous presence or absence of the species had already established (Mortelliti et al., 2009, 2010a, 2011) as our aim was to study long-term local colonization and extinction dynamics.

Dormice presence/absence data was collected from 2007 to 2013 through wooden nest-boxes (years 2008–09) or nest-tubes (years 2007 and 2010–13). We used a total of 118 nest-boxes and 452 nest tubes (75 in 2007, and 377 between 2010 and 2013). The number of nest-tubes/boxes in each patch increased with patch size (Mortelliti et al., 2011; see Tab. 1 for additional details on number of sampling occasions and survey timing). Nest-tubes/boxes were randomly distributed within each patch (minimum spacing: 70 m), and placed 1.5–2 m above ground. Nest-boxes (average size: $18 \times 21 \times 10 \text{ cm}$) were placed on trunk, with entrance hole (diameter: 3 cm) facing the tree. Nest-tubes

Table 1 – List of patches and number of nest-boxes/nest-tubes (secondary occasions) surveyed in each patch during a primary occasion. The number of nest-boxes/nest-tubes depended on the size of the patch; damaged and/or stolen nest-boxes/nest-tubes were replaced during the study. Here we reported only the nest-boxes/nest-tubes effectively surveyed during each primary occasion.

Patch	Primary occasion													
	Oct 2007	Apr 2008	May 2008	Jun 2008	Jul 2008	Oct 2008	Apr 2009	Nov 2010	Mar 2011	Mar 2012	Jun 2012	Oct 2012	Apr 2013	
	2007	2008	2008	2008	2008	2008	2009	2010	2011	2012	2012	2012	2013	
AR1	-	6	6	-	6	6	6	-	4	-	-	-	-	
AR2	-	8	8	8	8	8	8	-	15	2	8	4	9	
AR3	-	4	4	4	4	4	4	-	4	2	3	3	3	
AR5	-	9	9	9	9	9	9	-	8	-	-	10	4	
CP1	-	2	2	2	-	2	2	2	-	2	-	-	-	
CP2	-	2	2	2	-	2	2	5	-	5	-	-	-	
CP3	-	2	2	2	-	2	2	5	-	5	-	-	-	
CP4	-	-	-	-	-	-	-	5	-	5	-	-	-	
CP5	-	-	-	-	-	-	-	6	-	6	-	-	-	
CS1	-	6	6	6	6	6	6	-	4	3	7	5	9	
CS2	-	8	8	8	8	8	8	-	15	10	12	7	14	
CS3	-	4	4	-	-	4	4	-	9	8	2	-	-	
CS4	-	6	6	6	-	6	6	-	17	15	13	9	7	
CS5	-	4	4	4	4	4	4	-	6	6	5	4	2	
CS6	-	8	8	-	8	8	8	-	23	23	18	15	11	
IN3	-	10	10	10	-	10	10	21	-	21	-	-	25	
IN4	-	10	10	-	-	10	-	19	-	19	-	-	23	
PA1	-	6	6	-	-	6	6	-	12	9	12	-	11	
PA2	-	6	6	-	-	6	6	-	11	9	6	6	6	
RC1	-	7	7	7	7	7	7	-	7	7	7	6	6	
RC2	-	5	5	5	5	5	5	-	5	4	4	2	5	
RC3	-	3	3	3	3	3	3	-	4	2	5	3	4	
SI1	4	-	-	-	-	-	-	-	4	4	6	4	3	
SI10	4	-	-	-	-	-	-	-	8	8	12	6	12	
SI11	6	-	-	-	-	-	-	-	12	12	18	9	6	
SI2	4	-	-	-	-	-	-	-	2	2	3	2	2	
SI3	7	-	-	-	-	-	-	-	31	22	38	7	29	
SI4	10	-	-	-	-	-	-	-	10	10	24	8	9	
SI5	6	-	-	-	-	-	-	-	6	6	15	9	7	
SI6	4	-	-	-	-	-	-	-	4	4	6	4	3	
SI7	6	-	-	-	-	-	-	-	21	21	37	19	14	
SI8	15	-	-	-	-	-	-	-	24	24	38	18	16	
SI9	8	-	-	-	-	-	-	-	13	13	24	12	12	

Table 2 – List of predictor variables fitted in the multi-season occupancy models. x: the variable has been used to model the corresponding parameter. Probability of: γ : colonization; ϵ : extinction; p : detection.

Covariate group	Covariate	Description	γ	ϵ	p
Patch geometry	Area	Patch size (ha)	x	x	
	Shape Index	Shape Index: perimeter/area	x	x	
Patch Isolation	Mean Edge Distance in 1 km	Mean Edge Distance to patches within 1 km	x	x	
	Mean Edge Distance in 1.5 km	Mean Edge Distance to patches within 1.5 km	x	x	
	Proximity Index	Proximity Index	x	x	
	Connected Hedgerows	Number of hedgerows connected to other patches	x	x	
	Patches	Number of patches within 1 km	x	x	
	Autocovariate	Index of spatial autocorrelation	x	x	
Detection variables	Boxtube	Detection method: nest-box or nest-tube			x
	Year	Year of sampling			x
	Session	Primary occasion of sampling			x
	Season	Season (Spring: Mar-May; Summer: Jun-Aug; Fall: Sep-Nov)			x
	Lag	Months between consecutive primary occasions			x

(consisting of a removable wooden base inserted in a plastic square box) were placed on horizontal branches.

We considered the species detected when we found at least one individual or a new nest. The use of nest as a proxy to assess hazel dormouse's presence is a common technique for this species due to the characteristic structure and materials used by the individuals to build the nests (see Bright and Morris, 1990; Capizzi et al., 2002).

Explanatory variables related to landscape features and detection process were grouped in three categories: patch geometry, patch isolation and variables that were expected to influence the probability of detection, such as season (Tab. 2). The covariates in the first two groups were obtained from aerial photographs through ArcGIS 10 (ESRI, 2011). The aim of this analysis was to obtain information for the management of the species. We opted for using predictors that directly describe features of the landscape, instead of using an approach based on methods to summarize and reduce the number of variables (e.g. Principal Component Analysis). This facilitated the interpretation of the results and provides implications for management that are directly applicable. To avoid collinearity among variables, we checked for correlations using Spearman's correlation coefficient (Tab. 3). When pairs of variables had a correlation coefficient above ± 0.80 , we selected those

most biologically relevant based on previous knowledge on the natural history of the species. The final set of variables is listed in Tab. 2. All variables were standardized.

We fitted multi-season occupancy models (MacKenzie et al., 2003, 2006) to detection history data using *unmarked* package in R (Fiske and Chandler, 2011; R Core Team, 2015). These models estimate the initial probability of occupancy, detection, colonization and extinction probability taking into account imperfect detection — that is, failure in detecting a species when present (MacKenzie et al., 2003, 2006). We stress that accounting for imperfect detection when studying colonization and extinction rate is crucial; without disentangling true absence from failure in detection (using replicated surveys) the chances of overestimating extinction are relatively high. Occupancy modelling allows differences in sampling effort among sites and primary occasions, testing for differences on detection probabilities of multiple methods, and handling of missing data.

In this study, temporal replications within a sampling session (i.e. a year) were substituted with spatial replications. Consequently, we defined a primary occasion as a visit to the patches, and a secondary occasion as a visit to one of the nest-boxes/tubes within a patch. The

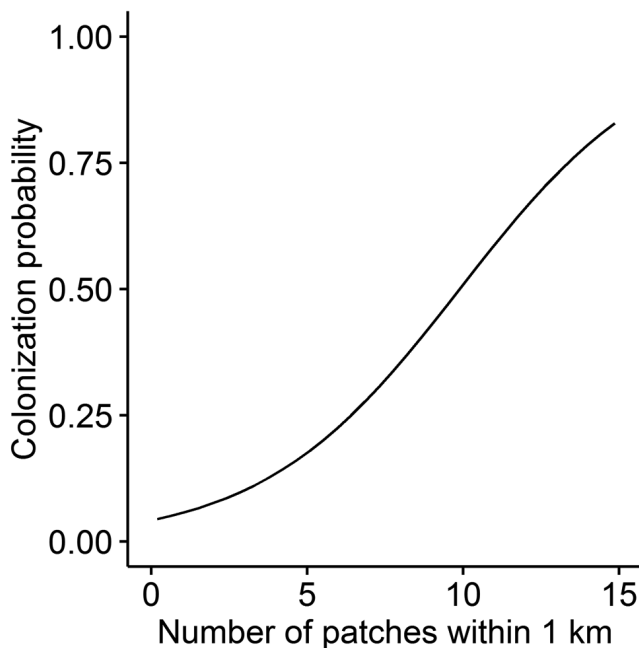
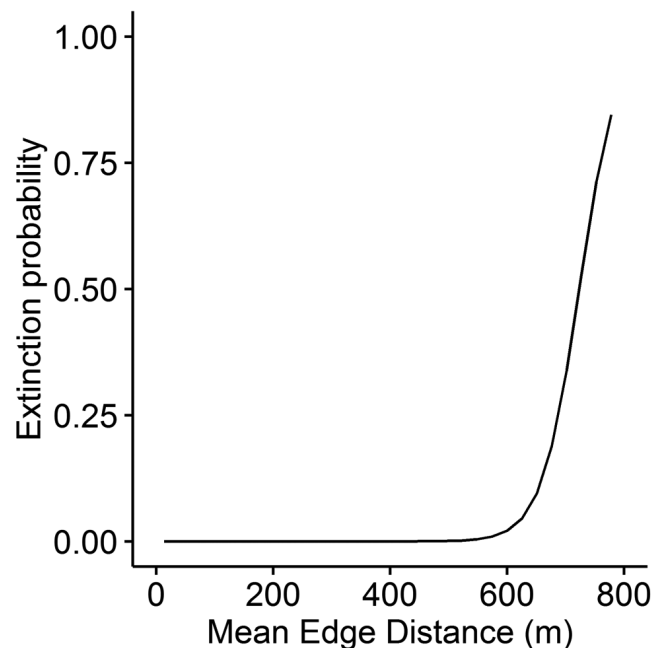
**Figure 2** – Colonization probability as a function of the number of patches within a 1-km buffer from the perimeter of the focal patch. The colonization probability of a patch increases with the increase of the number of patches within 1 km.**Figure 3** – Extinction probability in relation to the Mean Edge Distance between a focal patch and the surrounding patches within 1 km. The extinction probability steeply increases over a 600 meters average distance.

Table 3 – Spearman correlation coefficient between predictor variables used in the multiple season occupancy modelling.

	Shape Index	Mean Edge Distance in 1 km	Mean Edge Distance in 1.5 km	Proximity Index	Connected Hedgerows	Patches	Autocovariate
Area	-0.77	-0.1	-0.17	0.24	0.14	-0.07	-0.06
Shape Index		0.17	0.26	-0.16	0.1	0.32	0.21
Mean Edge Distance in 1 km			0.47	0	0.05	0.42	0.33
Mean Edge Distance in 1.5 km				-0.18	-0.18	0.23	0.22
Proximity Index					0.19	0.25	0
Connected Hedgerows						0.21	-0.24
Patches							0.23

number of secondary occasions ranged between 2 and 38 (8.13 ± 6.36 nest-boxes/tubes surveyed in each patch/primary occasion; Tab. 1).

Our primary goal was to estimate the colonization and extinction probabilities at the patch level. Since during the first year (2007) we were able to survey only 11 sites out of 33 due to technical constraints, we set the initial probability of occupancy as constant amongst sites. We started by modelling the detection probability parameter; predictor variables included: 1) data collection techniques (nest-box vs nest-tube: to test difference in detection probability of these two methods), 2) year, season and session in which the visit occurred (to test for yearly, seasonal and overall temporal trend, respectively). After selecting the relatively best detection probability model, we retained the covariates and then focused on assessing the relative importance of the patch geometry and connectivity on colonization and extinction probability (see Tab. 2). Models were ranked based on AIC (Akaike's Information Criterion) following Burnham and Anderson (2002).

Results

We detected *M. avellanarius* at least once in 22 out of the 33 patches and at least once in each of the seven landscapes surveyed.

For the detection probability parameter, none of the tested models showed a better fit compared to the model with constant detection probability in time and space; consequently, we kept detection probability constant in the subsequent modelling stages.

In the top ranked model (Tab. 4), the probability of colonization (γ) was positively affected by the number of surrounding patches in a 1 km

buffer from the focal patch (Patches; Tab. 5; Fig. 2). Hence, the probability of colonization was higher for patches that have a high number of forest fragments within a distance of 1 km from their perimeter (e.g. patches with only 2 fragments in the surrounding have less than 8% probability to be colonized, while the colonization probability increases over the 50% for patches closed to 10 fragments). The second ranked model showed that the colonization probability was also partially influenced by the number of hedgerows connecting a patch to the others (Connected Hedgerows; Tab. 4).

The probability of extinction (ϵ) increased with the increase of the mean edge distance between the focal patch and the surrounding patches within 1 km (Mean Edge Distance in 1 km; Tab. 4 and Tab. 5; Fig. 3). We caution the readers by emphasising that we observed high value of standard errors compared to the relative β estimates in the first ranked model in the extinction parameter (Tab. 5). However, Mean Edge Distance appeared as a predictor in the first four ranked models (and in both the models within $2\Delta AIC$), supporting the importance of this variable.

Discussion

Our work emphasizes the importance of habitat connectivity on colonization and extinction dynamics in the hazel dormouse. The level of isolation of a patch plays a key role for both the colonization and extinction parameters, affecting the colonization probability through the number of patches within 1 km and the extinction probability by the average distance to the closest patches (expressed as mean edge distance in 1 km).

These results confirm our hypothesis about the importance of connectivity for the probability of colonization (hypothesis 1). Our results show that low levels of isolation — high number of patches in the surrounding — promote the colonization of a patch, possibly due to a stepping-stone effect that increases the chances that individuals coming from other areas eventually reach a vacant patch. The number of patches in a landscape and the amount of forested habitat are inherently correlated and can be considered one the proxy of the other (Fahrig, 2003; Mortelliti et al., 2010b). Therefore, our result is consistent with previous knowledge on the spatial patterns of this species and could help explain why both landscape connectivity and forest cover have been found to affect the occurrence of the hazel dormouse (Capizzi et al., 2002; Mortelliti et al., 2011; Zapponi et al., 2013). Forest cover could in fact facilitate the occurrence of this species not only by an increased availability of habitat, but also by facilitating the colonization of vacant patches, as suggested by our findings. Here, for the first time,

Table 4 – Top ranked multi-season occupancy models. Colonization and extinction probability modelled as a function of variables related to patch geometry and isolation (reported in brackets; (.) : constant probability). Model ranking based on Akaike's Information Criterion. Only models within 5 ΔAIC are listed. nPars: number of parameters; AIC: Akaike's Information Criterion; ΔAIC : difference in AIC value between the model and the model with the lowest AIC value; AICwt: AIC weight of the model. Probability of: ϕ : initial presence; γ : colonization; ϵ : extinction; p: detection. Variables: Area: patch size; SH_IN: Shape Index; MED1000: Mean Edge Distance within 1 km; MED1500: Mean Edge Distance within 1.5 km; pr_in: Proximity Index; HDG_INT: number of connected hedgerows; PTC1000: number of patches within 1 km; AUTOCOV: Index of spatial autocorrelation.

Model	nPars	AIC	ΔAIC	AICwt
$\phi(.)\gamma(PTC1000)\epsilon(MED1000)p(.)$	6	684.22	0	0.19
$\phi(.)\gamma(HDG_INT)\epsilon(MED1000)p(.)$	6	685.6	1.38	0.09
$\phi(.)\gamma(.)\epsilon(MED1000)p(.)$	5	686.47	2.24	0.06
$\phi(.)\gamma(pr_in)\epsilon(MED1000)p(.)$	6	686.66	2.44	0.06
$\phi(.)\gamma(PTC1000)\epsilon(SH_IN)p(.)$	6	686.69	2.46	0.05
$\phi(.)\gamma(HDG_INT)\epsilon(HDG_INT)p(.)$	6	687.34	3.11	0.04
$\phi(.)\gamma(PTC1000)\epsilon(MED1500)p(.)$	6	687.65	3.43	0.03
$\phi(.)\gamma(MED1000)\epsilon(MED1000)p(.)$	6	687.65	3.43	0.03
$\phi(.)\gamma(PTC1000)\epsilon(.)p(.)$	5	687.68	3.46	0.03
$\phi(.)\gamma(MED1500)\epsilon(MED1000)p(.)$	6	687.73	3.51	0.03
$\phi(.)\gamma(PTC1000)\epsilon(Area)p(.)$	6	688.01	3.79	0.03
$\phi(.)\gamma(AUTOCOV)\epsilon(MED1000)p(.)$	6	688.32	4.1	0.02
$\phi(.)\gamma(SH_IN)\epsilon(MED1000)p(.)$	6	688.46	4.24	0.02
$\phi(.)\gamma(PTC1000)\epsilon(HDG_INT)p(.)$	6	688.57	4.34	0.02
$\phi(.)\gamma(PTC1000)\epsilon(AUTOCOV)p(.)$	6	688.67	4.45	0.02
$\phi(.)\gamma(PTC1000)\epsilon(PTC1000)p(.)$	6	688.77	4.54	0.02
$\phi(.)\gamma(HDG_INT)\epsilon(AUTOCOV)p(.)$	6	689.06	4.84	0.02

Table 5 – Top ranked model: parameters estimates and standard error. MED1000: Mean Edge Distance within 1 km; PTC1000: number of patches within 1 km.

	Parameter	Estimate	SE
Initial probability of presence	β_0	-0.37	0.74
Probability of colonization	β_0	-1.45	0.57
	$\beta_{PTC1000}$	1.41	0.67
Probability of extinction	β_0	-7.37	6.12
	$\beta_{MED1000}$	7.89	7.06
Probability of detection	β_0	-2.7	0.14

we demonstrate the importance of these features as key factors driving long-term spatial dynamics.

The probability of colonization is also partially influenced by the number of hedgerows connecting the focal patch (second ranked model), representing the structural connectivity of the landscape. This confirms that, even if the hazel dormouse can cross relatively high distances in open areas (Büchner, 2008; Mortelliti et al., 2013), the presence of a hedgerows network is still important to increase the overall connectivity.

We found that the local extinction probability is affected by the average distance to patches in 1-km buffer from the edge of a focal patch. The extinction probability increases steeply for mean distances greater than 600 meters; this value is slightly higher than the maximum distance movement reported for the species in treeless area (500 m; Büchner, 2008). This suggests an important role of individual movements through the matrix for the long-term persistence of fragmented populations. These inter-patch movements could avoid extinction events, maintaining genetic flow among single units of spatially structured population scattered across the landscape.

Conversely to what was expected (hypothesis 2) and as previously found by Mortelliti et al. (2014), patch size do not have an effect on the extinction probability for the species in this study area. However, we highlight that our results on this parameter are not conclusive: despite the large effort in data collection there is still a certain degree of uncertainty in the estimate of the extinction probability.

To the best of our collective knowledge this is the first study conducted at such a wide temporal and spatial scale aiming at investigating colonization and extinction patterns in the hazel dormouse. Our study strongly suggests that management or recovery plans for the hazel dormouse should consider the landscape structure of the area of interest and avoid (through forest preservation or reforestation) habitat fragments too isolated to support colonization events and avert local extinctions. ☞

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