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Original Investigation

Assessing environmental requirements effects on forest fragmentation sensitivity in two arboreal rodents

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ABSTRACT

The study of the effect of habitat fragmentation on species that inhabit residual patches requires the investigation of the relationship existing between species distribution and landscape components. To understand which components of landscape mosaics are more influential for species' persistence, we compared the distribution of two arboreal rodents proved to be sensitive to habitat fragmentation, the hazel dormouse Muscardinus avellanarius and the red squirrel Sciurus vulgaris. Their occurrence in residual oak woods in central Italy was studied with nest-boxes and hair-tubes, developing a new method for hair analysis. Their distributions were analysed considering patch, matrix composition and configuration, and landscape vegetation variables. The two species showed a different degree of plasticity, with the squirrel being significantly more specialised at the landscape scale. The comparison of the two distribution patterns highlighted the influence of different ecological constraints and the existence of different strategies to cope with fragmentation. Patch size and patch attributes were generally weaker determinants of occurrence, compared to landscape metrics. The squirrel presence was significantly influenced by the presence of shared perimeter between hedgerows and woods and by the lack of isolation of the residual patches, suggesting the use of several fragments to compensate the low habitat quality. Conversely the hazel dormouse seemed to be more affected by the internal management of the woods, and in particular by the mean DBH. Our results highlight how the recognition of the extrinsic constraints and the influence of multi-scale habitat selection may help guiding land use management, to ensure species conservation in profoundly exploited landscapes.

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Introduction

Mediterranean landscapes have been shaped by centuries of agriculture and exploitation, with an extensive human manipulation that probably spared only the sheerest areas (Blondel and Aronson 1999). The residual woods are often reduced to scattered patches, surrounded by crops, pastures and settlements, with landscape connectivity increasingly reduced by the growing impact of land use practices (Foley 2005). The study of the effect of woodland fragmentation on many wood dwelling species can no longer involve the simplistic dichotomy of habitat/non-habitat, of patches embedded in an homogenously adverse medium (Prugh et al. 2008). Patch area and isolation alone are weak determinants of species distribution, since the often human-biased concept of habitat suitability is not a black and white issue (Franklin and Lindenmayer 2009).

Understanding ecological correlates of local distribution patterns requires the identification of those individual constraints that influence patch use, such as boundary permeability, intraspecific density and trophic niche (Wiens et al. 1993). Home ranges, together with the size and configuration of landscape features, determine the actual use of the available resources (Macdonald and Rushton 2003). The effective conservation of fragmented landscapes entails the understanding of the value of the remaining vegetation and landscape elements for the fauna (Holland and Bennett 2009).

In the present study we investigate how long-term land management affects nowadays multi-scale responses of forest species. Since arboreal mammals are: (i) sensitive to landscape modification (Bright and Morris 1996), (ii) excellent indicators of ecosystem

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158 **Table 1**

Interspecific comparison of body mass, body length, home range and population density for the two target species.

Species	Body mass (g) ^a	Body length (mm) ^b	Mean home range (ha) ^{b,c}		Mean population density (ind/ha) ^{b,d}
			Male	Female	
Muscardinus avellanarius	15-40	65–90	0.783	0.503	5.725
Sciurus vulgaris	220-350	240-290	5.570	3.390	1.115

^a Capizzi and Santini (2007).

^b Amori et al. (2008).

^c Verbeylen et al. (2009).

^d Wauters et al. (1994).

health (Carey 2000), (iii) effective model-species of fragmentation studies (Koprowski 2005), the red squirrel, Sciurus vulgaris (Linnaeus, 1758) and the hazel dormouse, Muscardinus avellanarius (Linnaeus, 1758) were selected as target species. Besides, the comparison of two species that belong to the same trophic level, but show a different degree of habitat specialisation and a different spatial ecology (Table 1), allows the analysis of the effect ecological plasticity on distribution patterns. We hypothesise that woodland fragmentation may influence arboreal rodents in a non univocal way and therefore we test the following predictions: (1) as it has been highlighted by Swihart et al. (2003) the dispersal of generalist species should be less limited by the presence of certain matrix habitats, therefore we expect that the hazel dormouse should be less influenced in its distribution by landscape composition. Besides, we predict that the distribution of the two species should be shaped by different landscape elements: (2) while the presence of hedgerows and consequently a higher structural connectivity should be more influential for the hazel dormouse (Capizzi et al. 2002; Mortelliti et al. 2011), (3) the squirrel distribution should be more influenced by the lack of isolation (Celada et al. 1994; Rodríguez and Andrén 1999). Lastly, (4) recognising the high selectivity of the squirrel in terms of habitat quality (Van Apeldoorn et al. 1994) we expect this species to be more affected by forest habitat features.

Material and methods

Study area

The study was performed in central Italy $(43^{\circ}13'N - 12^{\circ}58'E, 43^{\circ}02'N - 13^{\circ}25'E)$, in an area of approximately 100,000 ha, with altitude ranging from 300 to 700 m a.s.l. (Fig. 1). The woods were mainly dominated by broad-leaf species (e.g., *Quercus cerris, Quercus pubescens, Ostrya carpinifolia*) and are coppiced. The matrix that surrounds the wood fragments was principally composed by crops (52%) and woods (34%), with scattered patches of shrubs (5%), anthropic areas (4%), hedges (3%) and grassland (2%) (Catorci et al. 2007). This area was selected since it offered the opportunity of comparing woodland fragments included in landscapes that have suffered a diverse human impact.

To reduce the variability due to sample units variability, the regional map of vegetation associations (Catorci et al. 2007) was used to generate a list of downy oak (*Q. pubescens*) woods larger than 1 ha, and a random sample of 23 wood patches was extracted. The "Abbadia di Fiastra" Natural Reserve, being the only wide wood of the area, was included among the sample sites to compare the patches with a more pristine and continuous condition. The scale adopted in this study can be defined patch-landscape that according to McGarigal and Cushman (2002) involves the use of patches as sample units and the inclusion of landscape metrics as explanatory variables.

Squirrel survey

The red squirrel survey was carried out from May 2008 until October 2009, using hair-tubes: plastic tubes that contain adhesive tape in both extremities and an attractive bait (Amori et al. 2012). It is a widespread (Bertolino et al. 2009) and low cost method that allows studying animal distribution at landscapescale (Sanecki and Green 2005). To reduce the probability of false absences, the sampling protocol has been designed according to Mortelliti and Boitani (2008). The number of hair tubes present in each site was therefore increased with the area of the sampled patch, starting with a minimum number of two, for a total number of 115 (see Table 1 of the Supplementary content for the number of hair-tubes in each patch). The tubes were baited with a mixture of maize, chocolate and hazelnuts (Mortelliti and Boitani 2008) and were placed in the 24 sample patches, attached to horizontal tree branches with metal wire. After 40 days the hair-tubes were removed, and the collected hairs were cleared from glue rests with a solvent and stored in 70% alcohol for microscopic examinations.

The hair samples were identified through comparison of morphological features (length, cuticular pattern and cross-section shape) with available literature (De Marinis and Agnelli 1993; Teerink 1991) and a reference collection. First, the hairs were measured using a stereomicroscope. Second, cuticular pattern casts were created following Quadros and Monteiro-Filho (2006) protocol. The casts were observed with an optic microscope (from $100 \times$ to $400 \times$) and classified according to the shape of the scales (Teerink 1991). Lastly, cross-sections of the hairs were obtained with a new method that involved embedding the samples in Optimal Cutting Temperature (O.C.T.) compound. Working in a cryostat (Leica, CM-3050S) at -20 °C, a base mould (7 mm \times 7 mm \times 5 mm moulds Simport Plastics, Cat no. 720-0820) was used to make a flat block of O.C.T. A straight cut was made on the surface of the block using a scalpel blade and the hair was placed in the cut. The edges of the cut were pressed down to keep the hair in place and the cut was sealed with an additional layer of O.C.T. The block was left to set in the cryostat and then trimmed. About 40 sections, 10 µm thick (tip, beginning and end of the shield) were obtained for each hair. The sections were collected on poly-lysine coated slides. The slides were kept at room temperature while working so that, upon collection, the frozen sections would melt and adhere when touching the warm slide. Once the glass slides had dried, pictures were taken using a Leica DMRB microscope, $40 \times$ air lens.

Dormouse survey

Presence and absence of hazel dormouse was assessed using nest boxes, a common technique for the monitoring of this elusive species (Büchner 2008; Juškaitis and Šiožinytė 2008). Nest boxes were assembled and positioned according to Bright and Morris (1989), attached to trees with metal wire, with the entrance facing the tree trunk. A total of 132 nestboxes were distributed in 22 L. Zapponi et al. / Mammalian Biology 78 (2013) 157-163



Fig. 1. Study area map with the distribution of the 24 forest fragments.

sample sites, according to the wood size (see Table 1 of the Supplementary content). Nestboxes were left in position and periodically visited every four months, from October 2008 until October 2010, being a year and a half the minimum survey duration to infer the species absence (Bright and Morris 1989).

Patch structure

Circular sample plots (n = 66) were distributed in the different sites, according to their size (Table 1 of the Supplementary content), ensuring a minimum distance of 200 m between plots. The metrics were selected following the international BioSoil protocol (Bastrup-Birk et al. 2007) and included list and cover for the herbaceous, shrub and tree layers, tree diameter (DBH), canopy height, canopy cover, number of strata, types of trees present and an estimate of the dead wood amount.

Landscape analysis

A buffer of 1-km was created around the patches, an extent considered suitable for landscape description for the target species considering their dispersal distance (Büchner 2008; Wauters et al. 2010). Vegetation maps (Catorci et al. 2007) and aerial photographs (Italian National Cartographic Portal, 2000) were used to digitalise habitat types with ArcMap 9.3 (ESRI, 1999–2008). We identified six classes of land cover: woodland, cropland, hedges, shrubs, grass-land and anthropic areas. Several metrics were extracted with Patch Analyst 0.9.5 (Ontario Ministry of Natural Resources, 2008) and IAN 1.0.23 (Department of Forest Ecology and Management, University of Wisconsin-Madison, 2010). The map of vegetation associations (Catorci et al. 2007) was also used to discriminate between the vegetation types present in the matrix and therefore evaluate their influence.

Statistical analysis

The explanatory variables, summarised in Table 2, were subdivided in three groups (patch structure, landscape configuration and landscape vegetation), appropriately transformed (Legendre and Legendre 1998) and tested for within-group collinearity. Only those variables non-significantly correlated with others of the same group were kept and used in the subsequent analyses. For both mammal species three sets with all alternative multiple logistic regression models were built, to which the presence–absence data were fitted. The resulting models were ranked using second order Akaike Information Criterion (AIC_c and Δ AIC_c) and the importance of the included parameters was evaluated with Akaike weights (*W_i*). The set of best models was identified as the subset which cumulative *W_i* was ≤0.95 (Burnham and Anderson 2002). The relative importance of the different variables was determined by the sum of the W_i (ΣW_i) of all the models in this subset where the parameter occurred. The integration of both parameters (ΔAIC_c and ΣW_i) allowed the estimation of the weight of evidence of the different variables considering the whole set of best models, and thus overcame the limits of multimodel selection uncertainty when no single model can be considered superior (Burnham and Anderson 2002). The analyses were performed using R 2.10.1 (The R Foundation for Statistical Computing 2009) with AICcmodavg package 1.25 (Marzerolle, 2008) and PASW Statistics 18 (SPSS Inc.).

Results

The new protocol for hair analysis, producing high quality images (Fig. 2), was fundamental for the final identification. The European red squirrel was detected in 46% of the sites (n=24), whereas the hazel dormouse was detected in the 36% of the wood patches (n=22).

The relative importance of the different variables included in the three sets of alternative models varied for the two target species, with a general higher fit (Nagelkerke's R^2) (Tables 3 and 4 of the manuscript and Tables 2 and 3 of the Supplementary content) and W_i segregation (Fig. 3) for what concerns the squirrel. For the models including the variables describing the patch characteristics, the most influential component was the amount of shrub cover ($\Sigma W_i = 0.43$, $R^2 = 0.14$) for the squirrel and the oak DBH (ΣW_i = 0.45, R^2 = 0.10) for the hazel dormouse. For the models derived using landscape composition and configuration variables, the amount of shared perimeter between woods and hedges was very influential for the squirrel ($\Sigma W_i = 0.72$), along with the amount of woodland in the matrix $(W_i = 0.57)$ that was relevant for the hazel dormouse as well ($\Sigma W_i = 0.45$). The model containing these two variables together was the best model for the squirrel ($R^2 = 0.35$). For the models that considered the vegetation present in the matrix, the amount of coniferous reforestations ($\Sigma W_i = 0.60$), *Quercus* sp. woods ($\Sigma W_i = 0.58$) and grassland ($\Sigma W_i = 0.53$) had the highest weight and fit for the squirrel ($R^2 = 0.53$), whereas all the vegetation types had similar W_i for the hazel dormouse (Fig. 3 of the manuscript and Table 4 of the Supplementary content).

Discussion

The prediction that the hazel dormouse would be less influenced by matrix habitats was confirmed by the two sets of models involving buffer elements composition and configuration. Even if the amount of habitat was a key driver for both species as in Mortelliti et al. (2011), landscape variables showed a clear relevance only for the squirrel. Unlike we predicted, hedgerows were influential only for the red squirrel. The presence of tree lines improved model

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Table 2

Description of the three sets of variables included in the models, with the applied transformations.

	Definition	Mean	S.D.	Т
Patch				
CANC	Canopy cover (%)	0.727	0.062	Arcsine
SHRC	Shrub cover (%)	0.607	0.254	Arcsine
HERC	Herbaceous cover (%)	0.506	0.226	Arcsine
ODBH	Oak diameter at breast height (cm)	42.305	23.352	Ln
DWOO	Dead wood amount	3.757	1.382	
SIZE	Area of the wood patch (ha)	10.897	20.468	Ln
Landscape composit	ion			
WHSP	Wood-hedge shared perimeter (m)	194.708	136.792	Ln
WOAM	Amount of woodland in the matrix (%)	0.325	0.199	Arcsine
WMNN	Wood mean nearest neighbour (m)	73.920	57.407	Ln
CON	Landscape contagion ^a	61.058	3.760	
PAC	Wood perimeter area ratio corrected (m ha ^{-1/2}) ^b	2.388	0.522	
CONI	Reafforestation with Pinus nigra (%)	0.053	0.120	Arcsine
Landscape vegetatio	n			
CAST	Woods characterised by the presence of Castanea sativa (%)	0.048	0.113	Arcsine
OSTR	Woods characterised by the presence of Ostrya carpinifolia (%)	0.419	0.244	Arcsine
QUER	Woods characterised by the presence of Quercus sp. (%)	0.303	0.128	Arcsine
RIPA	Riparian woods characterised by the presence of Salix alba (%)	0.084	0.101	Arcsine
SHRU	Shrublands mainly characterised by the presence of <i>Spartium junceum</i> and <i>Cytisus</i> sessifolius (%)	0.163	0.120	Arcsine
GRAS	Garigues characterised by the presence of Cephalaria leucantha and grasslands of <i>Bromus erectus</i> (%)	0.082	0.125	Arcsine

^a Riitters et al. (1996).

^b Baker and Cai (1992).

significancy for Verbeylen et al. (2003) as well, suggesting the critical role of this element to ensure species persistence through landscape structural connectivity. The squirrel selectivity at the landscape scale was further reinforced by the results of the models obtained with the map of vegetation associations, which showed a clear influence only for the red squirrel and indicated a preference for oak woods and coniferous reforestations. Even in a landscape naturally dominated by broadleaf species, where conifers covered less than the 2% of the study area, the squirrel confirms its preference for this element (Van Apeldoorn et al. 1994; Rima et al. 2010). Considering that in terms of landscape configuration, the most relevant factors were the length of shared perimeter between hedgerows and woods and the amount of woods, we can sustain the dominant role of landscape structure on occupancy patterns (Celada et al. 1994). As it has been previously observed for the squirrel by Koprowski (2005) and Verbeylen et al. (2009), the persistence in residual patches could be related to the contemporaneous use of several patches and supplemental food. Thus, the process of "landscape supplementation" (Dunning et al. 1992), or "habitat compensation" (Norton et al. 2000) could allow the squirrel to persit in an area of poor habitat quality patches with periodic extinctioncolonization dynamics (Celada et al. 1994; Swihart et al. 2003).

Even if we expected that the squirrel would be more specialised at the patch scale as well, the hazel dormouse showed a stronger segregation in the relevance of the variables for this set of models. The dependence of the hazel dormouse on the oak diameter supports the avoidance of young coppices and intensive thinning (Bright and Morris 1990; Juškaitis 2008). The area of the fragments was not a relevant predictor, contrary to what has been previously remarked for both the red squirrel (Rodríguez and Andrén 1999; Mortelliti et al. 2009) and the hazel dormouse (Greaves et al. 2006). This result could reflect the fact that when woodland patches are not very wide, as in this case where the average size <15 ha, the presence of connecting hedgerows (Wauters et al. 1994) and the lack of isolation exert a stronger effect.

The simultaneous consideration of the observed distribution patterns suggests the existence of different strategies of coping with landscape alteration. The extrinsic constraints (sensu Barbault and Stearns 1991) that arise in a highly fragmented and heterogeneous landscapes are key determinants of the mechanisms



Fig. 2. Hair cross-sections showing the shape of samples belonging to the two target species (a. Sciurus vulgaris, b. Muscardinus avellanarius), obtained with the new proposed method.

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Table 3

Model form of best logistic regression models for the hazel dormouse, ranked according to their second order Akaike Information Criterion (AICc). Goodness-of-fit assessed with Nagelkerke R^2 .

Model form	AICc	ΔAICc	w	β_1	SE1	β_2	SE ₂	R^2
Landscape configuration								
WOAM	31.55	0	0.16	3.438	2.592			0.12
WOAM + WMNN	31.98	0.44	0.13	5.59	3.19	0.79	0.60	0.24
WMNN	32.99	1.45	0.08	0.33	0.52			0.03
PAC	33.28	1.73	0.07	-0.39	0.89			0.01
WHSP	33.35	1.81	0.07	0.16	0.45			0.01
CON	33.47	1.92	0.06	-0.10	0.12			0.00
WOAM + PAC	33.75	2.20	0.05	3.75	2.63	-0.64	0.95	0.14
WOAM + WHSP	34.19	2.65	0.04	3.39	2.60	0.11	0.47	0.12
WOAM + CON	34.24	2.70	0.04	3.44	2.59	-0.01	0.12	0.12
Vegetation type								
RIPA	32.42	0.00	0.08	-4.79	4.87			0.06
CONI	32.86	0.43	0.07	-3.54	5.19			0.04
CAST	33.18	0.76	0.06	2.05	3.78			0.02
QUER	33.24	0.81	0.06	1.99	4.09			0.02
OSTR	33.42	0.99	0.05	0.43	1.84			0.00
GRASS	33.43	1.01	0.05	-0.72	3.70			0.00
SHRUB	33.45	1.02	0.05	0.74	4.54			0.00
QUER + RIPA	34.28	1.86	0.03	4.25	4.75	-6.81	5.74	0.11
CAST + RIPA	34.74	2.31	0.03	2.43	3.86	-5.14	5.03	0.09
Patch attributes								
ODBH	31.85	0.00	0.14	-1.54	1.33			0.10
SIZE	32.82	0.97	0.08	3.34	6.64			0.02
CANC	33.22	1.37	0.07	3.34	6.64			0.02
SHRC	33.44	1.59	0.06	-0.03	0.33			0.00
DWOO	33.46	1.61	0.06	-0.10	1.60			0.00
HERC	33.47	1.62	0.06	-0.10	1.62			0.00
CANC + ODBH	34.07	2.22	0.04	4.75	6.98	-1.64	1.33	0.13
ODBH + SIZE	34.47	2.62	0.04	-1.40	1.43	-0.18	0.61	0.10
ODBH + SHRC	34.47	2.62	0.04	-1.57	1.34	-0.40	1.44	0.10

governing the observed distributions, and hence the use of the matrix (Gehring and Swihart 2003). The red squirrel showed a higher degree of specialisation at the landscape scale and lower at the patch scale, confirming the effect of fragmentation on multi-scale habitat selection (Rima et al. 2010). In an area profoundly

alterated by habitat fragmentation the presence of landscape elements that both increase the structural connectivity and the availbility of resources probably determine the landscape grain (sensu Baguette and Van Dyck 2007) to which the squirrel responds. Conversely, the patch scale influenced the hazel dormouse more

Table 4

Model form of best logistic regression models for the squirrel, ranked according to their second order Akaike Information Criterion (AICc). Goodness-of-fit assessed with Nagelkerke R^2 .

Model form	AICc	$\Delta AICc$	w	β_1	SE1	β_2	SE ₂	β_3	SE ₃	R^2
Landscape configuration										
WOAM + WHSP	32.96	0.00	0.22	4.39	2.46	1.07	0.57			0.35
WHSP	34.13	1.17	0.12	0.80	0.51					0.18
WOAM + WHSP + PAC	35.06	2.10	0.08	4.59	2.55	1.32	0.71	0.93	1.05	0.39
WOAM + WHSP + CON	35.59	2.63	0.06	4.57	2.52	1.12	0.59	0.07	0.13	0.36
WMNN + WHSP	35.61	2.65	0.06	-0.49	0.51	0.83	0.51			0.24
WOAM + WMNN + WHSP	35.66	2.70	0.06	4.03	2.55	-0.24	0.55	1.06	0.57	0.36
WOAM	35.74	2.78	0.06	2.72	2.04					0.10
PAC+WHSP	36.03	3.08	0.05	0.83	0.98	1.00	0.61			0.22
RCO + WHSP	36.68	3.73	0.03	0.03	0.12	0.81	0.52			0.19
Vegetation type										
QUER + GRASS + CONI	31.05	0.00	0.22	12.27	6.59	-23.39	14.78	17.18	14.25	0.53
GRASS + CONI	33.15	2.10	0.08	-11.58	9.42	19.39	12.59			0.35
QUER + GRASS	33.32	2.27	0.07	11.73	5.51	-9.56	5.90			0.34
CONI	33.86	2.81	0.05	10.12	7.07					0.20
QUER	34.47	3.43	0.04	6.41	3.95					0.17
QUER + CONI	35.19	4.14	0.03	4.67	4.25	7.56	7.20			0.26
CAST + CONI	35.63	4.59	0.02	-4.13	4.99	9.74	7.28			0.24
QUER + RIPA + GRASS	35.65	4.60	0.02	12.54	5.78	4.18	5.60	-11.56	6.63	0.36
QUER + CAST	35.80	4.75	0.02	6.62	4.17	-4.97	4.87			0.23
Patch attributes										
SHRC	34.99	0.00	0.11	-2.27	1.51					0.14
DWOO + SHRC	36.24	1.25	0.06	-2.56	1.54	-0.39	-0.35			0.21
CANC	36.27	1.27	0.06	7.44	6.48					0.08
SIZE	36.35	1.36	0.06	0.56	0.52					0.07
SHRC + SIZE	36.60	1.61	0.05	-2.26	1.59	0.52	0.54			0.19
DWOO	36.64	1.65	0.05	-0.32	0.32					0.06
CANC + DWOO	36.71	1.72	0.05	10.82	7.13	-0.51	0.37			0.19
CANC + SHRC	36.88	1.89	0.04	5.74	6.82	-2.08	1.56			0.18
DWOO + SIZE	37.09	2.10	0.04	-0.47	0.37	0.80	0.61			0.17

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Fig. 3. Ranking of the explanatory variables included in the 95% confidence set according to their cumulative Akaike weight (W_i) for the red squirrel (*S. v.*) and hazel dormouse (*M. a.*). (a) Patch attributes, (b) matrix vegetation type, (c) matrix composition and configuration. See Table 2 for the definition of the explanatory variables abbreviations.

strongly. Landscape genetic analyses highlight that anthropogenic factors may limit its dispersal to a very reduced spatial scale, such as 1 km for Naim et al. (2012), tying the conservation of this species to the quality of the residual patches (Büchner 2008).

The presence/absence of the species in adjacent patches may be influenced by the proximity of the fragments (Mortelliti et al. 2010) and consequently by immigration processes. Unluckily, the short duration of the study does not allow us to infer the effect of metapopulation dynamics on the observed distribution patterns (Ovaskainen and Hanski 2004). Still, the non-random distribution of the species should not considered a bias but a reflection of the "spatially patterned environment" (Hawkins 2012). It should be taken into account that this is an observation-correlation study. Even if our results do not imply causation, the different strategies that can be identified from the comparison of the influence of patch and landscape attributes on the two species' presence/absence highlight the relevance of different factors. The identification of these components that could increase the probability of persistence is therefore key for their conservation. Semi-natural habitats (i.e. grasslands and hedgerows) may act as actual sources in landscapes

profoundly shaped by human intervention (Magrini et al. 2009; Fischer et al. 2011). The 96% of the trees in the coppiced broadleaf woods has a diameter below 12.5 cm (IPLA 2000): this intensive management may compromise the value of woodland for biodiversity conservation, to the extreme that residual woods may not be more suitable for the species than the rest of the matrix (Zapponi 2010). Policies should thus recognise the positive effect of these elements on biodiversity (Brady et al. 2011) and value the crucial role that the matrix may play if appropriately managed.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2012.08.005.

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