

Population and individual-scale responses to patch size, isolation and quality in the hazel dormouse

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Abstract. Patch size, isolation and quality are key factors influencing species persistence in fragmented landscapes. However, we still lack a detailed understanding of *how* these variables exert their effects on populations inhabiting fragmented landscapes. At which ecological scale do they have an effect (e.g., individuals versus populations) and, on which demographic parameters?

Answering these questions will identify the mechanisms that underlie population turnover rather than solely predicting it based on proxies (e.g., presence/absence data).

We report the results of a large-scale, three-year study focused on the relative effects of patch size, isolation and quality on individuals and populations of an arboreal rodent, the hazel dormouse (*Muscardinus avellanarius*). We examined 30 sites nested within three landscapes characterized by contrasting levels of habitat amount and habitat quality (food resources). We quantified the effects of patch size and quality on the response of individuals (survival and litter size) and populations (density and colonization/extinction dynamics). We identified demographic mechanisms which led to population turnover. Habitat quality positively affected survival (not litter size) and population density (measured through an index). We infer that the decline in survival due to patch quality reduced patch recolonization rather than increasing extinction, while extinction was mainly affected by patch size. Our findings suggest that the effect of patch quality on individual and population parameters was constrained by the physical structure of the surrounding landscapes. At the same time, our results highlight the importance of preserving habitat quality to help the persistence of entire systems of patches.

Key words: Central Italy; demography; habitat loss and fragmentation; habitat quality; landscape change; *Muscardinus avellanarius*; occupancy; patch isolation; patch quality; patch size; population ecology; survival.

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INTRODUCTION

Habitat loss and fragmentation are key drivers of global species loss (Fischer and Lindenmayer

2007). In fragmented landscapes species must survive in small and often isolated patches with local populations subject to a relatively high risk of extinction due to both deterministic and

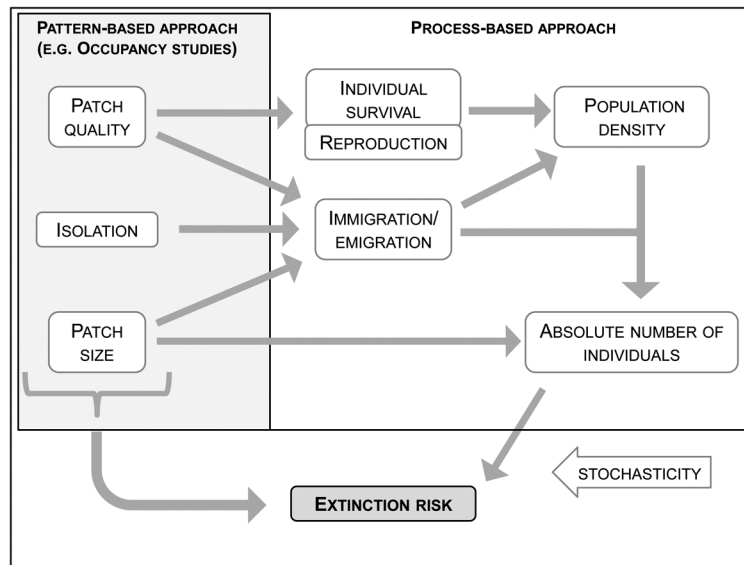


Fig. 1. Conceptual model of factors affecting species extinction risk in fragmented landscapes. We distinguished between a purely pattern-based approach (focused on snapshot presence/absence data) and the process-based mechanistic approach followed in this paper. A process-based approach should allow identifying the proximate causes of species' colonization/extinction in fragmented landscapes and thus illustrate at which ecological scale and by which demographic mechanisms the effects of patch quality and size are exerted. Arrows connect a subset of possible relationships (e.g., immigration/emigration may also have an effect on density).

stochastic forces (Hanski and Gaggiotti 2004, Fischer and Lindenmayer 2007). Although the processes of local extinction and colonization are a central theme in fragmentation ecology (Hanski and Gaggiotti 2004), the proximate factors which influence them are rarely quantified and therefore remain largely unknown.

Most knowledge on population dynamics in fragmented landscapes is centered on *pattern*-based rather than *process*-based studies (Lambin et al. 2004). That is, inferring processes driving local extinction from patterns of occurrence, such as snapshot presence/absence data, or focusing on population turnover (following a meta-population approach sensu Hanski and Gaggiotti 2004). Therefore, the majority of studies have focused on occupancy dynamics rather than on the demographic processes underlying spatial patterns of patch occupancy (Frey et al. 2012, Robles and Ciudad 2012). Hence, they have examined the ultimate effects rather than the proximate causes of population turnover (Fig. 1).

There is substantial literature showing that patch size, isolation and quality can play crucial roles in determining patch occupancy in frag-

mented landscapes (Fahrig 2003, Hanski and Gaggiotti 2004, Lindenmayer and Fischer 2006, Mortelliti et al. 2010a, Thornton et al. 2010). More mechanistic knowledge also has been gathered on the effects of patch variables on specific demographic parameters such as density and population size (e.g., Rabasa et al. 2008, Vögeli et al. 2010, Örvösy et al. 2012), immigration (Hanski and Gaggiotti 2004, Matter et al. 2009) and breeding success (Hinsley et al. 1999, Soga and Koike 2013). Some studies have targeted multiple demographic processes but at small scales such as within a single patch or single landscape (Zanette et al. 2000, Zanette 2000), whereas others working at larger scales have not explored the relationships between demography and colonization or extinction (Holland and Bennett 2010, Richmond et al. 2012). Occupancy (i.e., presence/absence) studies have been predominant in fragmentation research as it is very hard to conduct demographic studies over large areas.

Despite insights into the roles of local and landscape features on population dynamics in fragmented landscapes, we still have a limited

understanding of *how* patch variables influence populations inhabiting fragmented landscapes. Notably, we still do not know whether effects are exerted at an individual (e.g., survival) and/or population level (e.g., density) and how individual scale effects influence the response at the population level (Dooley and Bowers 1998).

We contribute to addressing this critical gap in ecological knowledge using a detailed large-scale field-intensive study encompassing 30 sites nested within three landscapes and monitored monthly for three years. We focused on the relative effects of landscape structure (habitat amount and configuration) and patch quality (here measured as resource abundance) on individuals (survival and litter size) and populations (an index of population density and colonization/extinction dynamics). Our target species was an arboreal rodent, the hazel dormouse (*Muscardinus avellanarius*).

Based on the conceptual model in Fig. 1 (which highlights the key differences between an occupancy-only study and a study including demographic and occupancy analyses), we posed four inter-linked questions on the effects of patch variables on individuals and populations. We stress that the key novelty of our approach is answering all the following questions in the same study (i.e., an holistic approach, *sensu* Lidicker 1988). The questions should not be treated independently but help guide understanding about how processes at the individual level influence patterns of occurrence at the population level (Sutherland and Freckleton 2013).

Question 1: What are the relative effects of patch size, isolation and quality in determining the risk of local extinction?—Previous studies have shown that patch size, isolation and quality all may influence spatial patterns of occupancy and their effects can be highly context-specific (Pellet et al. 2007, Mortelliti 2013). Our first question was aimed at understanding which factors prevail in our study area.

Question 2: Which factors affect the probability of local colonization?—Previous studies have shown that the colonization of a habitat patch may depend on two key events: (1) the chances that individuals reach the patch, mainly depending on its isolation and connectivity (e.g., number of corridors; Hanski and Gaggiotti 2004, Fischer and Lindenmayer 2007), and (2) the chances that

a population would establish in a patch which may depend on habitat quality (Mortelliti et al. 2010a). To answer question 2, we examined the relative role of patch size, isolation and quality in determining the probability of colonization of a habitat patch.

Question 3: How does population density respond to patch size, isolation and quality?—Previous studies in fragmented landscapes have found higher animal population densities in larger patches and in patches with higher habitat quality (Holland and Bennett 2010, Örvösy et al. 2012) whereas Matter et al. (2009) found lower density in more isolated patches. To answer question 3, we examined the effects of patch variables on an index of population density of hazel dormice.

Question 4: How do individuals respond to patch size, isolation and quality?—We identified a suite of target parameters to be measured on individuals to make inference on the possible individual-level causes of the population-level effects (questions 1–3). Previous studies have shown that patch quality may positively affect fecundity (Van Horne 1983) and apparent survival (Lin and Batzli 2001). Other studies have found a positive effect of patch size on breeding success (Hinsley et al. 1999) and survival (Bayne and Hobson 2002, Holland and Bennett 2010). To answer question 4, we evaluated the effects of patch variables on litter size and apparent survival, which was estimated through the application of capture-mark-recapture modeling.

MATERIALS AND METHODS

Study species

We selected the hazel dormouse as our target species for four reasons: (1) it is well documented as being sensitive to habitat loss and to the disruption of connectivity (Bright et al. 1994, Mortelliti et al. 2008, 2010b, Keckel et al. 2012), (2) it is a forest specialist that has similar responses to landscape change as several other vertebrate species (Bright and Morris 1996, Mortelliti et al. 2010b, Mortelliti 2013), (3) its food resources (fruit and flowers of shrub species) are well known (Juškaitis 2008) and relatively easy to estimate, and (4) by using nest-boxes, it is possible to directly estimate litter size of females (Juškaitis 2008). These four key characteristics make the

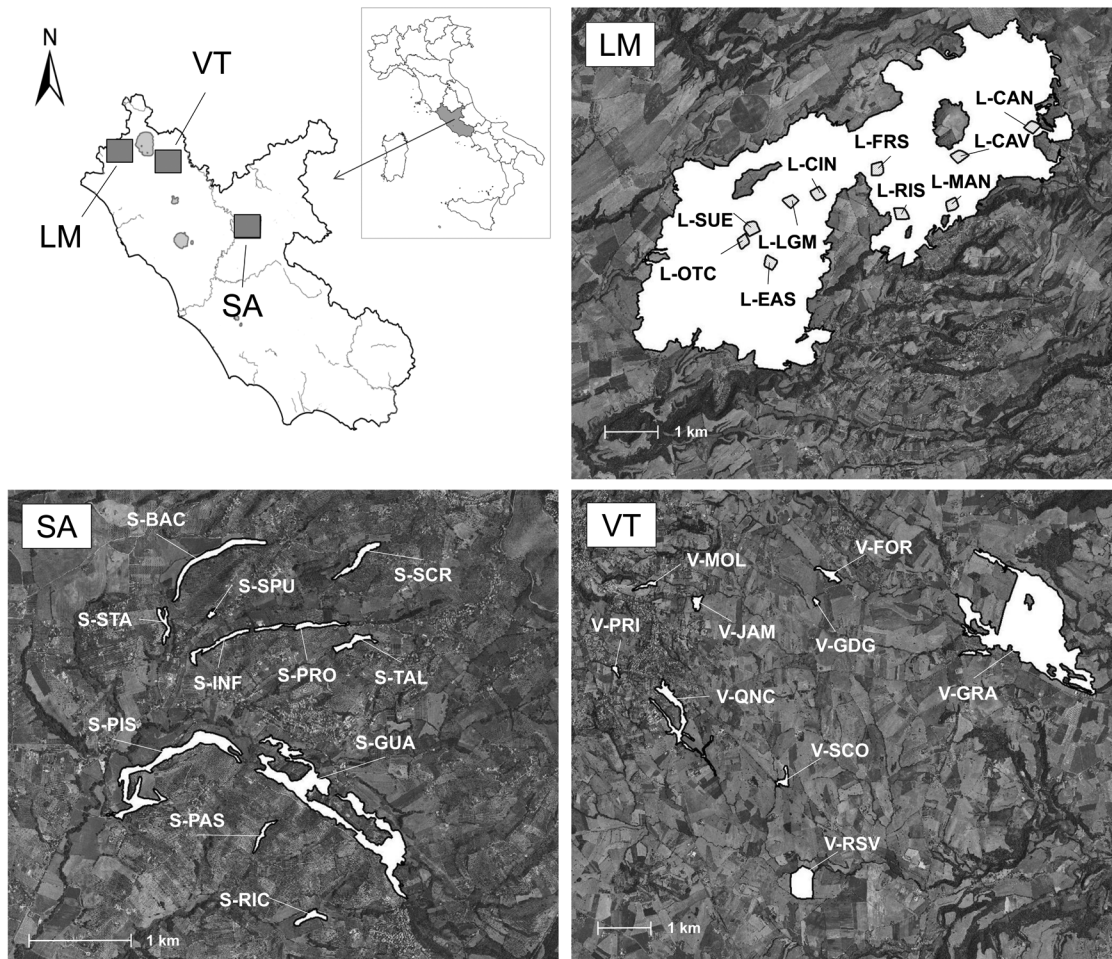


Fig. 2. Aerial photos of the three studied landscapes: VT = Viterbo (fragmented landscape), SA = Sabina (fragmented landscape), LM = Lamone (control landscape with continuous vegetation cover). The studied woodland patches are filled in white and labeled (information on each patch is provided in Appendix: Table A1).

hazel dormouse an ideal model species for evaluating the effects of patch variables on individuals and populations (Bright and Morris 1996). This species may occasionally disperse through the agricultural matrix, up to 500 m (Juškaitis 2008).

Study area

This study was conducted in the northern part of the Latium region, Central Italy (Fig. 2; mean annual precipitation: 955 mm). Three landscapes were studied and all were within 200 km from Rome and have been fragmented periodically over the past 2000 years. The ‘matrix’ between sampling woodland patches sites is relatively simple and is mainly composed of fields culti-

vated with cereals (wheat) and olive trees. The only remnant vegetation occurring are patches of oak woodland which are usually coppiced every 14–30 years. Coppicing may affect the diversity and richness of understory shrub species and thus the quality of habitat patches (more details on habitat quality for dormice are provided below). The terrain in the three landscapes is mainly flat (Lamone and Viterbo) or moderately undulated (Sabina), therefore no major topographical feature occurred between sites.

Study design

The study was conducted in three landscapes where the hazel dormouse was previously found (Mortelliti et al. 2011). These landscapes are

characterized by the same climax vegetation (mixed oak woodland with a dominance of *Quercus cerris* and *Quercus pubescens*). Two of these were relatively fragmented, the Sabina and Viterbo landscapes (18% and 13% residual forest cover, respectively), and one—the Lamone landscape—supported relatively continuous vegetation cover (>40% of residual forest cover).

The two fragmented landscapes were characterized by similar landscape structure in terms of habitat amount, size and isolation of patches (Fig. A1). We considered as “habitat” areas characterized by forest (deciduous oak woodland) or shrub vegetation according to the Corine Land Cover 2006. Patch size was measured as the size of the habitat patch (as measured from aerial photographs of the study area through Arcgis 10.1) whereas patch isolation was measured as the habitat cover in a 500 m (maximum recorded dispersal distance of hazel dormice in treeless areas; Juškaitis 2008) buffer around the patch (ha).

Eleven patches were sampled in the Sabina landscape and nine patches in the Viterbo landscape. Patches were selected to obtain, for each landscape and subject to availability, replicates for each of the following patch size classes: 0.4–2 ha, 2–5 ha, 5–10 ha, 10–25 ha and >100 ha (Table A1). Within each patch size class, patches to be sampled were randomly selected. The third area, which we consider to be our control area, is the regional park “Selva del Lamone,” a protected area with continuous (non-fragmented) forest subjected to several management regimes and thus different habitat quality (see below). Ten sites were sampled in this area to represent the variability in habitat quality. A summary of the characteristics of the 30 sampling sites is provided in Appendix: Table A1.

Dormice demographic parameters

To quantify the demography of the hazel dormouse, capture-mark-recapture (hereafter CMR) data were gathered, using grids of nest-boxes as sampling units. The standard grid was 4 ha (6 × 6 grids with nest-boxes 40 m apart) in all sites, with the exception of patches too small or too irregular in shape to accommodate a standard grid (Fig. 2; Appendix: Table A1). In those cases, the whole patch was sampled, but maintaining the same density of nest-boxes as in

standard grids so as to use a constant sampling effort/area in all sites. The distance between nest-boxes was the same as for other studies on this species (Juškaitis 2008). We selected 40 m because several nest-boxes may then be included in an individual’s home-range (Juskaitis 1997, Juškaitis 2006), increasing the chance of individual recapture. Further, higher density grids are not recommended for population ecology studies because more nest-boxes may influence population parameters (e.g., by increasing survival (Juškaitis 2006b). Wooden nest-boxes (average size 18 × 18 × 21 cm) had a standard entrance hole (3 cm in diameter) and were positioned on trees at a height of 1.5–2 m (Morris et al. 1990, Juškaitis 2008).

Nest-boxes were inspected monthly for three years (32 months) from May 2010 to December 2012; the period January–March was excluded due to hibernation of the hazel dormouse. To increase individual recaptures to provide additional data for supporting CMR model parameterization (details below), in the period May 2011–December 2012 (second and third year of the study) sampling effort was intensified by adding, on alternate months, two more visits to each grid (4 and 8 days after the first visit; e.g., in May 2011 a triple visit was carried out, in June 2011 a single visit, in July a triple visit, etc.). Based on our experience (including radio-tracking data), recapture of the same individual in the same nest-box is relatively uncommon because individuals have several nests (4–5) within their home-range (Juškaitis 2008) and tend to move to other nest-boxes following marking. In addition, previous knowledge gathered in the study area (Capizzi et al. 2002) and preliminary radio-tracking data suggest that nest-boxes are not a limiting factor as individuals still build their nest in understory vegetation even when nest-boxes are available; furthermore, individuals may share nest-boxes through most of the year (Juškaitis 2008).

The entrance of occupied nest-boxes was blocked and the content transferred to a plastic bag for further manipulation. Captured dormice were weighed, sexed, assigned to an age-class (adult/juvenile, based on body mass and fur characteristics, (Juškaitis 2008) and individually marked by means of PIT tags (Biomark 8 × 2 mm 134.2 KHz ISO; 2010) or ear tags (Michel suture clips 11 × 2 mm; 2011–2012). Dormice were

Table 1. Patch size, isolation and quality variables used as explanatory variables in models. Habitat quality variables were measured in quadrat plots (10 m²); number of plots increased with patch size but density of plots was kept constant. Cover of species was estimated according to the following classes (percentage of the plot covered by the ground projection of the target species, e.g., *Rubia peregrina*): 0, 1–25, 25–50, 50–75, 75–100. Selected shrub species are followed by a dagger (†); inclusion of species in the “selected shrubs” index was based on Amori et al. (2008) and Juškaitis (2008).

Factor	Variable	Description
Patch size	logHA	patch size (ha, logarithmic transformation)
Isolation	hab_buff	habitat cover in a 500 m (maximum recorded dispersal distance of hazel dormice in treeless areas; Juškaitis 2008) buffer around the patch (ha).
Patch quality	shrub_tot	Sum of the cover of the following shrub species (%) in the plots: <i>Crataegus</i> spp.,† <i>Corylus avellana</i> ,† <i>Cornus mas</i> ,† <i>Euonymus europeus</i> ,† <i>Ligustrum vulgare</i> ,† <i>Prunus spinosa</i> ,† <i>Rosa canina</i> ,† <i>Rubus</i> spp.,† <i>Ruscus aculeatus</i> ,† <i>Paliurus spina-christi</i> , <i>Ginestra</i> , <i>Sambucus nigra</i> , <i>Lonicera</i> spp., <i>Pistacia lentiscus</i> , <i>Phillyrea</i> spp., <i>Ilex aquifolium</i> , <i>Rubia peregrina</i> , <i>Smilax aspera</i> , <i>Viburnum</i> spp., <i>Clematis vitalba</i> , <i>Coronilla emerus</i> , <i>Bryonia dioica</i> , <i>Mespilus germanica</i> , <i>Asparagus acutifolius</i> , <i>Hedera helix</i> , <i>Prunus avium</i> , <i>Laurus nobilis</i>
	shrub_sel	Sum of the cover of the shrub species (with dagger) listed above
	rich	Number of shrub species detected in the patch
	Simps	Simpson's diversity index calculated on the shrub species in the patch
	vol_shrub	vertical cover of shrubs obtained by summing the percentage cover of shrubs at 0.5–1.2–4.8 m height

released in the nest-box where they were captured. Breeding females were not marked to minimize disturbance, therefore they did not contribute to survival estimates, but they were included in the total abundance of individuals. Pups were quickly counted, and released immediately with the mother in the nest-box to minimize stress.

Vegetation and food resource assessment

We assessed microhabitat structure and resource abundance in each sampled grid using 100 m² (10 × 10 m) quadrats. The number of quadrats increased with patch size and vegetation heterogeneity (Appendix: Table A1); location of quadrats was randomly selected. Both structural variables (e.g., percent canopy cover) and resource variables (e.g., cover of fruiting shrubs such as the hazel nut, *Corylus avellana*) were measured. Cover was estimated according to the following classes (percentage of the plot covered by the ground projection of the target shrub): 0, 1–25, 25–50, 50–75 and 75–100. Cumulative indices (e.g., shrub_tot in Table 1) were obtained by summing the cover of each species. We consider shrub cover as a reasonable proxy for shrub fruit biomass and therefore for resource abundance. Results of a pilot survey, during which fruit abundance was found to be correlated with shrub cover (P. Bartolommei, unpublished data: Spearman's rho =

0.606, $p < 0.001$) support the use of this proxy. An abundance index for preferred shrub species (shrub_sel) was also calculated because the hazel dormouse has known shrub preferences (e.g., *Corylus avellana*; Juškaitis 2007, 2008, Sarà and Sarà 2007, Amori et al. 2008) detailed in Table 1. Quadrats were surveyed in spring 2011 and 2012; data from both surveys were averaged. Following preliminary explorative analysis (univariate regressions and correlations), to reduce the number of predictors, we selected a subset of vegetation variables as habitat quality variables that we list in Table 1 (see Appendix: Table A2 for details on excluded variables).

We acknowledge that our study is focused on resources and did not take into account predation and competitor species which may affect species persistence in fragmented landscapes (Nupp and Swihart 2001, Ryall and Fahrig 2006). Hazel dormice are predated, mainly by nocturnal birds of prey. Nevertheless, the impact of predators on dormice populations has never been quantified and is therefore virtually unknown. We acknowledge that future studies should attempt to estimate the influence of predators on patch quality. Possible competitors (e.g., the edible dormouse *Glis glis*) are absent from the study area and we are therefore confident that effects of competitors were likely to have been limited.

Weather data

We gathered weather data to use as predictor variables in data analysis (details below). Daily weather data for the whole sampling period was obtained from the nearest (<5 km) available weather station (Sabina landscape, weather station number RI07SIE and RI10CME; Viterbo landscape: weather station number VT07SIE and VT20CME; Lamone landscape: weather station number VT22CME and VT25SIE).

Data analysis

Analyses were focused on quantifying the relationship between patch size, isolation and quality (see Table 1 for a list of tested variables) on the following response variables (the statistical approach adopted and the corresponding research question posed in the Introduction (Q) are detailed in the parentheses): (1) population turnover: colonization and extinction (Q1–2, multiple season occupancy modelling); (2) index of population density (Q3, generalized linear mixed models [GLMM] on the time-series of abundance data); (3) individual apparent survival (Q4, Cormack-Jolly-Seber Models); (4) litter size (Q4, generalized linear models on litter size);

Analyses were conducted on adults unless otherwise specified. To reduce collinearity, only sets of non-correlated variables (Spearman correlation coefficient between predictor variables <0.3) were included in each model (Appendix: Table A3).

For all analyses, except for GLMMs, the information theoretic approach was followed, ranking models according to the Akaike's information criterion corrected for small sample size (AIC_C) or, when required, the quasi-Akaike information criterion ($QAIC_C$). Models within $2\Delta AIC_C$ (or $QAIC_C$) were considered as the best model set, and parameters were averaged to obtain 'model averaged' estimates (Burnham and Anderson 2002). For GLMM we used Wald's tests for variable selection (Bolker et al. 2009) since AIC are less reliable for these models (Müller et al. 2013). Following Zuur et al. (2009), we started with the most parameterized model (including size, isolation and habitat quality terms) and sequentially removed non-significant terms.

Population turnover (occupancy models).—We conducted our analysis with occupancy models to determine which patch and habitat quality

factors influenced dormouse local extinction and colonization probability.

False absences (a species was present but was not detected) are a major source of bias in distribution studies (MacKenzie et al. 2003). We used multiple-season occupancy models (MacKenzie et al. 2003) fitted through the software PRESENCE (<http://www.mbr-pwrc.usgs.gov/software/presence.html>) to account for imperfect detection (p) and to estimate colonization (γ) and extinction (ϵ) probability.

Within the occupancy modeling framework sites are surveyed on multiple occasions and the outcome of each visit to a site is recorded as a detection/non detection. The resulting time-series of presence-absence data is called a *detection history*. The use of a detection history rather than a single presence/absence variable for each site (as applied by logistic regression) allows to estimate the probability of detecting the species and thus to take into account the risk of false absences in the data. Furthermore, we stress that colonization and extinctions are *probabilities* (i.e., colonization: the probability of an empty patch to become occupied; extinction: the probability of an occupied patch to become empty) and are estimated from detection history data after accounting for the uncertainty in detection (MacKenzie et al. 2003). Furthermore, we acknowledge that 'extinctions' also could be caused by emigrations of individuals to other patches.

To conduct a patch-level analysis, we pooled data from all the grids of the Lamone landscape, since they belonged to the same block of habitat (thus each grid should be viewed as a sample of the whole Lamone population). As a consequence, estimates of occupancy, detection, extinction and colonization probability, are to be referred to patches and not single grids.

Each inspection of a nest-box was considered as a 'visit' (sensu MacKenzie et al. 2003), one nest-box-check to all nest-boxes in a patch = one visit to the patch). Populations were assumed to be open (to colonization/extinctions) between months and closed within each monthly session (i.e., 3 visits within 8 days; see above for more details). Each monthly session (i.e., trapping period) was thus considered as a primary trapping period (sensu MacKenzie et al. 2003).

We followed a multi-step approach for building models:

- (1) We first modeled detection probability (p) to make the subsequent estimates of ψ_{i1} (initial probability of occurrence), γ (colonization) and ϵ (extinction) more reliable. Detection probability was modeled as a function of season (summer versus other months of activity) and weather (average, maximum, minimum temperature and mm of rain) during the sampling session to take into account the seasonal activity patterns of this species (Panchetti et al. 2004). We expected a decrease in detectability with increasing temperature, since in Mediterranean environments dormice tend to avoid nest-boxes in warmer weather (Panchetti et al. 2004). We retained the best covariates for p in the models. During this first step other parameters were kept constant.
- (2) We modelled colonization (γ) and extinction (ϵ) probabilities as functions of patch size, isolation and quality variables (Table 1). Main effects and their interactions were tested (interactions were tested when the two target variables ranked higher than the constant model at the early stages of modeling). To take into account the unequal time intervals between primary trapping periods (due to lack of sampling during the hibernation period), we modeled both extinction and colonization probabilities as function of the number of days between sampling events.
- (3) Possible spatial autocorrelation of distribution data was taken into account by incorporating a spatial autocovariate in colonization probability (γ) models, under the hypothesis that the chance of colonizing a focal patch could be influenced by the occupancy of surrounding patches in the previous time-interval. The autocovariate was calculated as a time-dependent covariate. For each time-step, we calculated the autocovariate following (Moore and Swihart 2005) as the weighted mean of the observed detection status (i.e.: 0 or 1) of all the patches in the landscape, weighted by $1/\text{distance}$ to the focal patch.

Occupancy probability in the first session (ψ_{i1}) was left constant to focus on population

turnover, determined by colonization and extinction events.

Index of population density.—The count of individuals captured during the first visit was modeled by fitting GLMM with a Poisson distribution (logarithmic link; Bolker et al. 2009). The inclusion of grid size as an “offset” variable made abundance values equivalent to density values (Zuur et al. 2009). We stress that our dependent variable should be considered an index of population density rather than an estimate (which would have been obtained by CMR models). We followed this approach to keep the CMR analyses (detailed in the following section) the least-parameterized as possible. To increase the reliability of our abundance indices on months with triple visits, we used only count data from the first visit so that in each month the sampling effort (and thus the abundance index) was consistent. Furthermore, we added a weather variable (average temperature in the time interval—30 days—preceding the sampling session) to account for seasonal activity patterns of this species (Panchetti et al. 2004). We fitted grid ($N = 30$) as a random effect to account for autocorrelation in the data (Zuur et al. 2009). To account for over-dispersion, we added an observation-level random effect (Elston et al. 2001). Landscape was treated as a fixed effect because of the small number of levels ($N = 3$) and because preliminary analyses suggested a close-to-zero variance component (Zuur et al. 2009). We also included months since first survey to take into account temporal trends in the population. Key predictor variables included in the model selection were patch size, isolation and habitat quality; following preliminary exploratory analyses we focused only on abundance of selected shrubs to keep number of predictors low (Table 1). Models were fitted using package ‘lme4’ ‘in R version 3.0.0 (R Development Core Team 2013).

Survival.—Survival probability of individuals was modeled using Cormack-Jolly-Seber approach for open populations; models were fitted through software MARK (<http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>). We stress that within the capture mark recapture framework ‘survival’ is defined as the probability that the animal is alive and remains on the study area and hence is available for recapture in the following sampling session.

Table 2. Parameter (β) estimates from the best occupancy model according to AIC_C (see Appendix: Table A4 for a list of tested models). Estimate and standard errors (SE) are reported for constant and covariate parameters (see Table 1 for details on the covariates).

Parameter	β and SE
psi - constant	-0.23 ± 0.55
gamma - constant	-2.64 ± 0.36
gamma - shrub_sel	1.15 ± 0.29
gamma - days	0.66 ± 0.22
eps - constant	-1.12 ± 0.33
eps - logHA	-1.17 ± 0.44
P - constant	0.69 ± 0.19
P - T_ave	-1.06 ± 0.23

Note: Abbreviations are: Psi = presence probability, gamma = colonization probability, eps = extinction probability, P = detection probability, shrub_sel = abundance index of selected shrubs (see Appendix: Table A2 for a checklist), logHA = logarithm of patch size in ha, T_ave = mean temperature during sampling.

The entire capture history was used (including single and triple visits), specifying the length of the time interval between samplings (i.e., 4 days or 30 days respectively for intra- and inter-session intervals). In this way, survival estimates were referred to the same time-scale (day) even with uneven time intervals (Amstrup et al. 2006). Furthermore, we used the Cormack-Jolly-Seber model instead of more complex and parameterized models (e.g., robust design models) as our CMR data required to keep parameterization as simple as possible. We first modeled recapture probability (p) as a function of season (i.e., summer versus other months of activity) and weather covariates (average, maximum, minimum temperature and mm of rain during sampling) to take into account seasonality in captures. We then modeled survival probability (ϕ) as a function of patch size, isolation and quality variables (Table 1). We also tested if survival varied with individual body mass (average value, since body mass is not known when an individual is not captured) with sex and between landscapes. We first included landscapes as a factor with three different levels (LM, VT and SA). Secondly, to test reciprocal differences between pairs of landscapes, we pooled them in pairs and tested models with only two levels (e.g., VT + SA versus LM). We used the value of $QAIC_C$ to rank models since the \hat{c} estimate was higher than 1 ($\hat{c} = 3$).

Litter size.—Litter size (count of the number of pups per female, a proxy for reproductive output) was modeled using generalized linear models (GLM) with a Poisson distribution. We opted for using GLM's rather than GLMM's because of the lack of temporal autocorrelation issues (litter size was never obtained from the same individual) and because multiple captures from the same patch were taken into account by the fixed factors. In addition to patch size, isolation and quality predictor variables (Table 1), a categorical variable was included to account for the effect of “age” of the litter (with presumed lower litter size with increasing age due to natural mortality: age 1 = body mass < 5 g, closed eyes; age 2 = mass 5–8 g, open eyes, low mobility; age 3 = mass > 8 g, mobile).

RESULTS

During the three years of the study we completed a total of 626 captures of hazel dormice (160 captures in 2010, 355 captures in 2011, and 111 captures in 2012). Five of the 30 sites were never occupied (all in the Sabina landscape), while apparent turnover was relatively high, particularly in the Viterbo (fragmented) landscape (Appendix: Fig. A2). Peaks in capture success occurred during spring and late autumn. The majority of dormice were captured in the Lamone landscape (control landscape with continuous vegetation cover: 64% of captures), followed by Viterbo (fragmented landscape: 34% of captures) and Sabina (fragmented landscape: 2% of captures). Mean body mass was 16.4 g (SD = 3.6). Average litter size was 4.16 (SD = 1.74; range 1–8, $N = 62$).

Occupancy models

Only one model was included in the best model set (see Appendix: Table A4 for a list of top ranking models). According to the first ranked model (Table 2), the best predictor for detection probability was the mean temperature during sampling (T_ave): as expected, in warmer months the species was more difficult to detect (Table 2).

After controlling for imperfect detection, the best predictor of extinction probability was patch size (logHA), with populations in larger patches being more persistent (lower extinction risk;

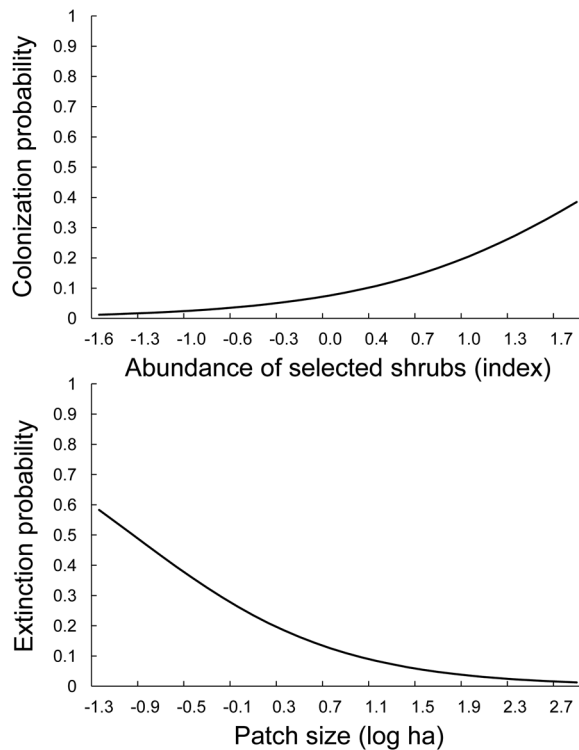


Fig. 3. Colonization probability increasing with the abundance of selected shrubs and extinction probability decreasing with patch size (log ha) as predicted by the best occupancy model. Abundance of selected shrubs and patch size were varied according to the range of values observed in the field.

Table 2, Fig. 3). Models including patch quality or its interaction with patch size were not included in the top model set (Appendix: Table A4).

The best predictor for colonization probability was patch quality (shrub_sel), with higher quality patches (those with a higher abundance of selected shrubs) being more likely to be colonized (Table 2, Fig. 3).

Patch isolation did not influence either extinction or colonization. Expected values of extinction and colonization probability of sampled patches are reported in Appendix: Fig. A3.

Index of population density

The number of captured dormice was influenced by patch quality and the average temperature, with the number of dormice caught in nest-boxes being higher with lower average temperature (i.e., in spring and autumn com-

pared to summer) and in sites with higher resource abundance (Table 3). We found that the index of dormice density was significantly lower in the fragmented Sabina and Viterbo landscapes when compared to Lamone (Table 3). Finally, we detected a negative temporal trend, with the index of population density across all landscapes significantly decreasing throughout our study period (months since beginning of the study; Table 3).

Survival

After controlling for seasonal differences in recapture probability, the best predictors of survival probability were individual body mass and Simpson's Index of shrub diversity, both contributing positively to survival (Table 4, Fig. 4; Appendix: Table A5). In addition, survival probability was different in the three landscapes, being higher in the Lamone landscape (control landscape with continuous vegetation cover) and lower in the Viterbo landscape; the Sabina landscape had intermediate survival values (Table 4; Appendix: Table A5). We found little support ($\Delta\text{QAIC}_C > 10$) for the model including sex-specific survival.

Litter size

We found no reproducing females in the Sabina landscape and therefore only data from Viterbo and Lamone were used for the GLM analysis ($N = 62$; data is shown in Appendix: Table A6). The only predictor variable affecting litter size was landscape, with females bearing significantly larger litters in the Lamone landscape (Wald test: $\chi = -2.1$; intercept $\beta = 1.51$ (0.07); landscape $\beta = -0.3$ (0.14), $p = 0.03$).

DISCUSSION

We found that the isolation of habitat patches (here measured as habitat in the buffer; Table 1) did not influence any of the investigated parameters (Appendix: Table A7). Patch quality was the main factor affecting individual survival and the index of population density, while occupancy dynamics were affected by both the size and the quality of habitat patches (Appendix: Table A7). Habitat quality matters; however its effects are clearly constrained by the geometrical properties of the surrounding patch since the risk of

Table 3. Model parameters predicting dormouse abundance showing the parameter (β) and standard error (SE) for each variable in the final model (N = 720 sampling occasions; 24 sessions on 30 grids). Fitted model: GLMM with a Poisson distribution with logarithmic link; variable significance was tested with a Wald test. The variable Lands is a categorical variable, with Lamone as reference category.

Term	β	SE	Wald's test	<i>p</i>	Variance	SD
Fixed effects						
Intercept	-1.22	0.34	-3.59	<0.001		
shrub_sel	0.60	0.14	4.30	<0.001		
T_ave	-0.08	0.02	-5.29	<0.001		
Lands (SA)	-2.47	0.62	-3.96	<0.001		
Lands (VT)	-1.81	0.65	-2.78	<0.01		
Month	-0.03	0.01	-3.02	<0.01		
Random effects						
Observation					1.11	1.05
Grid					0.43	0.66

Note: Abbreviations are: shrub_sel = abundance index of selected shrubs (see Appendix: Table A2 for a checklist), logHA = logarithm of patch size in ha; T_ave = mean temperature during sampling. SA = Sabina landscape, VT = Viterbo landscape.

extinction increases in smaller patches.

Our results provide one of the few examples investigating the demographic mechanisms by which habitat quality and the amount of habitat affect population turnover in fragmented landscapes. Furthermore we provide insights on the ecological scale at which their effects are most relevant, which has been an important debate in the last few years (Moilanen and Hanski 1998, Armstrong 2005, Mortelliti et al. 2010a). Unlike occupancy studies, detailed large scale demographic studies such as ours are not common in the literature. This is because of the intensity of sampling required (e.g., monthly surveys repeated over years) and the difficulty of estimating individual parameters (particularly with mammals, e.g., litter size).

The role of habitat quality

Patch quality (here measured as the diversity and abundance of shrub species) proved to be important for hazel dormice at the population and individual ecological scales (see also Bright and Morris 1996, Juškaitis 2008). At the population scale, resource abundance influenced colonization (which answers question 2 in *Introduction*). A population was less likely to establish in a patch if habitat quality was low. These results are consistent with similar pattern-based research on animal populations in fragmented landscapes (Franken and Hik 2004, Robles and Ciudad 2012). Our findings are also consistent with our individual-scale results on survival, suggesting that higher survival with increasing habitat quality mediates the establishment of a population. Hazel dormice may occasionally disperse up to 500 m in an agricul-

Table 4. Final set of Cormack-Jolly-Seber models ranked according to QAIC_C (only models with four Δ QAIC_C are shown). Covariates are represented in brackets (see Table 1 for details on the covariates).

Model	QAIC _C	Δ QAIC _C	QAIC _C wgt	N
phi(landscapeLM + body mass + simps), p(season)	278.19	0.00	0.13	6
phi(landscapeVT + body mass + simps), p(season)	278.68	0.50	0.10	6
phi(body mass + simps), p(season)	279.12	0.93	0.08	5
phi(body mass), p(season)	279.76	1.57	0.06	4
phi(landscapeLM + body mass + simps + logHA), p(season)	280.23	2.04	0.05	7
phi(landscape + body mass + simps), p(season)	280.24	2.05	0.05	7
phi(landscapeLM \times simps + body mass), p(season)	280.24	2.05	0.05	7
phi(body mass + simps \times logHA), p(season)	280.62	2.43	0.04	7
phi(landscapeSA + body mass + simps), p(season)	280.96	2.78	0.03	6
phi(T_ave + body mass), p(season)	281.49	3.31	0.02	5

Note: Abbreviations are: phi = survival probability, p = recapture probability, QAIC_C = quasi-likelihood adjustment of the Akaike's information criterion, QAIC_C wgt = Akaike's weight, N = number of estimated parameters, logHA = logarithm of patch size in ha, T_ave = mean temperature during sampling, simps = Simpson index, LM = Lamone landscape.

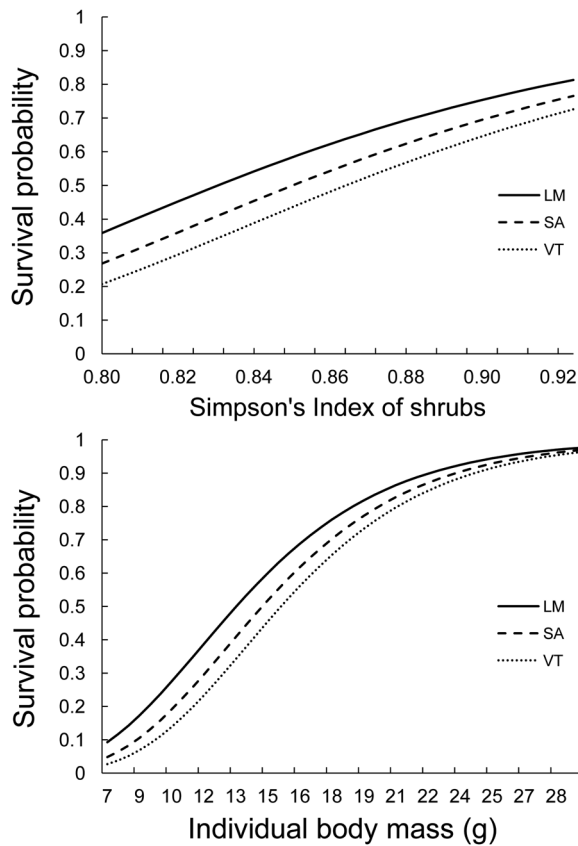


Fig. 4. Top: Monthly survival probability as function of the Simpson's diversity index of shrub species as predicted by the final Cormack-Jolly-Seber model. Each line represents a landscape (LM, SA, VT); Simpson's index was varied according to the range of values observed in the field; the other covariate (individual body mass) was kept constant at its average value. Bottom: Monthly survival probability as function of individual body mass as predicted by the final Cormack-Jolly-Seber model. Each line represents a landscape (LM, SA, VT); body mass was varied according to the range of values observed in the field; the other covariate (Simpson's index) was kept constant at its average value.

tural matrix (Büchner 2008, Mortelliti et al. 2013) and this may explain why our target populations showed no effect of isolation on colonization/extinction. These findings strongly suggest that the assumption that colonization can be predicted only by isolation is overly simplistic. In some cases, dispersal is not limiting and the chances of a population establishing in a patch may depend

predominantly on patch quality.

Besides influencing colonization, habitat quality also influenced patch-level demographics: high resource abundance led to a higher density of individuals (answer to question 3 in *Introduction*), which is in accordance with the basic biology of this species (Juškaitis 2008). As previously highlighted, habitat quality directly influenced individual parameters (which answers question 4 in *Introduction*). High diversity of shrubs could lead to high survival due to a more continuous food supply through the changing seasons (Bright and Morris 1996).

The relationship between body mass and survival in the hazel dormouse (larger body mass led to higher survival) was expected: fat is a crucial resource for this hibernating species (Juškaitis 2008). We stress that we have focused on the most relevant food resources for this species, which are flowers and fruits (Bright and Morris 1996, Juškaitis 2008). We acknowledge, however, that this species also may occasionally consume small invertebrates and bird eggs. We suggest that future studies focusing on habitat quality include an assessment of the availability of other food resources. Furthermore we suggest that future research should try to evaluate the effect of patch quality on the survival of different age-classes, which was not possible in this study.

Comparison among the studied landscapes

Survival was higher in the Lamone landscape, which may suggest that individuals survive more in non-fragmented landscapes. However, we stress that the "survival" considered here is "apparent survival" (Amstrup et al. 2006), which includes individual actual survival and emigration. Therefore, the lower survival in the two fragmented landscapes also may suggest higher level of emigration occurring in the patches nested in these two landscapes (Schtickzelle and Baguette 2003).

Larger litters were recorded in the non-fragmented area (Lamone) compared to the fragmented landscape (Viterbo). We suggest caution in interpreting the landscape-level results on litter size and survival, due to the small number of landscape-level replicates (Fahrig 2003). Further research is needed to establish a clearer relationship between habitat loss and/or fragmentation and litter size and/or survival.

The extinction process

Local extinction was due mainly to patch size (question 1 in *Introduction*; Table 2; Appendix: Table A5). The importance of patch size on dormouse occupancy has been highlighted by previous studies (Bright et al. 1994, Mortelliti et al. 2008, Keckel et al. 2012). Even if improved habitat quality led to higher individual survival and population density (as well as colonization chances, as above highlighted), these alone were not sufficient to ensure population persistence, which was ultimately related to the size of the habitat patch. We found no evidence that habitat quality (at least in the way we measured and tested it here) could offset the effects of small patch size to reduce extinction risk. The vulnerability of small populations to extinction is one of the key paradigms in conservation biology (Lande 1993, Hanski and Gaggiotti 2004). The amount of habitat at the patch level did not affect density, litter size or survival. These population properties and individual attributes were affected primarily by the availability and abundance of food resources, which were not correlated with patch or landscape variables (see also Knight and Fox 2000). The role of patch size was probably linked to absolute population size, which, in the landscapes we investigated, was low in small patches (tens of individuals, as inferred from our capture data; Appendix: Fig. A2), showing that even a high-performance (i.e., high vital rates) but still small population could be at risk of extinction.

Given that patch size was the best predictor of extinction risk, what was the likely underlying mechanism linking the size of a patch to local extinction? Populations persist only for a relatively short time (e.g., few months up to 1–2 years, therefore covering few breeding events) and therefore it is unlikely that inbreeding depression was the cause of local extinction. In addition, no major climatic or disturbance events occurred during the study. A combination of demographic and environmental stochasticity in small populations may have driven local extinctions (Hanski 1998, Hanski and Gaggiotti 2004) or the small population size may have triggered Allee effects (Stephens et al. 1999). Our results thus suggest that although high availability of resources may ultimately determine high individual survival and density, limitation in space

imposes a low absolute number of individuals. Therefore, a high density population with high individual survival can still face a high extinction risk if the overall population remains small because patch size is small.

We acknowledge that further studies with a longer time-frame (e.g., >5 years) thus encompassing a broader magnitude of fluctuations in the target populations will surely contribute with additional insights and more definitive conclusions on mechanisms affecting extinction risk in fragmented landscapes.

Persistence of populations in fragmented landscapes— the importance of multi-scale approach

The holistic approach that we have followed allowed us to show how the amount of habitat and habitat quality both play a role in the persistence of species in fragmented landscapes, influencing the performance of single populations and of the whole landscape system (extinction-colonization dynamics). These parameters exert their effects at different ecological scales with patch quality affecting both individuals and populations, whereas patch size mainly exerted its effects at the population level (on the probability of local extinction, as highlighted in Appendix: Table A7). Our findings suggest that individual-level effects of survival may translate into population-level effects (density and recolonization). Nevertheless, individual and population-level effects of patch quality appear to be overridden by the population-level effects of patch size. Furthermore, our results suggest that out of the two individual-level variables that we examined (survival and litter size), individual survival may be the key parameter linked to species persistence in fragmented landscapes since we found no effect on litter size (Appendix: Table A7).

As we have mentioned in the methods section the hazel dormouse is a forest specialist that has similar responses to landscape change as several other vertebrate species (Bright and Morris 1996, Mortelliti et al. 2010b, Mortelliti 2013) it is therefore likely that our conclusions may be applicable to a range of other species. The results of this study suggest that in the case of the hazel dormouse there is a need to manage the quality of habitat to ensure that colonization rates

counter local rates of extinction, thereby increasing the viability of the system. As we have shown, investing resources in increasing the quality of habitat may lead to increased performance of individuals and thus promote recolonization. Nevertheless, our findings also show that the effect of patch quality on individual and population parameters may be constrained by the physical structure of the surrounding landscapes, thus restoration to increase the amount of habitat, particularly increasing patch sizes, might be critical in landscapes that have been extensively cleared.

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SUPPLEMENTAL MATERIAL

APPENDIX A

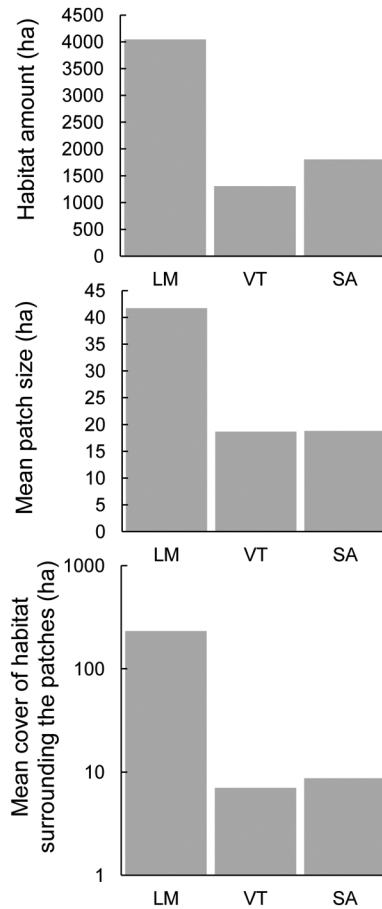


Fig. A1. Comparison of the structure of the three target landscapes. Each barplot shows a landscape variable (amount of habitat, mean size of patches, mean cover of habitat surrounding the patches) measured in a $10 \times 10 \text{ km}^2$ landscape centered on each study area. LM = Lamone landscape, VT = Viterbo landscape, SA = Sabina landscape.

Table A1. List of 30 sampling sites with their main characteristics.

Site code	Landscape	N plots	HA	Hab buffer	Shrub_tot	Shrub_sel	Rich	Simps	Vol_shrub
L-CAN	LM	15	2705.02	232.08	6.40	7.03	15	0.90	7.83
L-CAV	LM	12	2705.02	232.08	3.29	2.54	13	0.83	5.25
L-CIN	LM	25	2705.02	232.08	3.96	3.44	15	0.84	7.76
L-EAS	LM	13	2705.02	232.08	3.88	1.54	18	0.90	5.35
L-FRS	LM	13	2705.02	232.08	4.42	3.15	12	0.87	2.35
L-LGM	LM	8	2705.02	232.08	3.00	1.75	12	0.88	5.88
L-MAN	LM	25	2705.02	232.08	5.02	3.76	16	0.90	8.66
L-OTC	LM	8	2705.02	232.08	3.50	2.25	11	0.87	11.5
L-RIS	LM	15	2705.02	232.08	3.30	2.03	13	0.84	7.12
L-SUE	LM	13	2705.02	232.08	3.38	2.77	13	0.80	4.81
S-BAC	SA	18	6.85	1.49	5.69	3.47	20	0.90	9.28
S-GUA	SA	14	178.98	28.81	6.29	4.79	19	0.92	8.82
S-INF	SA	14	3.55	2.14	5.43	4.25	16	0.88	7.25
S-PAS	SA	5	1.33	4.24	6.00	4.9	15	0.91	8.45
S-PIS	SA	9	19.09	8.04	5.94	3.67	18	0.91	8.67
S-PRO	SA	6	1.98	17.11	5.25	3.17	16	0.90	6.17
S-RIC	SA	7	2.02	2.69	5.57	4.14	16	0.89	10.86
S-SCR	SA	5	2.37	0.00	4.30	2.20	13	0.89	8.10
S-SPU	SA	2	0.44	5.67	6.75	4.25	12	0.88	9.25
S-STA	SA	3	0.62	2.34	6.00	3.50	15	0.90	8.83
S-TAL	SA	5	2.62	4.83	6.50	4.07	15	0.90	6.42
V-FOR	VT	23	5.72	1.14	6.53	5.91	19	0.91	6.72
V-GDG	VT	11	1.20	1.75	7.44	8.22	15	0.89	13.25
V-GRA	VT	31	233.91	70.38	8.15	7.80	18	0.90	12.21
V-JAM	VT	8	3.80	0.00	6.69	6.38	13	0.88	9.75
V-MOL	VT	16	2.87	5.15	5.89	5.06	19	0.91	8.15
V-PRI	VT	13	1.74	0.00	7.89	7.35	19	0.91	9.79
V-QNC	VT	29	22.03	0.00	8.93	6.95	21	0.93	7.28
V-RSV	VT	8	21.50	0.00	6.81	7.08	13	0.88	12.08
V-SCO	VT	18	2.55	0.00	7.06	7.28	15	0.88	10.31

Note: Abbreviations are: N plots = number of plots for quality assessment; HA = patch size in ha; hab_buff = habitat amount in 500-m buffer, shrub_tot = abundance index of all shrub species obtained by summing the cover of each species, shrub_sel = abundance index of selected shrubs (see Appendix: Table A2 for a checklist), Rich = total number of shrub species in the site (grid), Simps = Simpson's diversity index of shrub species; vol_shrub = vertical cover of shrubs obtained by summing the percentage cover of shrubs at 0.5-1-2-4-8 m of height (see Table 1 for more details on variables).

Table A2. Microhabitat and resource abundance variables measured in each sampled site. Variables were measured in quadrat plots (100 m²); number of plots increased with patch size but density of plots was kept constant. Cover was estimated according to the following classes (percentage of the plot covered by the ground projection of the target variable, e.g., *Rubia peregrina*): 0, 1–25, 25–50, 50–75, 75–100. Selected shrub species are followed by a dagger (†).

Variable	Description
Age	Years since logging
Number of trees	Mean number of trees counted in the plots
Canopy	Mean canopy cover in the plots (%)
Canopy height	Mean height of the canopy (m)
Dominance of tree species:	Dominance of the following tree species: <i>Quercus cerris</i> , <i>Quercus pubescens</i> , <i>Fraxinus ornus</i> , <i>Ulmus minor</i> , <i>Ostrya carpinifolia</i> , <i>Carpinus betulus</i>
Dead trees	Mean number of dead trees in the plots
DBH	Mean diameter at breast height of trees in the plots (cm)
Herbaceous cover	Mean herbaceous cover in the plots (%)
Litter cover	Mean litter cover in the plots (%)
Naked soil	Mean cover of naked soil in the plots (%)
Cover of shrub species	Mean cover of the following shrub species (%) in the plots: <i>Crataegus</i> spp., † <i>Corylus avellana</i> , † <i>Cornus mas</i> , † <i>Euonymus europeaus</i> , † <i>Ligustrum vulgare</i> , † <i>Prunus spinosa</i> , † <i>Rosa canina</i> , † <i>Rubus</i> spp., † <i>Ruscus aculeatus</i> , † <i>Paliurus spina-christi</i> , <i>Ginestra</i> , <i>Sambucus nigra</i> , <i>Lonicera</i> spp., <i>Pistacia lentiscus</i> , <i>Phillyrea</i> spp., <i>Ilex aquifolium</i> , <i>Rubia peregrina</i> , <i>Smilax aspera</i> , <i>Viburnum</i> spp., <i>Clematis vitalba</i> , <i>Coronilla emeris</i> , <i>Bryonia dioica</i> , <i>Mespilus germanica</i> , <i>Asparagus acutifolius</i> , <i>Hedera helix</i> , <i>Prunus avium</i> , <i>Laurus nobilis</i>

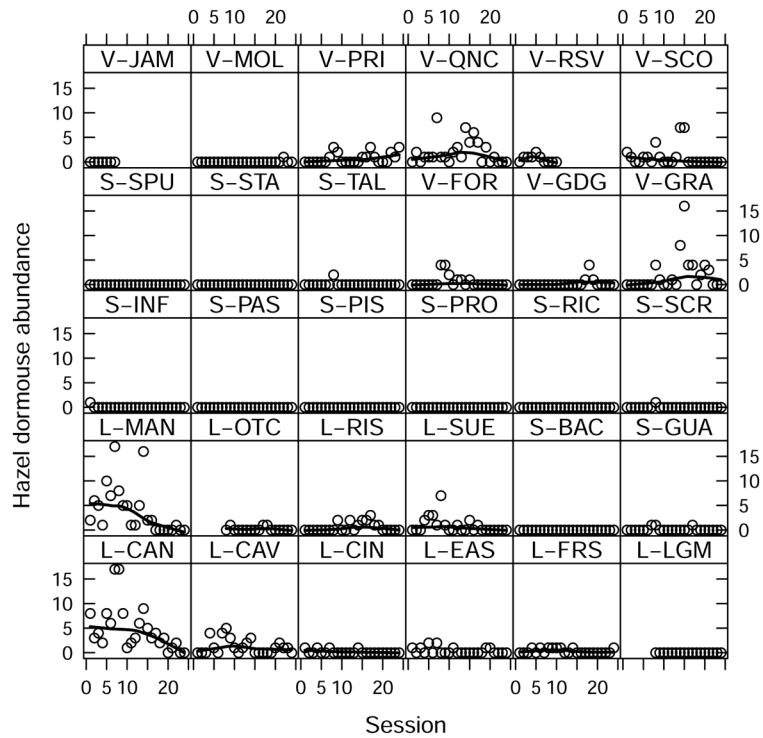


Fig. A2. Series of abundance (raw number of individuals captured) in each of the study sites. The first letter of the abbreviated code of each site specifies the landscape L = Lamone landscape (control), V = Viterbo landscape (fragmented), S = Sabina landscape (fragmented). A list of the main characteristics of each site is provided in Appendix: Table A1. A smoothing line (loess) was added to facilitate interpretation. We here used only first visits for the abundance data (to standardize between months with single and months with triple visits) therefore five sites (rather than nine) appear as occupied.

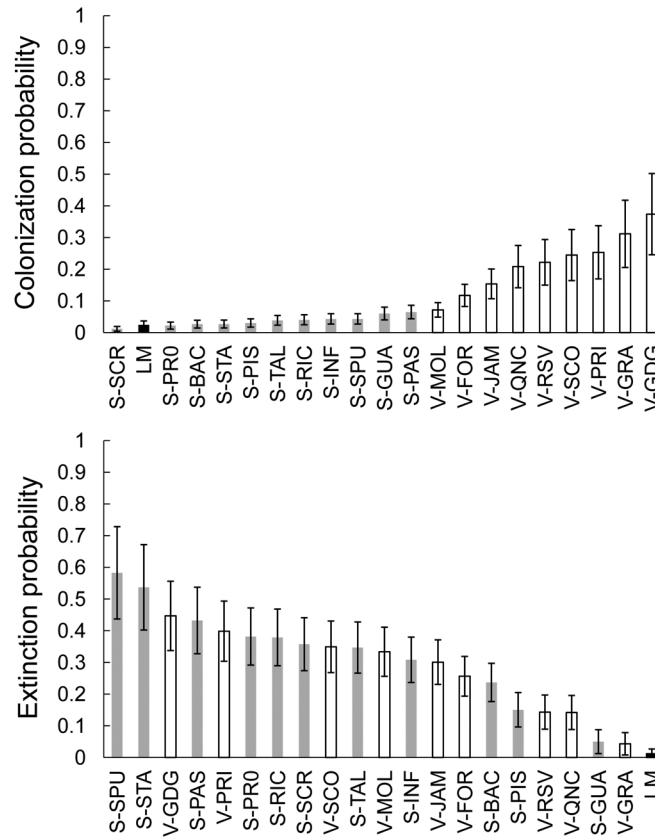


Fig. A3. Colonization and extinction probability in each sampled patch as predicted by the top ranked occupancy model (the graph includes model predictions and standard errors). Patches are sorted by shrubs (shrub_sel, colonization) and size (logHA, extinction); the three landscapes are represented with different colors (grey: S, black: L, white: V).

Table A3. Matrix of Spearman correlation coefficients of candidate predictor variables. Significant values ($p < 0.05$) are noted by an asterisk (*).

Variable	Shrub_tot	LogHA	Hab_buffer	Rich	Simpson	Vol_shrub
Shrub_sel	0.804*	0.040	-0.300	0.155	0.162	0.603*
Shrub_tot		-0.036	-0.282	0.186	0.255	0.625*
LogHA			0.173	0.343	0.132	-0.119
Hab_buffer				0.041	0.151	-0.210
Rich					0.752*	-0.119
Simpson						-0.162

Table A4. List of top ranked occupancy models, ranked according to AIC_C (only models within four ΔAIC_C are included. Covariates appear in parentheses (see Table 1 for more details on variables).

Model	AIC_C	ΔAIC_C	AIC_C wgt	N
psi, gamma(Shrub_sel,days), eps(logHA), p(T_ave)	526.40	0.00	0.50	8
psi, gamma(logHA, Shrub_sel,days), eps(logHA), p(T_ave)	528.77	2.37	0.15	9
psi, gamma(Shrub_sel,days), eps(logHA, Shrub_sel), p(T_ave)	530.20	3.80	0.08	9

Note: Abbreviations are: Psi = presence probability, gamma = colonization probability, eps = extinction probability, p = detection probability, AIC_C = corrected Akaike's information criterion, AIC_C wgt = Akaike's weight, N = number of estimated parameters.

Table A5. β averaged estimates of the final Cormack-Jolly-Seber model, obtained from models within two ΔQAIC_c . Estimate and standard error (SE) are reported for intercept and covariate parameters (see Table 1 for details on the covariates). Phi = survival probability, p = recapture probability.

Parameter	β	SE
phi - LM	4.47	0.14
phi - SA	4.21	0.24
phi - VT	4.03	0.24
phi - body mass	0.75	0.14
phi - simps	0.40	0.14
p - summer	-3.11	0.29
p - other seasons	-2.01	0.13

Table A6. Data on litter size for the 62 captures of mother with pups. L = Lamone, S = Sabina, V = Viterbo.

Grid	Date of capture	No. pups	Grid	Date of capture	No. pups
L-CAN	20 May 2010	4	L-MAN	10 Sep 2011	5
L-CAN	20 May 2010	4	L-MAN	4 Oct 2011	4
L-CAN	31 Aug 2010	8	L-MAN	12 Nov 2011	3
L-CAN	5 Oct 2010	8	L-RIS	6 Sep 2011	1
L-CAN	5 Oct 2010	4	L-RIS	6 Sep 2011	6
L-CAN	5 Oct 2010	6	L-RIS	10 Sep 2011	6
L-CAN	4 Aug 2011	5	L-SUE	1 Sep 2010	6
L-CAN	4 Aug 2011	4	L-SUE	30 Oct 2010	5
L-CAN	10 Sep 2011	6	L-SUE	10 May 2011	3
L-CAN	4 Oct 2011	3	L-SUE	10 May 2011	3
L-CAN	28 Apr 2012	3	L-SUE	14 May 2011	4
L-CAV	1 Sep 2010	3	V-FOR	2 Dec 2011	2
L-CAV	2 Aug 2012	6	V-GRA	5 Sep 2011	3
L-CAV	2 Oct 2012	3	V-GRA	7 Nov 2011	2
L-CIN	29 Jul 2010	5	V-GRA	7 Nov 2011	2
L-EAS	30 Oct 2010	5	V-GRA	7 Nov 2011	2
L-EAS	30 Oct 2010	6	V-GRA	2 Dec 2011	4
L-FRS	1 Sep 2010	4	V-GRA	2 Dec 2011	2
L-FRS	30 Oct 2010	7	V-GRA	2 Dec 2011	2
L-FRS	5 Aug 2011	5	V-QNC	13 Nov 2010	3
L-FRS	9 Sep 2011	4	V-QNC	13 Nov 2010	6
L-FRS	9 Sep 2011	6	V-QNC	3 Aug 2011	4
L-MAN	18 Jun 2010	3	V-QNC	3 Aug 2011	5
L-MAN	30 Jul 2010	1	V-QNC	5 Sep 2011	3
L-MAN	5 Oct 2010	3	V-QNC	5 Sep 2011	6
L-MAN	5 Oct 2010	2	V-QNC	5 Oct 2011	7
L-MAN	5 Oct 2010	8	V-QNC	7 Nov 2011	5
L-MAN	31 Oct 2010	5	V-QNC	26 Apr 2012	3
L-MAN	31 Oct 2010	5	V-QNC	6 Jul 2012	2
L-MAN	26 Nov 2010	5	V-SCO	7 Nov 2011	2
L-MAN	5 Aug 2011	4	V-SCO	3 Dec 2011	2

Table A7. Summary of the results on the influence of patch size, isolation and patch quality on the ecological levels investigated in the present study.

Parameter	Ecological level	Influenced by
Colonization	population	patch quality (abundance of resources)
Extinction	population	patch size
Abundance	population	patch quality (abundance of resources)
Survival	individual	patch quality (diversity of resources)
Litter size	individual	none