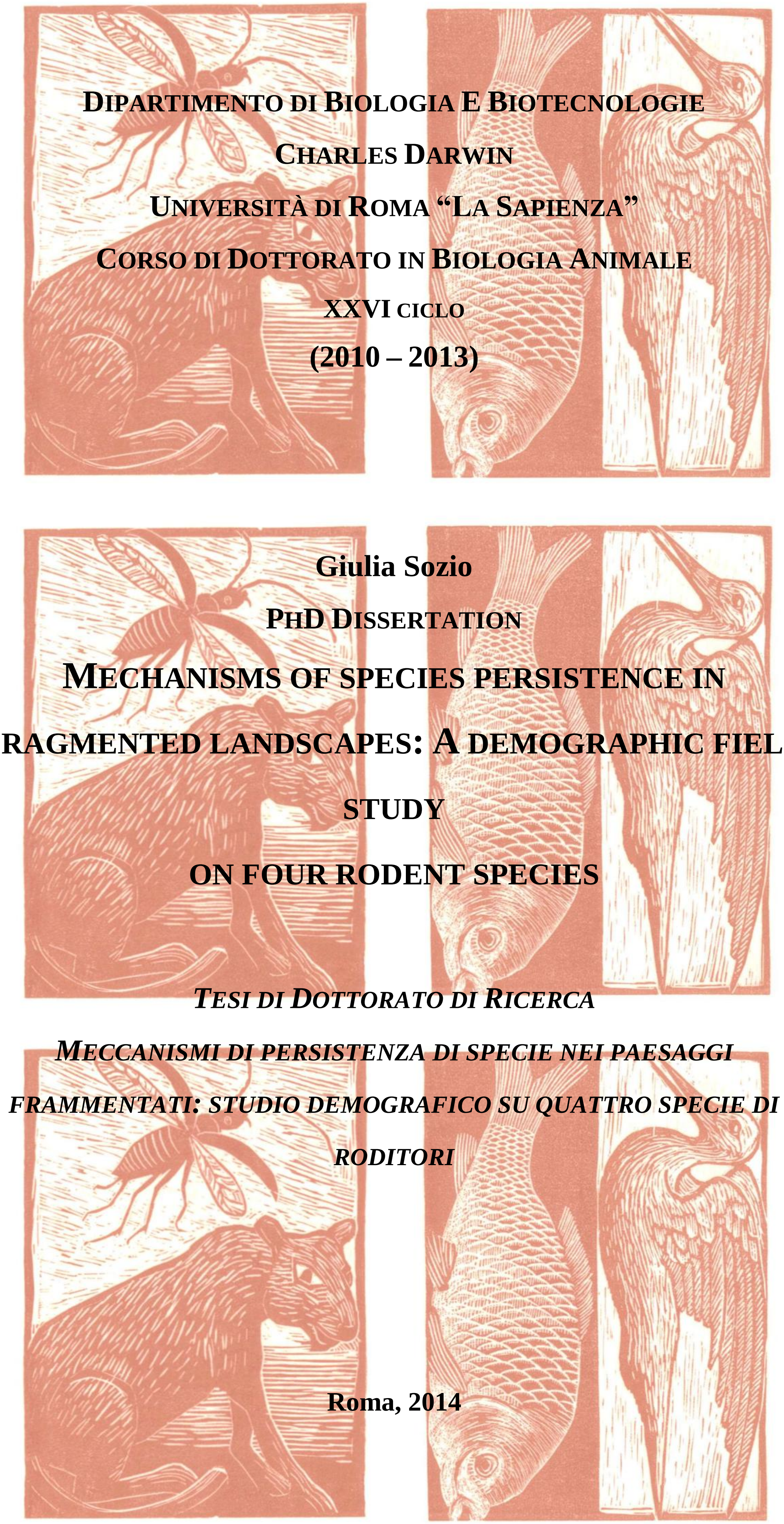

DIPARTIMENTO DI BIOLOGIA E BIOTECNOLOGIE

CHARLES DARWIN

UNIVERSITÀ DI ROMA “LA SAPIENZA”

CORSO DI DOTTORATO IN BIOLOGIA ANIMALE

XXVI CICLO

(2010 – 2013)

Giulia Sozio

PHD DISSERTATION

MECHANISMS OF SPECIES PERSISTENCE IN FRAGMENTED LANDSCAPES: A DEMOGRAPHIC FIELD STUDY

ON FOUR RODENT SPECIES

TESI DI DOTTORATO DI RICERCA

MECCANISMI DI PERSISTENZA DI SPECIE NEI PAESAGGI FRAMMENTATI: STUDIO DEMOGRAFICO SU QUATTRO SPECIE DI RODITORI

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ABSTRACT

Habitat loss and fragmentation are key drivers of global species loss. In fragmented landscapes species must persist in small, isolated and often degraded habitat patches where they can be subject to high risk of extinction due to deterministic and stochastic forces. Species respond to habitat fragmentation according to species-specific life-history traits, with habitat generalist, edge or mobile species being less impacted compared to specialists and less mobile species.

The impact of habitat fragmentation on species and their consequent probability of persistence depends on a series of key, concatenated events occurring at different biological and spatial scales. The response of single individuals to landscape change can translate into effects at the level of populations; coexisting species can reciprocally influence their responses through the alteration of interspecific relationships; inter-population dynamics can also occur, involving the movement of individuals between populations in different habitat fragments and affecting the persistence of entire systems of populations.

Given the complexity of factors involved, including direct and interacting responses, it is extremely difficult to understand the actual effects triggered by habitat fragmentation without a thorough knowledge of the underlying ecological mechanisms.

The aim of this PhD project was to contribute to understanding the mechanisms underlying the response of species to habitat fragmentation. By following a holistic approach, I used a set of mechanistic field studies on four rodent species specifically designed to investigate the series of key events involved in the persistence of species in fragmented landscapes:

<u>1) Population and individual scale responses of small mammals to patch size, isolation and quality.</u>

The aim of this section was to determine the relative effects of landscape structure (habitat amount and configuration) and patch quality (here measured as abundance of shrub resources) on individuals (survival and litter size) and populations (density and colonization/extinction dynamics). A large-scale demographic field study was conducted, encompassing 30 woodland sites nested within three landscapes and surveyed monthly for three years by means of a capture-mark-recapture protocol. Model species was an arboreal rodent, the hazel dormouse (*Muscardinus avellanarius*), known to be sensitive to habitat loss and fragmentation. Habitat quality influenced populations at different biological scales by concatenated effects: it enhanced individual survival, increased the chances of colonizing vacant patches and sustained higher population densities. It was therefore related to the performance of single populations and systems of populations through re-colonization dynamics. Habitat quality, however, did not influence local extinction probability, which was ultimately related to the extent of available habitat, likely due to the absolute size of populations: a high absolute number of individuals reduces the chances of population extinction.

2) The role of interspecific interactions in shaping small mammal communities in fragmented landscapes.

The aim of this section was to evaluate the strength of interspecific interactions as a shaping force of animal communities in fragmented landscapes. A large-scale demographic field study was conducted to measure the degree of competitive interference between species. Model system was constituted by the community of forest-dwelling ground rodents of central Italy, including the species *Apodemus sylvaticus*, *Apodemus flavicollis* and *Myodes glareolus*. Populations, inhabiting 29 wood patches in a fragmented landscape, were surveyed for two years by means of a capture-mark-recapture protocol. I modeled species' distribution as a function of landscape (habitat cover and connectivity provided by hedgerows) and habitat variables (vegetation structure and food resources) to look for evidences of competitive spatial segregation. Then I tested for each species the effect of competitors on several biological parameters: survival, recruitment, reproduction, body mass, population density. Even though populations' relative distribution was consistent with a mechanism of competitive spatial segregation, with habitat specialists being favored by high-quality, well-connected fragments and generalists exploiting more isolated and degraded patches, results on demographic parameters did not fully confirm this result. The strongest competitive effects were exerted by *A. sylvaticus* on *A. flavicollis*, whereas a little degree of interference was found between *Apodemus* spp. and *M. glareolus*. Nevertheless, competitive effects were weak, acting on a few biological parameters and not translating into strong effects at the level of populations (density of individuals).

These results suggest that populations were mainly distributed according to their ecological requirements; competitive exclusion of specialists from isolated and degraded fragments was actually acting but was likely to play a minor role in determining the observed pattern of distribution.

3) Perceptual range and movement ability of small mammals in fragmented landscapes.

The aim of this section was to broaden our understanding of animal orientation and movements in the agricultural matrix, with a special attention on the use of plantation rows as navigation cues. Experiments consisted in releasing individuals of forest-dwelling small mammals (species *A. flavicollis, A. sylvaticus, M. glareolus*) in fields characterized by different types of matrices: a bare field, a grass field with random pattern of vegetation, and a wheat field at three different stages of growth. Animals (N=119) were marked with fluorescent powder and released at progressive distances from target wood fragments; in this type of experiments individuals are assumed to go directly toward the wood as soon as they perceive it. Animal tracks were then analyzed to determine perceptual ranges and movement abilities. Perceptual ranges were species-specific, with habitat specialists perceiving woods at smaller distances compared to generalists. The presence of vegetation in the fields (either grass or wheat) strongly reduced perceptual ranges of all species by obstructing individuals' view. Furthermore, wheat plantation rows drastically influenced animal movements, possibly facilitating or hampering the reaching of a wood. Individuals of all species, in fact, followed the direction of wheat rows at any stage of growth, even if they were not directed toward the target wood.

This study is one of the few examples investigating in detail the demographic mechanisms of response of species to habitat fragmentation. The holistic approach allowed me to provide an overview on the process by which factors such as landscape features, habitat characteristics, and co-occurring species affect the performance of populations in fragmented landscapes. Interspecific interactions play a minor role in shaping the community of small mammals in the studied system. A major role, instead, is played by landscape characteristics (such as habitat cover, connectivity, matrix properties) and local features (such as food resources and habitat structure), in both cases depending on species-specific life-history traits. Increased individual performance (e.g. due to habitat quality) can help to increase the viability of systems of populations; at the same time animals are constrained by the physical structure of the landscape where they live, and individual-scale effects are not necessarily transferred to the level of population. Results suggest that in order to increase the viability of animal systems in fragmented landscapes there is the need to manage the quality of habitat, which proves to be a major determinant of animal populations' performance. Nevertheless, findings also strongly suggest not to ignore the overall landscape context where populations are embedded. In landscapes that have been extensively cleared, restoration aimed to increase the amount of habitat and management of outside-patch landscape elements (hedgerows, agricultural fields) might also be a critical step to ensure the persistence of animal communities.

RIASSUNTO

Perdita e frammentazione degli habitat sono tra le principali minacce per la biodiversità a livello mondiale. Nei paesaggi frammentati le popolazioni animali sopravvivono all'interno di frammenti di habitat residuali di ridotte dimensioni, isolati e spesso degradati, dove il rischio di estinzione è alto a causa di fattori stocastici e deterministici. L'impatto della frammentazione dell'habitat è legato alle caratteristiche delle singole specie: le specie più generaliste, di margine o dotate di maggiori capacità dispersive sono solitamente meno soggette ad impatti negativi rispetto agli specialisti o alle specie meno mobili.

La risposta delle specie alla frammentazione degli habitat, e di conseguenza la loro persistenza, dipendono da una serie di eventi chiave che si verificano a diverse scale biologiche e spaziali. La risposta dei singoli individui alle modifiche del paesaggio può essere tradotta in conseguenti effetti a livello di popolazione; specie coesistenti all'interno della stessa area possono influenzarsi a vicenda tramite l'alterazione delle interazioni interspecifiche; anche il movimento di individui tra popolazioni diverse può influenzare la risposta e la persistenza dell'intero sistema di popolazioni favorendo ad esempio dinamiche di ricolonizzazione.

Data la complessità dei fattori coinvolti, che comprendono risposte dirette, indirette e interagenti tra loro, è estremamente difficile comprendere e prevedere le effettive conseguenze della frammentazione dell'habitat senza una approfondita conoscenza dei meccanismi ecologici sottostanti.

Lo scopo di questo progetto è contribuire alla comprensione dei meccanismi alla base della risposta delle popolazioni animali alla frammentazione degli habitat. Seguendo un approccio olistico ho utilizzato una serie di studi, su quattro specie di roditori forestali, appositamente

disegnati per investigare gli eventi chiave coinvolti nel meccanismo di persistenza delle specie nei paesaggi frammentati:

1) Risposta di individui e popolazioni alla dimensioni dei frammenti, al grado di isolamento e alla qualità dell'habitat.

Lo scopo di questa sezione era determinare gli effetti relativi della struttura del paesaggio (copertura di habitat e sua configurazione spaziale) e della qualità dei patch (misurata in termini di abbondanza di risorse arbustive) su alcuni parametri biologici a scala di individuo e di popolazione: sopravvivenza, dimensione delle nidiate, densità di individui e dinamiche di colonizzazione / estinzione.

La specie modello è il moscardino (*Muscardinus avellanarius*), roditore arboricolo sensibile a perdita e frammentazione dell'habitat, sul quale è stato impostato uno studio demografico a larga scala comprendente 30 siti appartenenti a tre paesaggi (due paesaggi frammentati e un'area continua). I dati sono stati raccolti mensilmente per tre anni tramite un protocollo di cattura - marcatura - ricattura.

La qualità dell'habitat è risultata influenzare le popolazioni di moscardino a diverse scale biologiche, aumentando la probabilità di sopravvivenza degli individui, la probabilità di colonizzazione di siti vacanti, e sostenendo più alte densità di popolazione. La qualità dell'habitat è risultata quindi determinante non soltanto per la performance delle singole popolazioni ma anche per interi sistemi di popolazioni tramite dinamiche di ricolonizzazione. La probabilità di estinzione, tuttavia, non è risultata influenzata dalla qualità dell'habitat ma soltanto dalla quantità di habitat disponibile. Questo risultato è probabilmente legato alla dimensione assoluta delle popolazioni supportate da una maggiore quantità di habitat, che aiuta a ridurre le probabilità di estinzione.

2) Il ruolo delle interazioni interspecifiche nel determinare la struttura delle comunità di piccoli mammiferi nei paesaggi frammentati.

Lo scopo di questa sezione era valutare il ruolo delle interazioni competitive come forza plasmante delle comunità animali nei paesaggi frammentati. Il sistema modello è costituito dalla comunità di roditori forestali terricoli del centro Italia, comprendente le specie *Apodemus sylvaticus*, *Apodemus flavicollis*, *Myodes glareolus*. L'area di studio comprende 29 frammenti boschivi nei quali le popolazioni di roditori sono state seguite per due anni, a intervalli di due mesi, tramite un protocollo di cattura - marcatura - ricattura mirato alla misurazione del grado di interferenza competitiva tra le specie. Dapprima è stata modellizzata la distribuzione relativa delle tre specie in funzione di caratteristiche del paesaggio (cover boschivo e connettività fornita dalle siepi) e dell'habitat (struttura della vegetazione e risorse alimentari), al fine di cercare supporto per un meccanismo di segregazione spaziale competitiva. Successivamente, per ogni specie è stato testato l'effetto dei competitori su una serie di parametri biologici rappresentativi della performance di individui e popolazioni: sopravvivenza, recruitment, riproduzione, massa corporea, densità di popolazione.

Sebbene la distribuzione relativa delle popolazioni risultasse compatibile con un meccanismo di segregazione competitiva (specialisti legati a siti di alta qualità, poco isolati, e generalisti legati a siti più isolati e degradati), tuttavia, i risultati demografici non hanno confermano pienamente questo risultato. Gli effetti competitivi più forti sono stati rilevati da parte di *A. sylvaticus* nei confronti di *A. flavicollis,* mentre tra *Apodemus* spp. e *M. glareolus* è risultato un basso grado di interferenza competitiva. Tuttavia gli effetti competitivi, rilevati su alcuni parametri biologici a livello dell'individuo (come una ridotta sopravvivenza e un ridotto peso corporeo), sono risultati complessivamente deboli, e non sono stati rilevati effetti corrispondenti forti a livello di popolazione (densità di individui). Questi risultati suggeriscono che la distribuzione delle popolazioni di roditori fosse determinata prevalentemente dalle esigenze ecologiche specie-specifiche, mentre i meccanismi di esclusione competitiva, sebbene non da escludere, giocassero un ruolo minore nel determinare i pattern osservati.

3) Raggio di percezione e capacità di movimento di roditori in paesaggi frammentati.

Lo scopo di questa sezione era contribuire alla comprensione dei meccanismi di orientamento e delle capacità di movimento degli animali attraverso le aree di matrice agricola, con una particolare attenzione all'uso delle linee di coltivazione dei cereali come elementi guida per gli spostamenti.

Lo studio è basato su una serie di esperimenti di rilascio di roditori forestali (*A. sylvaticus*, *A. flavicollis*, *M. glareolus*) in campi agricoli caratterizzati da diversi tipi di matrice: un campo brullo, un prato incolto e un campo di grano a tre stadi di crescita. Gli individui (N=119) sono stati marcati con polvere fluorescente e rilasciati a distanze progressive da frammenti boschivi target; in questo tipo di esperimenti si assume che gli individui si dirigano verso il bosco non appena riescono a individuarlo. Le tracce fluorescenti lasciate dagli animali hanno permesso di determinare la traiettoria degli individui, il loro raggio di percezione e le capacità di movimento. I raggi di percezione sono risultati altamente specie-specifici (gli specialisti individuavano i frammenti boschivi a distanze inferiori rispetto ai generalisti). La presenza di vegetazione (sia prato incolto che grano) che ostruisse la visione a distanza riduceva fortemente i raggi di percezione di tutte le specie. Inoltre, i movimenti animali sono risultati influenzati drasticamente dalle linee di coltivazione del grano, che costituivano la direzione preferenziale di movimento per gli individui di tutte le specie. Gli individui, infatti, mostravano di muoversi lungo le linee del grano anche nel caso in cui queste non fossero rivolte nella direzione del bosco, suggerendo il loro ruolo nel facilitare oppure impedire il raggiungimento dei frammento boschivi.

Questo è uno dei pochi studi ad esaminare in dettaglio i meccanismi demografici di risposta delle specie alla frammentazione dell'habitat. L'approccio olistico mi ha permesso di fornire una visione d'insieme sui processi attraverso cui i fattori come le caratteristiche del paesaggio, dell'habitat e la presenza di specie competitrici influiscono sulla performance delle popolazioni nei paesaggi frammentati. Le interazioni interspecifiche giocano un ruolo minore nel plasmare la comunità di piccoli mammiferi nel sistema studiato, mentre un ruolo maggiore è giocato dalle caratteristiche del paesaggio (come cover boschiva, connettività, proprietà della matrice) e locali (come struttura dell'habitat e risorse alimentari), in entrambi i casi con modalità specie-specifiche. La performance degli individui (ad esempio in relazione ad una buona qualità dell'habitat) può aiutare ad aumentare la vitalità dei sistemi di popolazioni; allo stesso tempo, tuttavia, le specie animali sono vincolate alla struttura fisica del paesaggio in cui vivono, per cui gli effetti positivi a livello individuale non si traducono necessariamente in corrispondenti effetti a livello di popolazione.

I risultati suggeriscono che per aumentare la persistenza dei sistemi animali nei paesaggi frammentati non si può prescindere da una gestione corretta della qualità dell'habitat all'interno dei singoli frammenti residuali. Allo stesso tempo, i risultati suggeriscono anche che non si può prescindere dal contesto del paesaggio in cui le popolazioni vivono. In paesaggi in cui la copertura di habitat è stata fortemente ridotta, il ripristino dell'habitat e la gestione di elementi esterni ai frammenti (come siepi e campi agricoli) può costituire un passaggio fondamentale per la persistenza delle comunità animali.

1. INTRODUCTION

1.1. General introduction ad thesis outline

Habitat loss and fragmentation are key drivers of global species loss (Foley et al. 2005, Fischer and Lindenmayer 2007). In fragmented landscapes species must survive in small, isolated and often degraded habitat patches in which their demography (e.g. survival, reproduction, growth rate) is disrupted and population size limited (Fahrig 2003). Local populations are therefore subject to a relatively high risk of extinction due to both deterministic and stochastic forces (Hanski and Gaggiotti 2004, Fischer and Lindenmayer 2007). Populations are more or less connected by individuals' dispersal, which depends on their ability to move through a sub-optimal and often hostile man-made environment (e.g. the agricultural matrix). A high dispersal ability may increase the persistence of species by allowing re-colonization of fragments or by maintaining high immigration rates (Hanski and Gaggiotti 2004).

Several studies showed that habitat fragmentation impact species according to their natural history traits (Henle et al. 2004): habitat specialists or less mobile species, which strictly rely on native habitat for living and reproducing and are not able to exploit or move through the surrounding matrix, are expected to be highly and negatively impacted. On the contrary, generalist, edge, or highly mobile species are expected to be poorly impacted or even advantaged by fragmentation-induced landscape modifications (e.g. Mac Nally and Brown 2001, Gibb and Hochuli 2002, Ripperger et al. 2014).

The impact of habitat fragmentation on species and their consequent probability of persistence depends on a series of concatenated key events occurring at different biological and spatial scales. The response of single individuals to landscape change can translate into effects at the level of populations; coexisting species can reciprocally influence their responses through the alteration of interspecific relationships (e.g. Gibbs and Stanton 2001, Gibb and Hochuli 2002, Robertson et al. 2013b). Inter-population dynamics can also occur, involving the movement of individuals between populations in different habitat fragments and affecting the persistence of entire systems of populations.

Given the complexity of factors involved, including direct and interacting responses, it is extremely difficult to understand and predict the actual effects triggered by habitat fragmentation without a thorough knowledge of the underlying ecological mechanisms (Holland and Bennett 2010, Godsoe and Harmon 2012). A holistic approach aimed at dissecting the different events involved in the response of populations would provide a more comprehensive overview of the whole process compared to studies focusing on single aspects. Such holistic studies, however, are still lacking in the literature on habitat fragmentation.

The aim of this PhD project was to contribute to understanding the mechanisms underlying the response of species to habitat fragmentation. By following a holistic approach, I used a series of mechanistic field studies specifically designed to investigate a set of concatenated, key events involved in the persistence of species: a) the response of individuals to habitat fragmentation; b) the translation of individual responses into population-level dynamics; c) the interacting dynamics of different co-occurring species; d) the movement of individuals among populations.

I selected as a model system a set of forest-dwelling small mammals, including the species *Muscardinus avellanarius*, *Apodemus sylvaticus*, *Apodemus flavicollis*, *Myodes glareolus*.

M. avellanarius is an arboreal specialist known to be sensitive to the loss and fragmentation of woodlands (e.g. Mortelliti et al. 2008); furthermore, it does not have main competitors, as *Glis glis* is absent in the study area. For these reasons, it was particularly suited as a model species to isolate the demographic effects of fragmentation at several scales, from individuals to populations to systems of populations.

A. sylvaticus, *A. flavicollis* and *M. glareolus* constitute the main components of the guild of forest-dwelling, ground rodents in central Italy. They lie on a gradient of specialization to forest habitat and they are known to share part of their niche, being potential competitors (e.g. Amori et al. 2008). Given their characteristics, they were selected as a model system to study the role of competitive interactions in determining the response of species to habitat fragmentation. Furthermore, given their differences in life-history traits and dispersal abilities, they were also particularly suited to investigate movement ability of species in fragmented landscapes.

Below I present the general outline of the thesis, including three main sections aimed at investigating the afore-mentioned key topics:

1) Population and individual-scale responses of small mammals to patch size, isolation and quality.

The aim of this section was to determine 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 (density and colonization/extinction dynamics). A large-scale demographic field study was conducted, encompassing 30 woodland sites nested within three landscapes and surveyed monthly for three years by means of a capture-mark-recapture protocol. Model species was the hazel dormouse (*M. avellanarius*).

2) The role of interspecific interactions in shaping small mammal communities in fragmented landscapes.

The aim of this section was to evaluate the strength of interspecific interactions as a shaping force of animal communities in fragmented landscapes. A large-scale demographic field study was conducted to measure the degree of competitive interference between species. The model system was constituted by the community of forest-dwelling ground rodents of central Italy, including the species *A. sylvaticus*, *A. flavicollis* and *M. glareolus*. Populations, inhabiting 29 wood patches in a fragmented landscape, were surveyed for two years by means of a capture-mark-recapture protocol.

3) Perceptual range and movement ability of small mammals in fragmented landscapes.

The aim of this section was to broaden our understanding of animal orientation and movements in the agricultural matrix, with a special attention on the use of plantation rows as navigation cues.

Experiments consisted in releasing individuals of forest-dwelling small mammals (*A. flavicollis, A. sylvaticus, M. glareolus*) in fields characterized by different types of matrices to observe their movements and reveal their perceptual range and movement abilities.

Specific theoretical background on each topic is provided in the remainder of this chapter. In order to facilitate readers and to help following each section as a stand-alone study addressing specific questions, specific details on each part including materials and methods, details on species' biology functional to the study, results and discussions are provided in separate sections of the corresponding chapters.

1.2. Population and individual-scale responses to patch size, isolation and quality.

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 (Robles and Ciudad 2012, Frey et al. 2012). Hence, they have examined the ultimate effects rather than the proximate causes of population turnover (Figure 1).

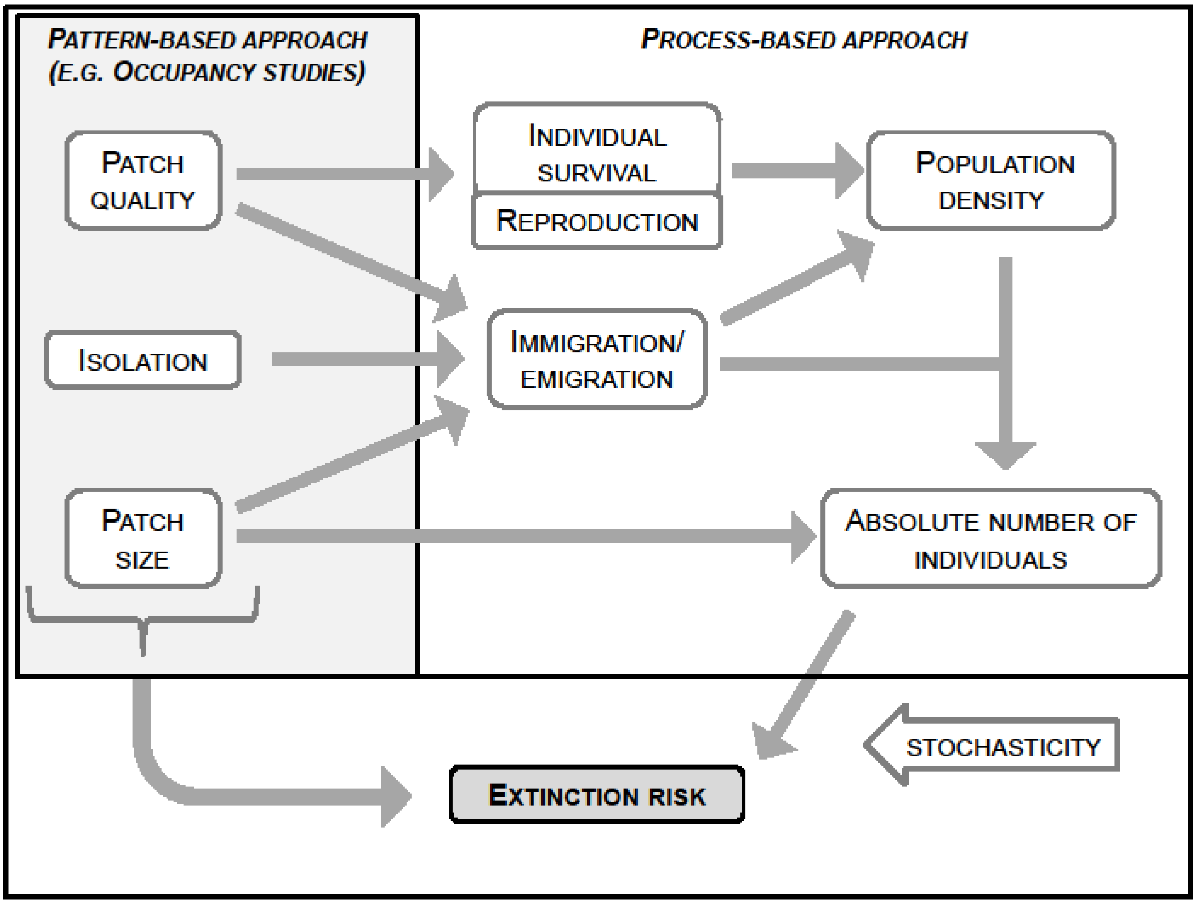


Figure 1. Conceptual model of factors affecting species extinction risk in fragmented landscapes. I distinguished between a purely pattern-based approach (focused on snapshot presence/absence data) and the process-based mechanistic approach followed in this paper. A process-based approach should allow 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).

There is substantial literature showing that patch size, isolation and quality can play crucial roles in determining patch occupancy in fragmented landscapes (Fahrig 2003, Hanski and Gaggiotti 2004, Lindenmayer and Fischer 2006, Mortelliti et al. 2010, Thornton et al. 2011). More mechanistic knowledge also has been gathered on the effects of patch variables on specific demographic parameters such as density and population size (Rabasa et al. 2008, Vögeli et al. 2010, Örvössy 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).

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, including whether effects are 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).

I contributed 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. I 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 (density and colonization/extinction dynamics). The target species was an arboreal rodent, the hazel dormouse (*Muscardinus avellanarius*).

Based on the conceptual model in Figure 1 (which highlights the key differences between an occupancy-only study and a study including demographic and occupancy analyses), I posed four inter-linked questions on the effects of patch variables on individuals and populations. I stress that the key-novelty of this 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). The first question was aimed at understanding which factors prevail in the 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: a) 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 b) the chances that a population establish in a patch, which may depend on habitat quality (Mortelliti et al. 2010). To answer question 2, I examined the relative role of patch variables 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, Örvössy et al. 2012) whereas Matter et al. (2009) found lower density in more isolated patches. To answer question 3, I examined the effects of patch variables on the density of hazel dormice.

Question 4. How do individuals respond to patch size, isolation and quality?

I 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, I evaluated the effects of patch variables on litter size and apparent survival, which was estimated through the application of capture-mark-recapture modeling.

1.3. The role of interspecific interactions

Despite the extensive scientific literature measuring fragmentation-induced effects on species and communities (Fahrig 2003, Lindenmayer and Fischer 2006, Collinge 2009), the role of interspecific interactions in determining such negative effects, and the underlying demographic mechanisms, are still far from being clear (Amarasekare 2003, Holland and Bennett 2010).

Several theoretical studies describe possible mechanisms regulating the coexistence or exclusion of species in modified landscapes, but empirical confirmation to theory is poor and based on indirect inference (Chesson 2000, Amarasekare 2003, Boeye et al. 2014).

A few studies examined interspecific interactions in fragmented landscapes by looking at static distribution patterns (e.g. Nupp and Swihart 2001, Brown 2007, Kath et al. 2009, Youngentob et al. 2012, Fisher et al. 2013, Robertson et al. 2013a). However, competition is a dynamic process which shapes animal populations so that they tend to avoid interference. For this reason, it is extremely hard to detect competition in action unless using removal experiments (e.g. Ginger et al. 2003, Brunner et al. 2013, but see Dugger et al. 2011). Such experiments, however, are hard to conduct over the large-scale required to investigate fragmentation-related processes. Inferring competition processes from pattern-based studies can lead to misleading conclusions as it is extremely difficult to understand whether what looks as an apparent competitive response is instead due to a response to habitat or landscape characteristics. Likewise the risk of underestimating the effect of competition in comparison to patch and landscape variables is high. To detect competition in action, a demographic approach is required. In fact, by focusing on the effect of competitors on the vital rates of a target species we can quantify the immediate response of species to competitors and thus partition its effect from the effect of the surrounding landscape characteristics. There are no large-scale empirical studies directly measuring the effect of competitors on the performance of populations in fragmented landscapes.

To contribute in filling the critical knowledge gap on the role of interspecific interactions on species' extinction in fragmented landscapes, I conducted a large-scale demographic study specifically designed to measure the degree of ongoing competitive interference between species. My aim was to evaluate the strength of interspecific interactions as a shaping force of animal communities in fragmented landscapes. I used as a model system the terrestrial small mammal community inhabiting deciduous oak woodlands in central Italy, which includes the species *A. sylvaticus*, *A. flavicollis* and *M. glareolus*. These species have been extensively studied in the past and are known to compete (Andrzejewski and Olszewski 1963, Hoffmeyer 1973, Montgomery 1978, 1981, Wójcik and Wolk 1985, Canova 1993, Cihakova and Frynta 1996, Abt and Bock 1998, Fasola and Canova 2000). The populations inhabiting 29 woodland patches in a fragmented landscape were surveyed every other month for two years. This frequent sampling interval allowed me to measure the response of one species to variation in abundance of the other two species, approaching what can be defined as a "natural experiment". I focused on a set of key ecological parameters that would allow me to measure the response of individuals and populations (body mass, survival, reproduction, recruitment, population density) (e.g. Dooley and Bowers 1998, Bowers and Dooley 1999, Holland and Bennett 2010).

I hypothesized species to segregate according to their competitive strength and specialization to forest habitat, following the competition-colonization trade-off hypothesis (Amarasekare 2003). In particular, based on this hypothesis:

1) I expected habitat specialists to be confined in large, well-connected, high quality patches, and generalists to exploit small, isolated, low-quality patches, where they could take advantage from competition release. To test the first prediction I modeled the distribution of species as a function of habitat cover, habitat quality and connectivity provided by hedgerows (Objective 1).

2) Further, to test whether the observed distributions were due to a mechanism of competitive segregation rather than being a species-specific response to habitat characteristics, I measured the response of the target vital rate parameters to the increase or reduction in the abundance of competitor species (Objective 2).

1.4. Perceptual range and movement ability

Dispersal ability is one of the main factors determining the sensitivity of species to habitat fragmentation. The dispersal ability of a species depends, among other factors, on its orientation skills, such as its perceptual range (Prevedello and Vieira 2010) which is defined as the maximum distance at which an animal can perceive the surrounding landscape elements such as a woodland patch (Zollner and Lima 1997). A higher perceptual range can increase the ability of an individual to detect a habitat fragment and to move directly towards it, reducing time spent in the hostile matrix, where the survival probability is lower (Zollner and Lima 2005). The perceptual range is not only a species-specific characteristic, it is also highly dependent on the environmental context (Prevedello et al. 2010). The type of matrix or the environmental conditions during dispersal have a strong influence on animals' ability to perceive habitat fragments. Perceptual range is higher in the presence of wind (e.g. for species orienting with smell), or in the presence of moonlight and in a matrix that does not obstruct the view (e.g. for visually oriented species) (Zollner and Lima 1997, Prevedello et al. 2011).

Although conservation actions are predominantly targeted towards increasing habitat structural connectivity, matrix management is important because (1) even strictly forest species cross the agricultural matrix (e.g. Mortelliti et al. 2013), (2) habitat oriented conservation actions are expensive, therefore matrix management may often be the only feasible conservation action. From this perspective, a long-standing question in conservation ecology is: what makes a matrix more permeable to animal movements?

To date, many studies have demonstrated that animal species have different ways to orient and guide their movements in known or unfamiliar areas, such as magneto-reception (Wiltschko and Wiltschko 2005) or use of visual landmarks (Lipp et al. 2004). As demonstrated by Prevedello & Vieira (2010) forest marsupials tend to follow manioc (*Manihot esculenta*) plantation rows during their movements through the matrix, suggesting appropriate orientation of cultivation rows as a possible means to increase functional connectivity between habitat fragments.

The study by Prevedello and Vieira (2010) was carried out in manioc plantations on relatively large marsupial species. While manioc is an important crop in tropical habitats ($3.4*10^6$ hectares globally; FAO, 2012), cereal cultivations (e.g. wheat *Triticum* spp.) are the most important crop in more temperate or dry environments ($2.2*10^8$ hectares of wheat plantations globally in 2010; FAO, 2012).

The goal of this section was to broaden our understanding of plantation rows as navigation cues in agricultural landscapes. I focused on testing whether the orientation of wheat rows acts as a dispersal route during three stages of the wheat plant maturation. Such aspect is not trivial: while manioc has long pre-harvesting periods (up to one year and over), on the opposite wheat is normally harvested 110-130 days after sowing. The longer animals use plantation rows as navigation routes, the more likely their use will coincide with dispersal events.

I chose as model species two forest rodents (*A. flavicollis* and *M. glareolus*) and a habitat generalist (*A. sylvaticus*), which are characterized by different degrees of dispersal ability (Marsh and Harris 2000, Mortelliti et al. 2009).

The experimental design followed three conceptual phases:

1) determination of the perceptual range of the model species in different matrix types;

2) test on the influence of wheat plantation rows on animal movement (hypothesis: animals will follow plantation lines as navigation cues);

3) control test in a grass field (hypothesis: due to obstructed view combined with lack of orientation pattern in grass vegetation, animals will not follow any preferential direction).

2. MATERIALS AND METHODS

2.1. Population and individual-scale responses to patch size, isolation and quality.

2.1.1. Study species

For this part of the work I selected the hazel dormouse as a target species for four reasons: 1) it is well documented as being sensitive to habitat loss and to the disruption of connectivity (Bright and Morris 1996, Mortelliti et al. 2008), 2) it is a forest specialist that has similar responses to landscape change as several other vertebrate species (Bright and Morris 1996, 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 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).

2.1.2. Study area

This study was conducted in the northern part of the Latium region, Central Italy (Figure 2). Three landscapes were studied; they are all within 200 km from Rome and have been fragmented periodically over the past 2000 years. These landscapes are characterized by the same climax vegetation (mixed oak woodland with a dominance of *Quercus cerris* and *Quercus pubescens)*. Patches of woodland, usually coppiced every 14-30 years, are embedded in an agricultural matrix mainly cultivated with cereals (wheat) and olive trees.

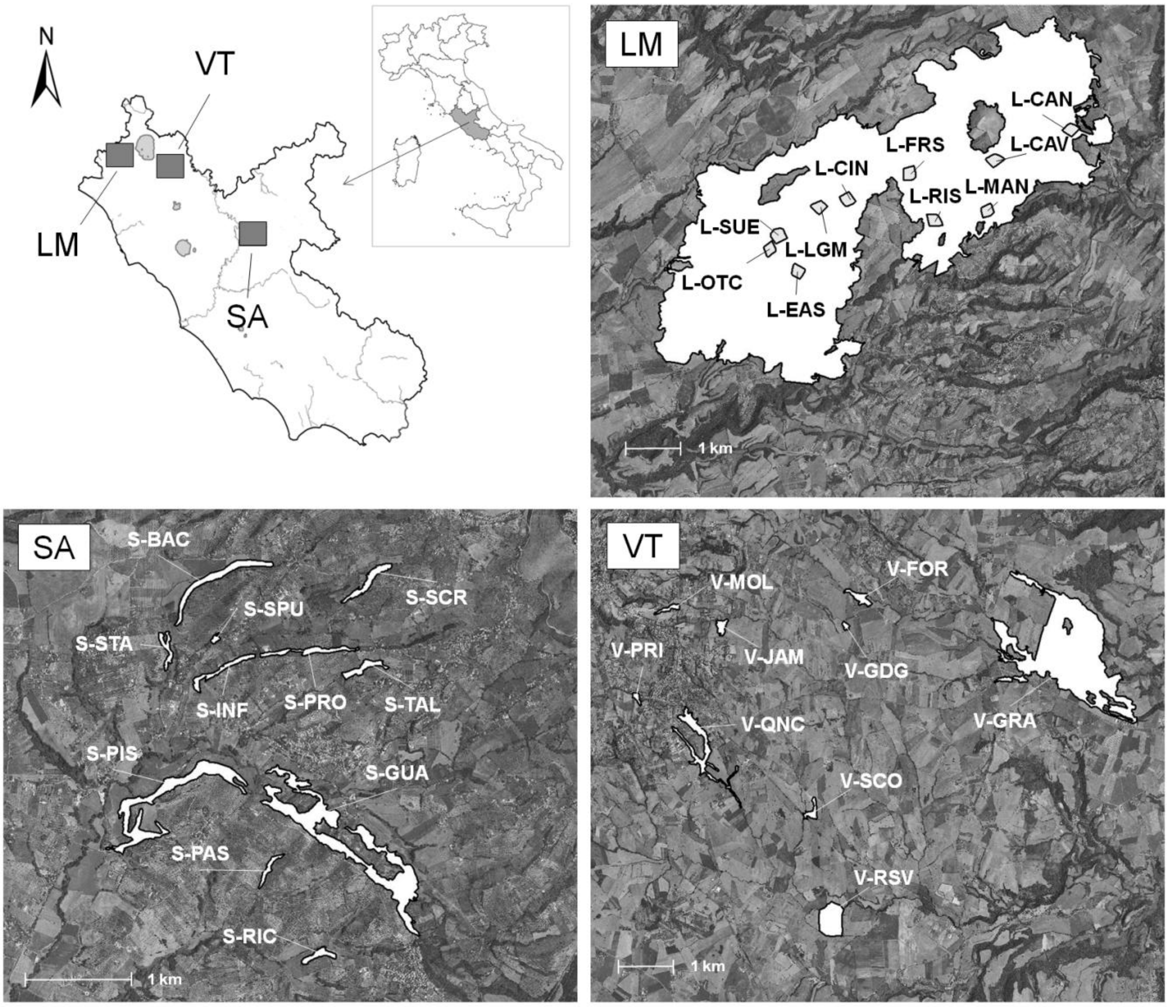
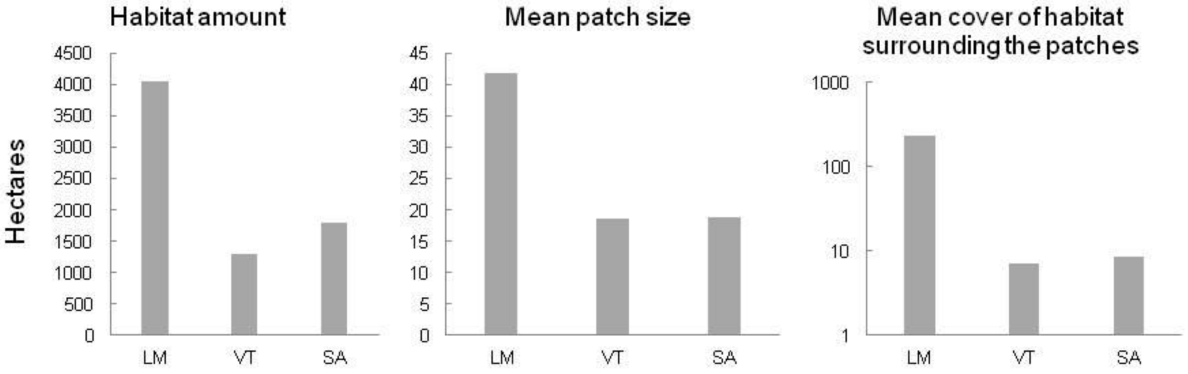


Figure 2. Aerial photos of the three studied landscapes: VT = Viterbo, SA = Sabina, LM = Lamone. The studied woodland patches are filled in white and labeled (information on each patch is provided in Table 1).

2.1.3. Study design

The study was conducted in three landscapes where the hazel dormouse was previously found (Mortelliti et al. 2011). 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 (Figure 3). Mean distance between neighboring fragments was 117 m (range 8 - 716 m) for Viterbo landscape and 126 m (range 7 - 780 m) for Sabina landscape. I 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 Quantum GIS 18.0) 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.


Habitat amount

Mean patch size

Mean cover of habitat surrounding the patches

Figure 3. 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 in a 500 m buffer) measured in a 10x10 Km^2 landscape centered on each study area. LM= Lamone landscape, VT=Viterbo landscape, SA= Sabina landscape.

Eleven patches were sampled in the Sabina landscape and 9 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 1). Within each patch size class, patches to be sampled were randomly selected. The third area, which I consider to be a 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 Table 1.

Table 1. List of 30 sampling sites with their main characteristics. N plots = number of plots for quality assessment; HA = patch size (hectares); Hab buffer = habitat amount in a 500 meters buffer around the patch, shrub_tot = abundance index of all shrub species obtained by summing the cover of each species, shrub_sel = abundance index of selected shrubs, Rich = total number of shrub species in the site, Simps = Simpson's Diversity Index of shrub species; vol_shrub = vertical cover of shrubs visually quantified by an index ranging from 0 to 16 (more details in the text). See Table 2 for more details on variables.

Site code	landscape	N plots	HA	Hab buffer	shrub_tot	shrub_sel	Rich	Simps	vol_shrub
L-CAN	LM	15	2705.02	232.08	8.83	7.03	15	0.9	7.83
L-CAV	LM	12	2705.02	232.08	3.83	2.54	13	0.83	5.25
L-CIN	LM	25	2705.02	232.08	4.90	3.44	15	0.84	7.76
L-EAS	LM	13	2705.02	232.08	3.77	1.54	18	0.9	5.35
L-FRS	LM	13	2705.02	232.08	4.62	3.15	12	0.87	2.35
L-LGM	LM	8	2705.02	232.08	3.88	1.75	12	0.88	5.88
L-MAN	LM	25	2705.02	232.08	6.02	3.76	16	0.9	8.66
L-OTC	LM	8	2705.02	232.08	4.38	2.25	11	0.87	11.5
L-RIS	LM	15	2705.02	232.08	3.90	2.03	13	0.84	7.12
L-SUE	LM	13	2705.02	232.08	4.15	2.77	13	0.8	4.81
S-BAC	SA	18	6.85	1.49	8.03	3.47	20	0.9	9.28
S-GUA	SA	14	178.98	28.81	9.39	4.79	19	0.92	8.82
S-INF	SA	14	3.55	2.14	6.96	4.25	16	0.88	7.25
S-PAS	SA	5	1.33	4.24	7.90	4.9	15	0.91	8.45
S-PIS	SA	9	19.09	8.04	7.67	3.67	18	0.91	8.67
S-PRO	SA	6	1.98	17.11	6.42	3.17	16	0.9	6.17
S-RIC	SA	7	2.02	2.69	7.21	4.14	16	0.89	10.86
S-SCR	SA	5	2.37	0.00	7.10	2.2	13	0.89	8.1
S-SPU	SA	2	0.44	5.67	9.50	4.25	12	0.88	9.25
S-STA	SA	3	0.62	2.34	8.00	3.5	15	0.9	8.83
S-TAL	SA	5	2.62	4.83	7.78	4.07	15	0.9	6.42
V-FOR	VT	23	5.72	1.14	7.73	5.91	19	0.91	6.72
V-GDG	VT	11	1.2	1.75	11.19	8.22	15	0.89	13.25
V-GRA	VT	31	233.91	70.38	10.19	7.8	18	0.9	12.21
V-JAM	VT		3.8	0.00	9.13	6.38	13	0.88	9.75
V-MOL	VT	16	2.87	5.15	8.30	5.06	19	0.91	8.15
V-PRI	VT	13	1.74	0.00	10.82	7.35	19	0.91	9.79
V-QNC	VT	29	22.03	0.00	11.20	6.95	21	0.93	7.28
V-RSV	VT		21.5	0.00	8.54	7.08	13	0.88	12.08
V-SCO	VT	18	2.55	0.00	9.86	7.28	15	0.88	10.31

Table 2. Patch size, isolation and quality variables used as explanatory variables in models. Habitat quality variables were measured in quadrat plots (10 m^2). 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 an asterisk.

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: *Crataegus spp.*, Corylus avellana*, Cornus mas*, Euonymus europeaus*, Ligustrum vulgare*, Prunus spinosa*, Rosa canina*, Rubus spp.*, Ruscus aculeatus*, Paliurus spina-christi, Ginestra, Sambucus nigra, Lonicera spp., Pistacia lentiscus, Phillyrea spp., Ilex aquifolium, Rubia peregrina, Smilax aspera, Viburnum spp., Clematis vitalba, Coronilla emerus, Bryonia dioica, Mespilus germanica, Asparagus acutifolius, Hedera helix, Prunus avium, Laurus nobilis*
	shrub_sel	Sum of the cover of the shrub species (with asterisk) 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 visually quantified by an index ranging from 0 to 16

2.1.4. 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 hectares (6 x 6 grids with nest-boxes 40 meters apart) in all sites, with the exception of patches too small or too irregular in shape to accommodate a standard grid (Table 1, Figure 2). 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). A distance of 40 meters was selected because several nest-boxes may then be included in an individual's home-range (Amori et al. 2008), 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 2006). Wooden nest-boxes (average size 18x18x21 cm) had a standard entrance hole (3 cm in diameter) and were positioned on trees at a height of 1.5-2 m (Amori et al. 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 previous 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 (Amori et al. 2008, Juškaitis 2008) and tend to move to other nest-boxes following marking (Morris et al. 1990). 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 share nest-boxes through most of the year (Amori et al. 2008). Nest-boxes are used by males, females, adults and juveniles (Morris et al. 1990), suggesting that all individuals are potentially able to access them. I cannot exclude, however, that a part of the population never enters the boxes; such possible un-detected part of the population may vary depending on the abundance of natural nests. For this reason, abundance of individuals captured with nest-boxes should be considered as a population index rather than an estimate.

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; Amori et al. 2008) and individually marked by means of PIT tags (Biomark 8x2 mm 134.2 KHz ISO; 2010) or ear tags (Michel suture clips 11x2 mm; 2011-2012). PIT tags were only used on individuals weighing more than 13 g; smaller individuals were marked by fur-clipping (as this marking method is temporary and not individual, fur-marked individuals were not used for capture-mark-recapture analyses). Before PIT-tagging, individuals were anesthetized with a small dose of ethyl ether. After handling, dormice were released in the nest-box where they were captured. In the case of anesthetized individuals, entrance of the nest-box was closed for a few hours to allow a full awakening of the individual. PIT-tagging is a commonly used method to mark small mammals (e.g. Chanin and Gubert 2011, 2012, Trout et al. 2012, Verbeylen 2012). However, for logistic and ethical reasons, in 2011 and 2012 it was preferred to use a less invasive and less expensive method (ear-tagging) which did not require anesthetizing the individuals. 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 (calculated as the minimum number of animals alive). Pups were quickly counted, and released immediately with the mother in the nest-box to minimize stress. It is known that in some cases, disturbed females may move litters to other nests. Even though the level of disturbance was kept as small as possible, I cannot exclude that a few litters were moved and counted multiple times during subsequent nest-box checks. However I consider this event unlikely.

2.1.5. Vegetation and food resource assessment

Microhabitat structure and resource abundance in each sampled grid was assessed using 100 m^2 (10 x 10 m) quadrats. The number of quadrats increased with patch size and vegetation heterogeneity (Table 1); 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, Table 2) were obtained by summing the cover of each species. I 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 (Bartolommei, unpublished data: Spearman's rho = 0.606, N = 12, $p < 0.001$) 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*; Amori et al. 2008, Juškaitis 2008), detailed in Table 2. Vertical structure of shrubs was visually quantified by an index ranging from 0 to 16. For this quantification, four vertical layers were considered, at the height of 0.5 m, 1 m, 2 m and 4 m. For each layer, it was visually quantified what percentage of shrub vegetation reached the corresponding height. A value from 0 to 4 (corresponding to percentage classes: 0%, 0.1-25%, 25.1%-50%, 50.1%-75%, 75.1%-100%) was assigned to each layer. The overall vertical structure of shrubs was obtained by summing values of all layers, obtaining an index ranging from 0 o 16. Quadrats were surveyed in spring 2011 and 2012; data from the two surveys were averaged. Following preliminary explorative analysis (univariate regressions and correlations), to reduce the number of predictors, I selected a subset of vegetation variables as habitat quality variables that are listed in Table 2 (see Table 3 for details on excluded variables).

Table 3. Microhabitat and resource abundance variables. Variables were measured in quadrat plots (100 m^2). 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 an asterisk.

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: *Quercus cerris, Quercus pubescens, Fraxinus ornus, Ulmus minor, Ostrya caripinifolia, Carpinus betulus*
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: *Crataegus spp.*, Corylus avellana*, Cornus mas*, Euonymus europeaus*, Ligustrum vulgare*, Prunus spinosa*, Rosa canina*, Rubus spp.*, Ruscus aculeatus*, Paliurus spina-christi, Ginestra, Sambucus nigra, Lonicera spp., Pistacia lentiscus, Phillyrea spp., Ilex aquifolium, Rubia peregrina, Smilax aspera, Viburnum spp., Clematis vitalba, Coronilla emerus, Bryonia dioica, Mespilus germanica, Asparagus acutifolius, Hedera helix, Prunus avium, Laurus nobilis*

I acknowledge that this study was focused on resources and did not take into account predator 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. I 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 I am therefore confident that effects of competitors were likely to have been limited.

2.1.6. Weather data

I 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).

2.1.7. Data analysis

Analyses were focused on quantifying the relationship between patch size, isolation and quality (see Table 2 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 brackets):

- population turnover: colonization and extinction (*Q1-2*, multiple season occupancy modeling);
- density of individuals (*Q3,* Generalized Linear Mixed Models on the time-series of abundance data);
- individual apparent survival (*Q4,* Cormack-Jolly-Seber Models);
- 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 (Table 4).

Table 4. Matrix of Spearman correlation coefficients of candidate predictor variables. Significant values ($p<0.05$) are in bold.

	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

For all analyses, except for Generalized Linear Mixed Models (hereafter GLMM), 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 (QAICc). Models within 2ΔAICc (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, following Zuur et al. (2009), I started with the most parameterized model (including size, isolation and habitat quality terms) and sequentially removed non-significant terms.

2.1.7.1. Population turnover (occupancy models)

I commenced analyses with occupancy modeling to determine what 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). I used multiple-season occupancy models (MacKenzie et al. 2003) fitted through the software PRESENCE (http://www.mbr-pwrc.usgs.gov/software/presence.html) to take into account imperfect detection probability (p) and to estimate colonization (gamma) and extinction (eps) 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 estimating the probability of detecting the species and thus to take into account the risk of false absences in the data. Furthermore, I stress that colonization and extinctions are *probabilities* and are estimated from detection history data after accounting for the uncertainty in detection (MacKenzie et al. 2003). Furthermore, I acknowledge that ‘extinctions’ also could be caused by emigrations of individuals to other patches. To conduct a patch-level analysis, I 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 nest-boxes 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).

I followed a multi-step approach for building models:

1) I first modeled detection probability (p) to make the subsequent estimates of psi1 (initial probability of occurrence), gamma (colonization) and eps (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 (Amori et al. 2008). I expected a decrease in detectability with increasing temperature, since in Mediterranean environments dormice tend to avoid nest-boxes in warmer weather (Amori et al. 2008). I retained the best covariates for p in the models. During this first step other parameters were kept constant.
2) I modeled colonization (gamma) and extinction (eps) probabilities as functions of patch size, isolation and quality variables (Table 2). 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), I 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 (gamma) 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, I calculated the autocovariate following (Moore and Swihart 2005) as the weighted mean of the observed occupancy values (0 or 1) of all the patches in the landscape, weighted by 1/ distance to the focal patch.

Occupancy probability in the first session (psi1) was left constant to focus on population turnover, determined by colonization and extinction events.

2.1.7.2. Index of population density

Density of individuals was modeled by fitting GLMM with a Poisson distribution (logarithmic link; Bolker et al. 2009) on the time-series of abundance (count of individuals actually captured in each site). The inclusion of grid size as an "offset" variable made abundance values equivalent to density values (Zuur et al. 2009). I stress that the dependent variable should be considered an index of population density rather than an estimate (obtained by CMR models). I followed this approach to keep the CMR analyses (detailed in the following section) the least-parameterized as possible. To increase the reliability of abundance indices on months with triple visits, I used only count data from the first visit so that in each month the sampling effort (and thus the abundance index) was consistent. Furthermore, I 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 (Amori et al. 2008). I fitted grid (N=30) as a random effect to account for autocorrelation in the data (Zuur et al. 2009). To account for over-dispersion, I 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). I 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 I focused only on abundance of selected shrubs to keep number of predictors low (Table 2).

Models were fitted using package lme4 (Bates et al. 2011) for R (release 2.15.2, R Core Team 2012).

2.1.7.3. 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). 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, I used the Cormack-Jolly-Seber model instead of more complex and parameterized models (e.g. robust design models) as CMR data required to keep parameterization as simple as possible. I 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. I then modeled survival probability (phi) as a function of patch size, isolation and quality variables (Table 2). I also tested if survival varied with individual body mass (average value, since body mass is not known when an individual is not captured) and between landscapes. I first included landscapes as a factor with three different levels (LM, VT and SA). Secondly, to test reciprocal differences between pairs of landscapes, I pooled them in pairs and tested models with only two levels (e.g. VT+SA versus LM). I used the value of QAICc to rank model since the c-hat estimate was higher than 1 (c-hat=3).

2.1.7.4. 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. I 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 2), 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).

2.2. The role of interspecific interactions

2.2.1. Study species

For this part of the work I focused on the three components of the guild of forest-dwelling ground rodents in central Italy (*A. sylvaticus*, *A. flavicollis*, *M. glareolus*). These species lie on a gradient of specialization to forest habitat and sensitivity to habitat fragmentation, with *A. sylvaticus* being the most generalist and least sensitive (Amori et al. 2008, Mortelliti et al. 2009). Several studies provided empirical evidence of potential competition between these species. *A. sylvaticus* and *A. flavicollis* have highly overlapping trophic niches, mainly constituted by tree and shrub seeds and animal items (invertebrates) (Canova 1993, Abt and Bock 1998); they also have overlapping daily activity rhythms, with a single or occasionally double peak of nocturnal activity (Greenwood 1978, Wójcik and Wolk 1985, Canova 1993). *A. flavicollis* is known to behaviorally dominate *A. sylvaticus* both in field and experimental conditions (Hoffmeyer 1973, Hoffmeyer and Hansson 1974, Montgomery 1978, Cihakova and Frynta 1996). A behavioral dominance of *A. flavicollis* is also known over *M. glareolus* (Andrzejewski and Olszewski 1963, Buchalczyk and Olszewski 1971, Kalinowska 1971), whereas there is no clear dominance hierarchy between *A. sylvaticus* and *M. glareolus* (Lambin and Bauchau 1989). Niche overlapping between *M. glareolu*s and *Apodemus* spp. is less pronounced as *M. glareolus* shows more herbivore habits, preferring items such as leaves and fruits (Abt and Bock 1998). Furthermore, *M. glareolus* has a different pattern of daily rhythms compared to *Apodemus* spp., showing multiple peaks of activity during both night and day (Wójcik and Wolk 1985, Canova 1993). However, this species tends to be more active during the day in presence of both *Apodemus* species, showing at least a certain degree of competitive interference (Andrzejewski and Olszewski 1963, Greenwood 1978). The three species are all common prey for the same set of predators (e.g. Sidorovich et al. 2010, Sunde et al. 2012, Rugiero et al. 2012), making the study system particularly suited to the scope, allowing me to focus on competitive effects.

2.2.2. Study area

The study was conducted in one of the two fragmented landscapes of central Italy (Viterbo) used for the dormouse study (see previous paragraphs) (Figure 4). Woodland fragments, constituted by mixed deciduous forest dominated by *Q. pubescens* and *Q. cerris*, were embedded in an agricultural matrix (mainly wheat fields) crossed by a network of hedgerows providing structural connectivity to habitat patches (Figure 4).

2.2.3. Experimental design and site selection

Twenty-nine wood patches were selected following a gradient in patch size and habitat structure (range 0.56 ha to 234 ha; Table 5). Patch size was measured from aerial photographs through Quantum GIS 18.0, whereas habitat structure was initially quantified by a field inspection to the sites and subsequently confirmed by more detailed measures (see following details on habitat variables). I focused on the structure of the shrub component of vegetation which is known to be very important both as a source of food (fruits, leaves, seeds) and as protection from predators (Amori et al. 2008, Buesching et al. 2008). The goal of the design was to obtain a gradient in structure non-correlated with patch size (Table 6, Figure A 1).

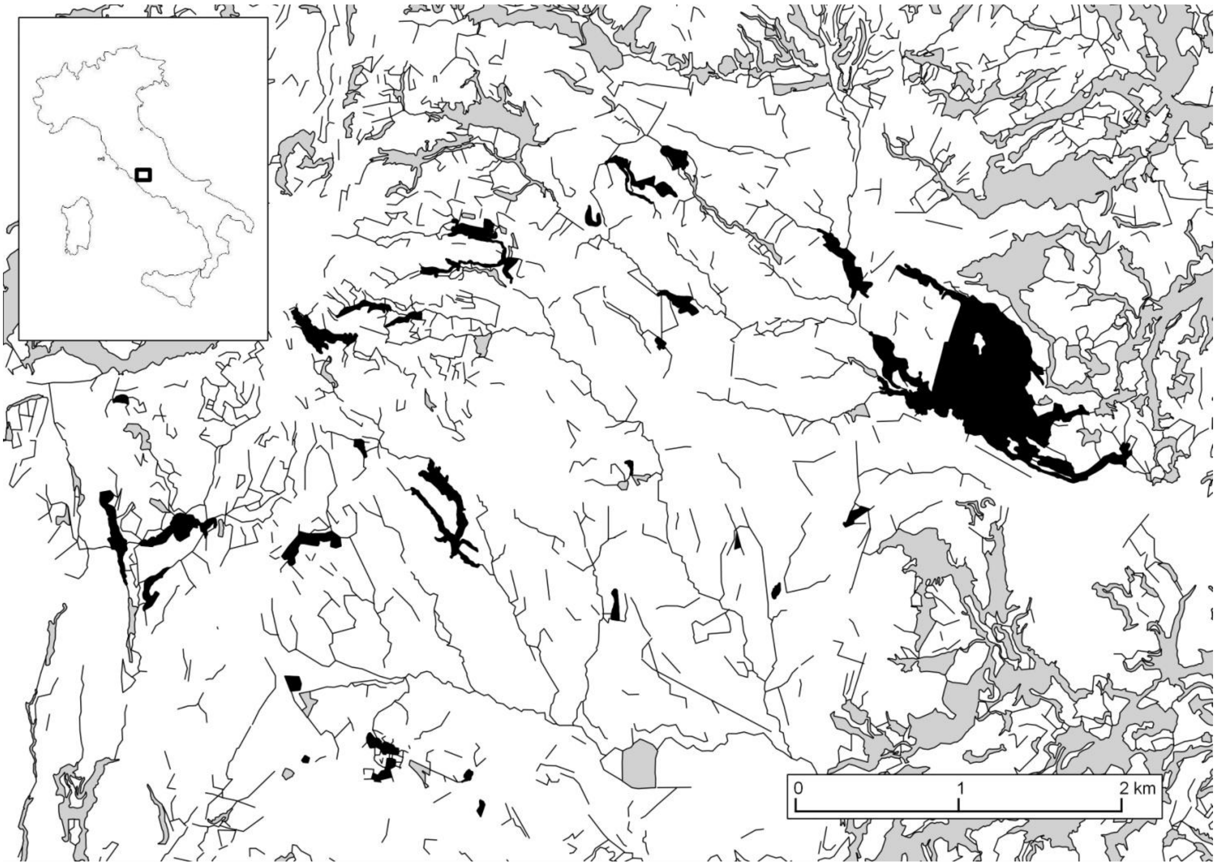


Figure 4. Study area located in central Italy. Black shapes = sampled wood fragments; grey shapes = not sampled wood fragments; white areas = agricultural matrix; lines = hedgerows.

In each habitat patch a squared trapping grid was set up (7x7 with 10 m of distance between traps; Figure 5). Where the size or shape of the patch did not allow building a regular 7x7 grid, sampled area was modified accordingly but maintaining the same trap density as regular grids (100 traps/hectare). Grids ranged from 14 to 49 trap points. Patches with grids with <49 traps were sampled entirely.

Table 5. Summary of the characteristics of 29 grids located in 29 wood patches in a fragmented landscape in central Italy. Simpson = shrubs diversity index; Shrub structure = index of vertical complexity of shrubs; Acorns Qc = biomass of *Q. cerris* acorns (g/m2); Acorns Qp = biomass of *Q. pubescens* acorns (g/m2); Patch size = size of the wood fragment (hectares); Habitat 100 and 1000 = wood cover (hectares) in a 100 or 1000 m buffer around the grid; Hedgerows 100, 900 and 1000 = total length of hedgerows (m) in a 100, 900 or 1000 m buffer around the grid.

Grid	Simpson	Shrub structure	Acorns Qc	Acorns Qp	Patch size	Habitat 100	Habitat 1000	Hedgerows 100	Hedgerows 900	Hedgerows 1000
1FA	0.87	3.25	121.38	123.20	2.26	1.50	14.55	0	7517	8615
2VO	0.91	6.63	46.78	1.75	4.38	1.38	21.17	102	13092	15189
ALB	0.86	12.50	34.83	137.27	17.21	1.91	26.18	0	10230	12682
API	0.90	13.50	58.67	0.00	2.74	2.11	6.44	0	6751	7964
BRU	0.83	13.13	256.45	44.69	5.73	1.78	20.34	75	7567	9088
CAS	0.89	7.63	258.23	12.53	14.08	3.09	31.89	0	13276	15596
CAT	0.83	2.88	0.00	145.63	12.81	1.98	21.13	0	9309	11943
CRI	0.81	8.25	0.00	113.85	0.83	0.83	3.38	35	7108	8337
CRO	0.88	11.50	0.00	316.30	0.75	0.67	1.95	202	7252	8765
FDT	0.89	12.25	137.95	262.00	9.66	1.79	21.39	0	7330	9200
FOR	0.88	7.57	13.19	19.81	5.72	1.82	6.93	91	8214	9027
GDG	0.88	12.25	0.00	0.00	1.20	1.20	6.93	71	6177	8117
GOK	0.87	8.88	0.00	106.92	1.01	1.00	4.69	0	3958	4488
GRA	0.88	10.63	236.85	0.00	233.91	3.09	195.62	0	549	1265
IUG	0.88	7.38	191.26	92.49	3.54	1.69	11.95	148	6233	6938
MIC	0.88	12.75	103.53	0.00	5.07	1.78	23.08	30	7204	9059
MOL	0.91	6.33	24.02	0.00	2.87	1.46	17.63	252	15042	17322
MOZ	0.89	13.25	303.56	2.25	11.71	2.91	36.16	16	10967	13410
PEG	0.90	9.63	0.00	0.00	1.05	1.03	7.25	0	3810	5232
PRI	0.90	8.13	69.76	5.48	1.74	1.30	6.44	67	9213	11078
QNC	0.91	4.50	106.08	0.00	22.09	2.21	21.92	0	4073	5645
RIG	0.91	8.88	21.39	25.42	10.64	2.11	10.71	46	10385	13458
SCA	0.84	11.63	19.18	2133.93	0.56	0.56	11.50	0	3902	5815
SCO	0.89	5.13	78.77	0.00	2.55	1.32	2.55	108	5954	7694
TAN	0.90	7.63	149.90	157.94	13.65	2.97	23.05	0	5763	7080
TES	0.87	8.86	39.78	76.77	1.20	1.05	1.95	75	6979	9029
VER	0.88	9.63	190.97	365.49	2.85	1.63	20.87	44	5970	6929
VIP	0.89	4.43	56.46	156.07	1.46	1.34	50.64	71	5976	8307
YEA	0.90	6.13	0.00	655.73	4.72	2.07	14.36	119	7824	8964

Table 6. Spearman's correlation coefficients between pairs of predictors. Simpson = shrubs diversity index; Shrub structure = index of vertical complexity of shrubs; Acorns Qc = biomass of *Q. cerris* acorns (g/m2); Acorns Qp = biomass of *Q. pubescens* acorns (g/m2); Patch size = size of the wood fragment (hectares); Habitat 100 and 1000 = wood cover (hectares) in a 100 or 1000 m buffer around the grid; Hedg 100, 900 and 1000 = total length of hedgerows (m) in a 100, 900 or 1000 m buffer around the grid. Significant ($p < 0.05$) correlations are in bold.

	Shrub structure	Acorns Qc	Acorns Qp	Patch size	Habitat 100	Habitat 1000	Hedg 100	Hedg 900	Hedg 1000
Simpson	-0.205	0.120	**-0.393**	0.233	0.320	0.145	0.156	0.156	0.159
Shrub structure		0.136	-0.100	-0.033	0.005	-0.001	-0.215	-0.083	-0.014
Acorns Qc			-0.147	**0.534**	**0.550**	**0.574**	-0.166	0.038	0.059
Acorns Qp				-0.164	-0.158	0.002	-0.039	-0.007	-0.032
Patch size					**0.922**	**0.724**	-0.281	0.319	0.310
Habitat 100						**0.655**	-0.321	0.266	0.221
Habitat 1000							-0.367	0.152	0.190
Hedg 100								0.297	0.266
Hedg 900									**0.960**

2.2.4. Sampling protocol

Demographic data were collected following a capture-mark-recapture (hereafter CMR) protocol. Twelve trapping sessions were conducted, one every other month from April 2011 to February 2013. During each session grids were activated for three consecutive nights. Such timing followed Pollock's (1982) robust design: between consecutive sessions populations were considered open, i.e. births, deaths, immigrations and emigrations were considered likely given the biology of these rodents. During the three consecutive nights within a session, instead, populations were considered closed. Closure assumption in each session was confirmed by Closure Tests by Stanley and Burnham (1999) and Otis et al. (1978) ($p > 0.05$), both implemented in CloseTest software (Stanley and Richards 2004).

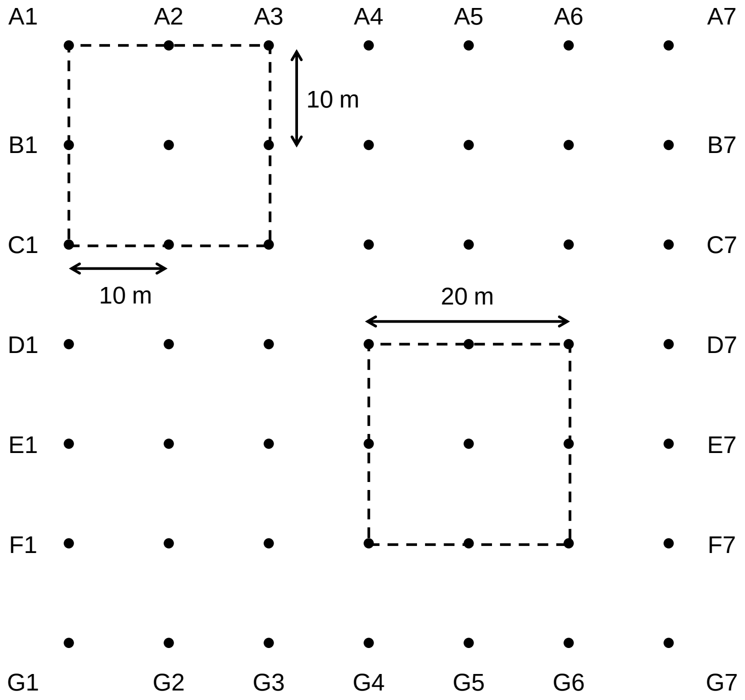


Figure 5. Scheme of a regular sampling grid (0.36 ha). Dots represent trap locations and are individually identified by an alphanumeric code (A1, A2, A3, etc); dashed lines represent quadrats used for vegetation sampling.

Trapping was conducted with a mix of Longworth and Sherman live traps, which were distributed homogeneously with a ratio Longworth:Sherman = 1:5 in all grids to ensure an homogeneous sampling effort per area unit.

Traps were baited with a mix of sunflower seeds, peanut butter and apple; trap bedding was provided for thermoregulation; traps were checked daily early in the morning. Trapped individuals were identified to species, sexed, aged, weighed and individually marked by toe-clipping (or, if already marked, individually identified); reproductive status was assessed by observing external sexual characters. Toe-clipping is a commonly-used method to mark small mammals and several studies found that it does not affect individual vital parameters (such as body weight, survival, etc.) and recapture rate (Ambrose 1972, Fairley 1982, Pavone and Boonstra 1985, Korn 1987, Wood and Slade 1990, Braude and Ciszek 1998, McGuire et al. 2002, Schradin and Pillay 2005, Fisher and Plomberg 2009). In this study there was the need to permanently mark a high number of individuals while avoiding tag-losses. For these reasons, toe-clipping was preferred to other commonly-used marking methods, such as PIT-tagging (an expensive and moderately invasive method which requires anesthetizing animals, not applicable to several thousands of individuals) or ear-tagging (subject to tag loss and known to cause an increase in tick infestation rates; e.g. Ostfeld et al. 1993). A small sample of ear tissue was also collected for molecular confirmation of *Apodemus* spp., conducted following Michaux et al. (2001). Molecular analyses were performed on a sub-sample of individuals having morphological characteristics (e.g. intermediate fur color or body size) which did not allow a reasonably certain identification of species. Individuals were disinfected and released at the capture site.

2.2.5. Habitat and food resource variables

The quality of habitat is a crucial factor affecting the viability of species in fragmented landscapes (Armstrong 2005, Mortelliti et al. 2010). The majority of fragmentation studies measure the quality of habitat through gross proxies; however, such an approach may lead to biased results (Mortelliti et al. 2010). In this study I tried, where possible, to measure key habitat and resource variables directly. In particular I focused on shrubs and on acorns, which are known to be a crucial resource for the three target species (Amori et al. 2008, Harris and Yalden 2008).

The protocol for vegetation surveys was similar to the protocol used for the hazel dormouse (see previous paragraphs) with a few differences due to the smaller size of sampling grids.

Habitat features of each grid were sampled in two squared 400mq-plots (hereafter quadrats) systematically located within each grid (Figure 5). Each quadrat was subdivided in four 100mq-subplots (analogous to plots used in the study on the hazel dormouse, see paragraph 2.1.5), where the cover of each shrub species was measured through the modified Braun-Blanquet scale (cover classes: 0%, 0.1-25%, 25-50%, 50%-75%, 75-100%). I then summarized the cover of all species through the Simpson's Index of diversity to obtain a measure of shrubs abundance-diversity in each grid. Vertical structure of shrubs was also measured; it was visually quantified through an index ranging from 0 (absence of shrubs in all vertical layers) to 16 (maximum vertical complexity). For more details on the method, see paragraph 2.1.5. Vegetation assessment was conducted in spring 2012.

Further, productivity of oaks was measured by quantifying the biomass of acorns fallen on the ground. Under each productive oak (*Q. pubescens* and *Q. cerris*) within the quadrats two circular sub-plots were located (0.5 m of radius) where all acorns found on the ground were collected, counted and weighed. The size of the canopy of each productive oak was also estimated by measuring the two main axes and then calculating the area of the ellipse. A small sample (10% in each plot) of acorns was subsequently desiccated at 70C° for 48 hours to obtain the plot-specific dry/wet biomass ratio, which was then used to obtain an estimate of the total dry acorns biomass per area unit in each plot. Biomass values were multiplied by the area of the canopy of the corresponding oaks and then used to estimate the total production in each grid. Acorn sampling was conducted in Autumn 2011 and 2012 in the period immediately following the fall of acorns. As the analysis of inter-annual differences in acorn production was beyond the scope of this work, I averaged data from the two years to obtain a mean index of productivity.

2.2.6. Landscape variables

Previous literature has shown how species respond to the amount and configuration of habitat at different scales (Wiens 1989, Holland et al. 2004, Fahrig 2013, Thornton and Fletcher 2013).

I conducted a series of preliminary analyses to select the spatial scales with the strongest effect on the abundance of each target species, following the approach suggested by (Fahrig 2013).

Habitat amount and connectivity were measured in ten concentric buffers around the grids, with radius ranging from 100 m to 1000 m. In each buffer, habitat amount was measured as the total cover of woods and connectivity was measured as the total length of hedgerows. Hedgerows provide connectivity in fragmented landscapes for the three species (e.g. Zhang and Usher 1991, Kotzageorgis and Mason 1997). I fitted generalized linear mixed models (Poisson distribution, log link) to model the series of estimated individual abundances of *A. sylvaticus*, *A. flavicollis* and *M. glareolus* (29 sampling grids and 12 sampling sessions) as function of habitat amount and connectivity at the different scales (one model for each variable for each scale). I used grid size as an offset variable, and grid ID and sampling session as random factors.

For each variable (Habitat or Hedgerows) I selected the spatial scale corresponding to the model with the lowest AICc (Akaike's Information Criterion). Results are provided below in Tables 7 and 8. I retained the selected scales for all of the following analyses.

Table 7. Ranking of GLMM (Poisson distribution, log link) models on individual abundance of the three species as a function of wood cover in a series of concentric buffers from 100 m to 1000 m around the grids. Habitat = total wood cover (hectares, $\log_{10}$-transformed); K = number of parameters; AICc = Akaike's Information Criterion; AICcWgt = Akaike's weight; LL = log-likelihood.

Model	K	AICc	Delta AICc	AICcWgt	LL
A. sylvaticus					
Habitat 1000	4	2665.91	0	0.55	-1328.12
Habitat 900	4	2668.86	2.95	0.13	-1329.6
Habitat 700	4	2669.56	3.65	0.09	-1329.95
Habitat 800	4	2670.08	4.17	0.07	-1330.21
Habitat 600	4	2670.24	4.33	0.06	-1330.29
Habitat 500	4	2671.49	5.58	0.03	-1330.91
Habitat 400	4	2672.67	6.76	0.02	-1331.5
Habitat 100	4	2672.72	6.81	0.02	-1331.53
Habitat 200	4	2673.12	7.21	0.01	-1331.73
constant	3	2673.62	7.71	0.01	-1333.33
Habitat 300	4	2673.73	7.82	0.01	-1332.03
A. flavicollis					
Habitat 100	4	3266.43	0	0.53	-1628.38
Habitat 200	4	3267.77	1.34	0.27	-1629.05
Habitat 300	4	3271.43	5	0.04	-1630.88
Habitat 400	4	3272.05	5.62	0.03	-1631.19
Habitat 900	4	3272.91	6.48	0.02	-1631.62
Habitat 500	4	3273	6.57	0.02	-1631.67
Habitat 800	4	3273.08	6.65	0.02	-1631.71
Habitat 1000	4	3273.17	6.74	0.02	-1631.75
Habitat 600	4	3273.28	6.85	0.02	-1631.81
Habitat 700	4	3273.46	7.03	0.02	-1631.9
constant	3	3274.88	8.45	0.01	-1633.96
M. glareolus					
constant	3	2054.75	0	0.26	-1023.85
Habitat 100	4	2057.12	2.37	0.08	-1023.65
Habitat 1000	4	2057.12	2.37	0.08	-1023.65
Habitat 900	4	2057.23	2.48	0.08	-1023.7
Habitat 500	4	2057.23	2.48	0.08	-1023.71
Habitat 200	4	2057.26	2.51	0.07	-1023.72
Habitat 800	4	2057.32	2.57	0.07	-1023.75
Habitat 600	4	2057.36	2.61	0.07	-1023.77
Habitat 700	4	2057.37	2.62	0.07	-1023.77
Habitat 400	4	2057.39	2.64	0.07	-1023.78
Habitat 300	4	2057.46	2.71	0.07	-1023.82

Table 8. Ranking of GLMM (Poisson distribution, log link) models on individual abundance of the three species as a function of total length of hedgerows in a series of concentric buffers from 100 m to 1000 m around the grids. Hedgerows = total length of hedgerows (m); K = number of parameters; AICc = Akaike's Information Criterion; AICcWgt = Akaike's weight; LL = log-likelihood.

Model	K	AICc	Delta AICc	AICcWgt	LL
A. sylvaticus					
constant	3	2673.62	0	0.23	-1333.33
Hedgerows 1000	4	2675.02	1.4	0.11	-1332.67
Hedgerows 900	4	2675.14	1.52	0.11	-1332.74
Hedgerows 800	4	2675.35	1.73	0.10	-1332.84
Hedgerows 700	4	2675.89	2.27	0.07	-1333.11
Hedgerows 100	4	2676.04	2.42	0.07	-1333.19
Hedgerows 600	4	2676.09	2.47	0.07	-1333.21
Hedgerows 500	4	2676.11	2.49	0.07	-1333.22
Hedgerows 400	4	2676.18	2.56	0.06	-1333.26
Hedgerows 300	4	2676.27	2.65	0.06	-1333.3
Hedgerows 200	4	2676.32	2.7	0.06	-1333.33
A. flavicollis					
Hedgerows 900	4	3273.09	0	0.18	-1631.71
Hedgerows 800	4	3273.3	0.21	0.16	-1631.82
Hedgerows 1000	4	3273.59	0.5	0.14	-1631.96
Hedgerows 700	4	3273.82	0.73	0.12	-1632.08
Hedgerows 600	4	3274.47	1.38	0.09	-1632.4
Hedgerows 400	4	3274.67	1.58	0.08	-1632.5
Hedgerows 500	4	3274.81	1.72	0.07	-1632.57
constant	3	3274.88	1.79	0.07	-1633.96
Hedgerows 300	4	3276.35	3.26	0.03	-1633.34
Hedgerows 200	4	3276.86	3.77	0.03	-1633.6
Hedgerows 100	4	3277.04	3.95	0.02	-1633.69
M. glareolus					
Hedgerows 100	4	2053.86	0	0.30	-1022.02
constant	3	2054.75	0.89	0.19	-1023.85
Hedgerows 200	4	2056.23	2.37	0.09	-1023.2
Hedgerows 300	4	2056.82	2.96	0.07	-1023.5
Hedgerows 400	4	2057.17	3.31	0.06	-1023.68
Hedgerows 500	4	2057.47	3.61	0.05	-1023.83
Hedgerows 900	4	2057.51	3.65	0.05	-1023.85
Hedgerows 600	4	2057.51	3.65	0.05	-1023.85
Hedgerows 700	4	2057.51	3.65	0.05	-1023.85
Hedgerows 800	4	2057.52	3.66	0.05	-1023.85
Hedgerows 1000	4	2057.52	3.66	0.05	-1023.85

2.2.7. Data analysis

Below I present the rationale and design of the analyses. Specific details on each analysis are provided in the subsequent paragraphs.

Objective 1) To identify the main factors affecting the distribution of each species I tested the effect of habitat and resource variables (Simpson's Index of shrubs diversity, index of shrub vertical structure, acorn biomass) and landscape variables (habitat cover and connectivity within the buffers) on population abundance of each species. The overarching goal of this analysis was to look for evidence of spatial segregation due to competitive interactions. A summary of all tested predictors is provided in Table 9.

Objective 2) I then tested the effect of the density of competitor species (estimated number of individuals/grid area) on a set of parameters selected as representative of the performance of individuals and populations (survival, recruitment, reproduction, body mass, population density). To take into account a possible time-lag in the response to competitors, I conducted preliminary analyses to test the effect of competitors' density both in the same and in the previous session. I found that for all the biological parameters there was a stronger effect with a lag of 1 session (e.g. the effect of the abundance of *A. flavicollis* on the survival of *A. sylvaticus* was stronger when the predictor was the abundance of *A. flavicollis* in the previous trapping session). Consequently I here report results relative to the abundance of competitors in the previous session.

For all analyses I followed the Information Theoretic Approach to model selection, ranking models according to the Akaike's information criterion corrected for finite samples (AICc). Among each set of hypothesis, I selected the model with the lowest AICc as the most supported.

CMR analyses were conducted with program MARK (White and Burnham 1999); for all other analyses I used software R (R Core Team 2013), packages: Hmisc (Harrell 2013), lme4 (Bates *et al.* 2013), AICcmodavg (Mazerolle 2013), languageR (Baayen 2013).

Table 9. Summary of habitat (Simpson, Shrub structure, Acorns Qc, Acorns Qp) and landscape (Habitat 100, Habitat 1000, Hedgerows 100, Hedgerows 900, Hedgerows 1000) variables used as predictors for abundance, survival, recruitment, reproduction and body mass of *A. sylvaticus*, *A. flavicollis*, *M. glareolus*. Description, units and descriptive statistics (minimum, maximum, mean value; N=29) for each variable are provided.

Variable	Description	Min	Max	Mean
Simpson	Simpson's Index of shrub diversity	0.81	0.91	0.88
Shrub structure	Index of shrub vertical complexity	2.88	13.50	8.80
Acorns Qc	Biomass of *Q. cerris* acorns (g/m^2)	0.00	303.56	86.86
Acorns Qp	Biomass of *Q. pubescens* acorns (g/m^2)	0.00	2133.93	170.88
Habitat 100	Total cover of woods in a 100 m buffer around the grid (hectares)	0.56	3.09	1.71
Habitat 1000	Total cover of woods in a 1000 m buffer around the grid (hectares)	1.95	195.62	22.16
Hedgerows 100	Total length of hedgerows in a 100 m buffer around the grid (m)	0.00	252.48	53.52
Hedgerows 900	Total length of hedgerows in a 900 m buffer around the grid (m)	548.78	15041.75	7504.25
Hedgerows 1000	Total length of hedgerows in a 1000 m buffer around the grid (m)	1264.69	17322.20	9180.61

2.2.7.1. Population abundance

I estimated population size in each grid and session by fitting CMR models (robust design Pradel models with Huggin's parameterization). To increase the accuracy of abundance estimates, I modeled capture and recapture probabilities as function of sampling effort (number of active traps in the grids, i.e. to account for traps inactivated by animals, weather, etc.) and season variables (temperature and mm of rain during sampling). In this way I could take into account possible variation in trapping efficiency during the year and between sites (Smith et al. 1975).

I fitted generalized linear mixed models (hereafter GLMM) with Poisson distribution (log link) to model the time-series of estimated individual abundances (29 sites and 12 sampling sessions) as function of habitat, food resources and landscape variables (Table 9). I used grid size as an offset variable to take into account sampled area (ranging from 0.18 ha to 0.52 ha), so that the response variable corresponded to the density of individuals per area unit (Zuur et al. 2007). I also used grid and sampling session as random factors to account for the non-independence of data from the same site and during the same period of the year.

After identifying the main environmental factors influencing the abundance of each species, I retained the best model and added the effect of the density of the two competitor species.

2.2.7.2. Survival and recruitment

I fitted CMR models (robust design Pradel models with Huggin's parameterization) to test the effect of competitors' density on survival and recruitment probability. In this context, survival is intended as "apparent" survival, including both actual survival and emigration and corresponding to the probability that an individual remained in the sampled area from one session to the following one. Similarly, recruitment represents the rate of production of new individuals from one session to the following one (= number of new individuals at time t per individuals at t-1) and it includes individuals actually born in the study area and immigrated (Amstrup et al. 2006).

2.2.7.3. Body mass

I fitted linear mixed models (hereafter LMM) to test the effect of competitors' density on individual body mass, an index of body conditions (e.g. Montgomery 1981, Fasola and Canova 2000). I chose to use body mass, instead of more complex indexes for body condition taking into account skeletal measures of body size (e.g. scaled mass index; Krebs and

Singleton 1993, Schulte-Hostedde et al. 2005, Peig and Green 2009) for several reasons. First, the only measure of body size that it was possible to measure on awake animals was the hind foot length. Following preliminary analyses conducted on a sample of dead individuals, I found that hind foot length was not strictly correlated with overall body size. Furthermore, in order to rule out the effect of individual growth, only adult individuals were used for the analysis, excluding pregnant females. I also used session and individual ID as random factors to control for non-independence of multiple data from single individuals. This way, the possible effect of seasonality in body condition and intrinsic differences between individuals should have been ruled out. I did not use sampling grid as a random factor as preliminary analyses showed that it was redundant with individual ID (explained variance ~ zero).

2.2.7.4. Reproduction

I fitted GLMMs with binomial distribution (logit link) to test the effect of competitors on the probability of reproduction of females (e.g. Montgomery 1981, Fasola and Canova 2000), which reflects a possible inhibition of reproduction in presence of competitors. Response variable was coded as 1 when a female was in reproductive status (pregnant or in lactation) and as 0 when it was not reproductive; only adult females were included in this analysis. As for body mass, I used session and individual ID as random factors.

2.3. Perceptual range and movement ability

2.3.1. Study area

This part of the study was carried out in a third fragmented landscape of central Italy (different from those used for dormice and competition studies) from March to June 2012. The area is characterized by residual mixed oak (*Quercus* spp.) forest fragments embedded in an agricultural matrix (residual wood cover < 10%; agricultural fields cover > 80%) (Figure 6; see Figure A 2 and Figure A 3 for some pictures of the study area). The majority of fields are conventionally managed and cultivated with cereals, especially wheat. A small proportion of fields are periodically left uncultivated. Spring wheat is sown in February-March and harvested in July, when it reaches its maximum height (about 120 cm).

Experiments were carried out in a bare field, a grass field and a wheat field at three maturation stages (20 cm, 60 cm and 120 cm in height). All the studied fields were characterized by completely flat terrain. Wheat plants were cultivated along rows spaced approximately 20 cm. Within the same line, plants were closer (1.5-2 cm) but distant enough not to create a barrier for small rodents, which could easily pass through lines in any direction (as testified by the multiple crossings observed during a pilot experiment). In the grass field the distribution of herbaceous plants did not follow any regular pattern.

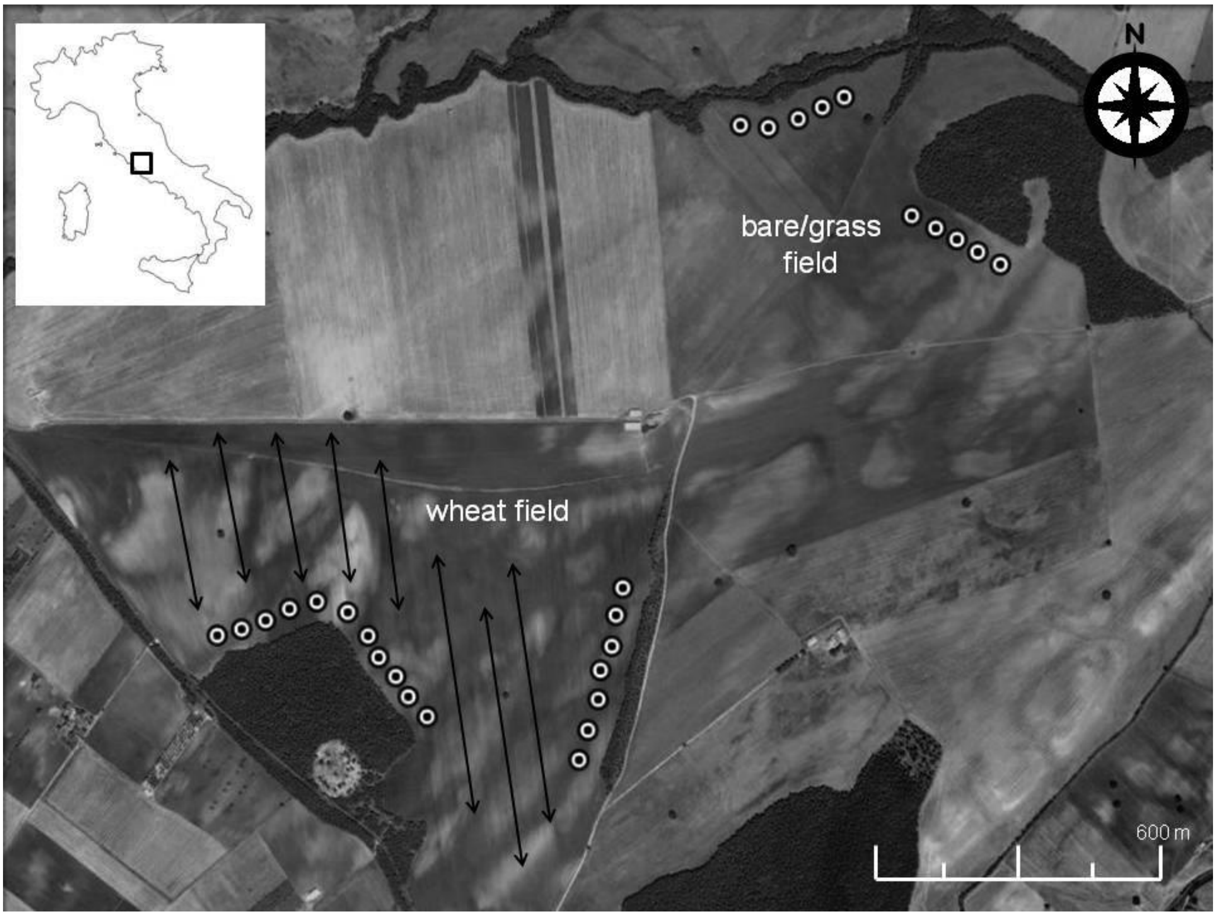


Figure 6. Study area located in central Italy, including a wheat field and a bare/grass field (depending on the period of the year). Dots represent release points along the edge of wood fragments. Black arrows represent the direction of wheat plantation rows.

2.3.2 Experimental protocol and data collection

Experiments consisted in releasing individuals (*A. flavicollis, A. sylvaticus, M. glareolus*) in the fields in order to observe their movements through the matrix. I assumed that when released in an hostile open matrix, individuals would go toward the wood as soon as possible, with their movements and orientation revealing their ability to perceive it (Zollner and Lima 1997). I considered this assumption valid also for the habitat generalist *A. sylvaticus,* which is known to prefer woodland habitat due to predation risk in open environment (Tattersal et al. 2001, Amori et al. 2008).

Individuals were first released in the bare field (March) at progressive distances from the target habitat patch (20 m, 40 m and 100 m; Table 21) and in a wheat field at three maturation stages (respectively in March, May and June; see Figure A 4 for an example). At the earlier maturation stage individuals were released at 40 m of distance from the wood; since none of the species perceived the wood at this distance (see Results chapter), in the following (more obstructed) maturation stages I reduced distances to 20 m in order to detect a possibly lower perceptual range. In the case of *A. flavicollis*, due to a higher number of captured individuals, in the intermediate wheat field I was able to extend the experiment at the distance of 10 m (Table 21), whereas for the other two species I did not obtained enough individuals. Individuals were also released in the grass field (May; 60 cm in height) at 20 m of distance from the wood. For *A. flavicollis* I extended the experiment at the distance of 10 m (Table 21). In order to vary the direction of the wheat plantation rows relative to the edge of the wood and the position of the target woods relative to the release points, two different sides of the fields adjacent to different habitat patches were used for the experiment.

Individuals were captured with Sherman and Longworth traps. In order to avoid homing behavior (Zollner and Lima 1997), animals were captured in forest fragments distant more than 13 Km from the release landscape. The landscape where species were captured was similar to that of release in terms of agricultural matrix composition, type and cover of residual forest fragments. Only healthy looking adult and sub-adult (following Gurnell and Flowerdew, 2006) individuals were used for the experiment. Field determination of the two *Apodemus* species was confirmed through molecular analysis following Michaux et al. (2001).

Individuals were kept in cages and fed for a maximum of 72 hours before being released; each individual was released only once. Release mechanism was designed to reduce the observer-induced disturbance on animals' behavior. It was constituted by a glass jar (10 x 10 x 15 cm; Figure A 5) with a wooden lid connected to a 20 meters long string. Individuals were put into the jars immediately before the release and remotely released by pulling the string. The transparent walls of the jars increased animals’ propensity to abandon the mechanism, while the opening situated on the top allowed not influencing their initial movement in any direction. Immediately before being placed in the cases individuals were disoriented by gently spinning their cage (covered with a blanket) and then marked with fluorescent powders (pigments F002, F008, F016, F019 Abralux Colori Beghè srl, Italy; Figure A 5, A 6, A 7). Release occurred within a few minutes; field workers abandoned the area minimizing disturbance. Experiments were carried out during night time with moonlight (moon phase between 70 and 100 %) in order to maximize perceptual ability of the individuals, avoiding windy and cloudy nights in order to reduce confounding factors (Prevedello et al. 2011). Individuals released in the same night were spaced along the edge of the wood at least 50 m from the others in order to reduce possible intersection of their trajectories.

Few hours after the release animal routes were tracked by illuminating powder fallen from each individual with ultra-violet light (Figure A 7), in accordance with standard procedures (Zollner and Lima 1997). Tracks were followed until no additional powder was detected or until the reaching of the wood. Individual paths were recorded through GPS devices.

2.3.3. Data analysis

Unlike other authors (Prevedello et al. 2011), who often analyze only the first few meters of each path to determine the initial orientation of individuals, I chose to analyze entire paths in order to understand if, when released at certain fixed distances, individuals were likely to reach the wood or not. Therefore I subdivided each individual route in segments (at least 1 m long) and then I calculated weighted mean vectors of each route, with segments lengths as weights. Following Zollner and Lima (1997) perceptual range was determined as the maximum distance at which released individuals showed to perceive the forest fragment, going directly towards it (V-test for the significance of mean angles around a specified direction). I also tested if, in the grass field, individuals were significantly oriented towards any direction (Hotelling's second order test on mean vectors of individual paths; Zar 1998). Then I tested whether individuals followed plantation rows while moving through the wheat field (V-test with mean angles as axial data; (Prevedello and Vieira 2010). Analyses were performed using Oriana 4 software (Kovach Computing Services).

3. RESULTS

3.1. Population and individual-scale responses to patch size, isolation and quality.

During the three years of the study a total of 626 captures of hazel dormice were completed (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 landscape (Figure 7; Table A 1). Peaks in capture success occurred during spring and late autumn. The majority of dormice were captured in the Lamone landscape (64 % of captures), followed by Viterbo (34 % of captures) and Sabina (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).

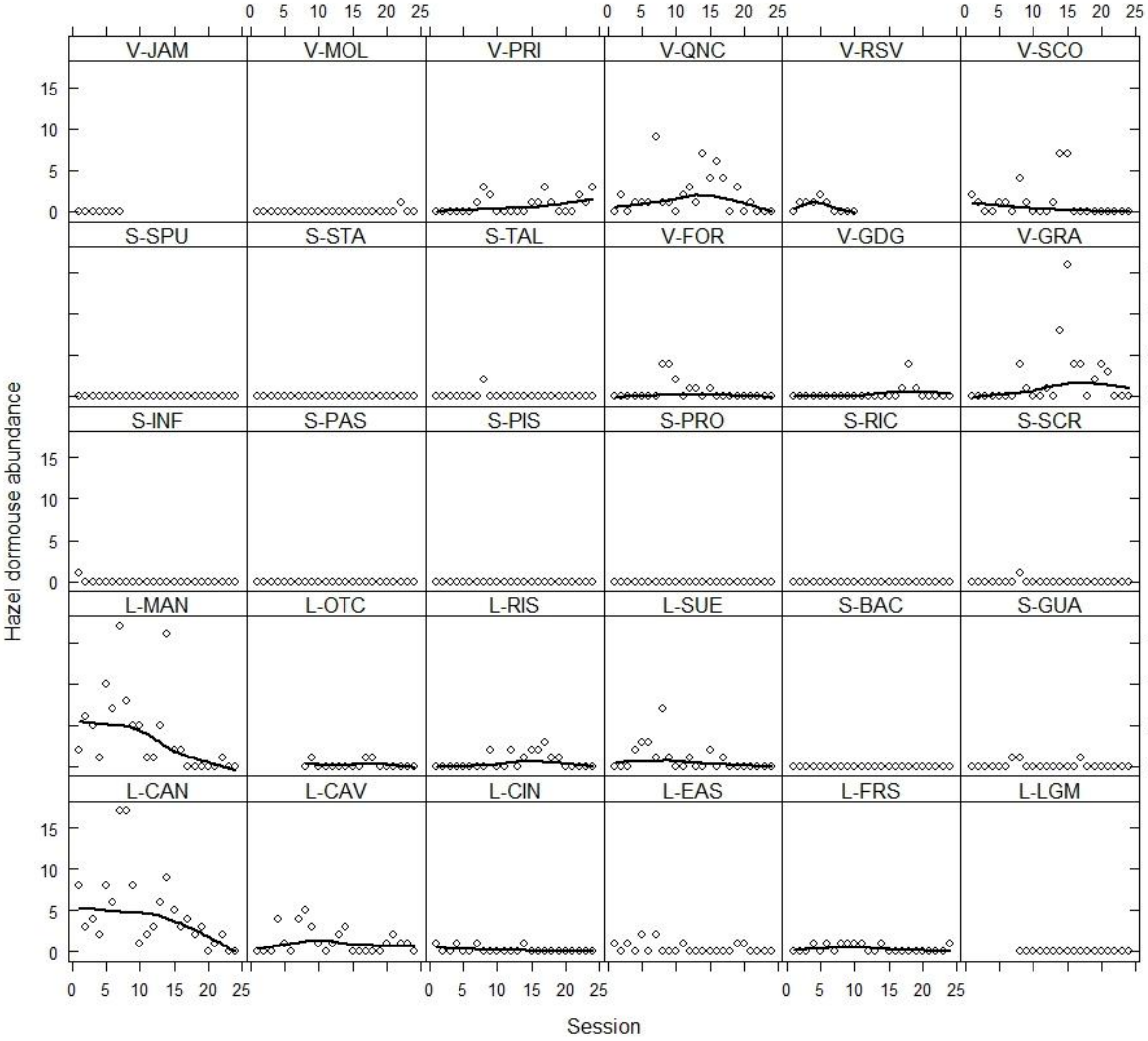


Figure 7. Series of abundance (raw number of individuals captured) in each of the study sites. The first letter of the abbreviated code of each site specifies the landscape L = Lamone landscape, V= Viterbo landscape, S= Sabina landscape. A list of the main characteristics of each site is provided in Table 1. A smoothing line (loess) was added to facilitate interpretation. I 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.

3.1.1. Occupancy models

Only one model was included in the best model set (see Table 10 for a list of top ranking models). According to the first ranked model (Table 11), 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 11).

Table 10. List of top ranked occupancy models, ranked according to AIC_C (only models with 4 ΔAIC_C are included. Covariates are in brackets (see Table 2 for more details on variables). 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.

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

Table 11. Parameter (β) estimates from the best occupancy model according to AIC_C. Estimate and standard errors (SE) are reported for constant and covariate parameters (see Table 2 for details on the covariates). Psi = presence probability, gamma = colonization probability, eps = extinction probability, P = detection probability. shrub_sel = abundance index of selected shrubs, logHA = logarithm of patch size in ha; T_ave= mean temperature during sampling.

β	estimate	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

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, Table 11). Models including patch quality or its interaction with patch size were not included in the top model set (Table 10).

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 11). Patch isolation did not influence either extinction or colonization. Expected values of extinction and colonization probability of sampled patches are reported in Figure 8.

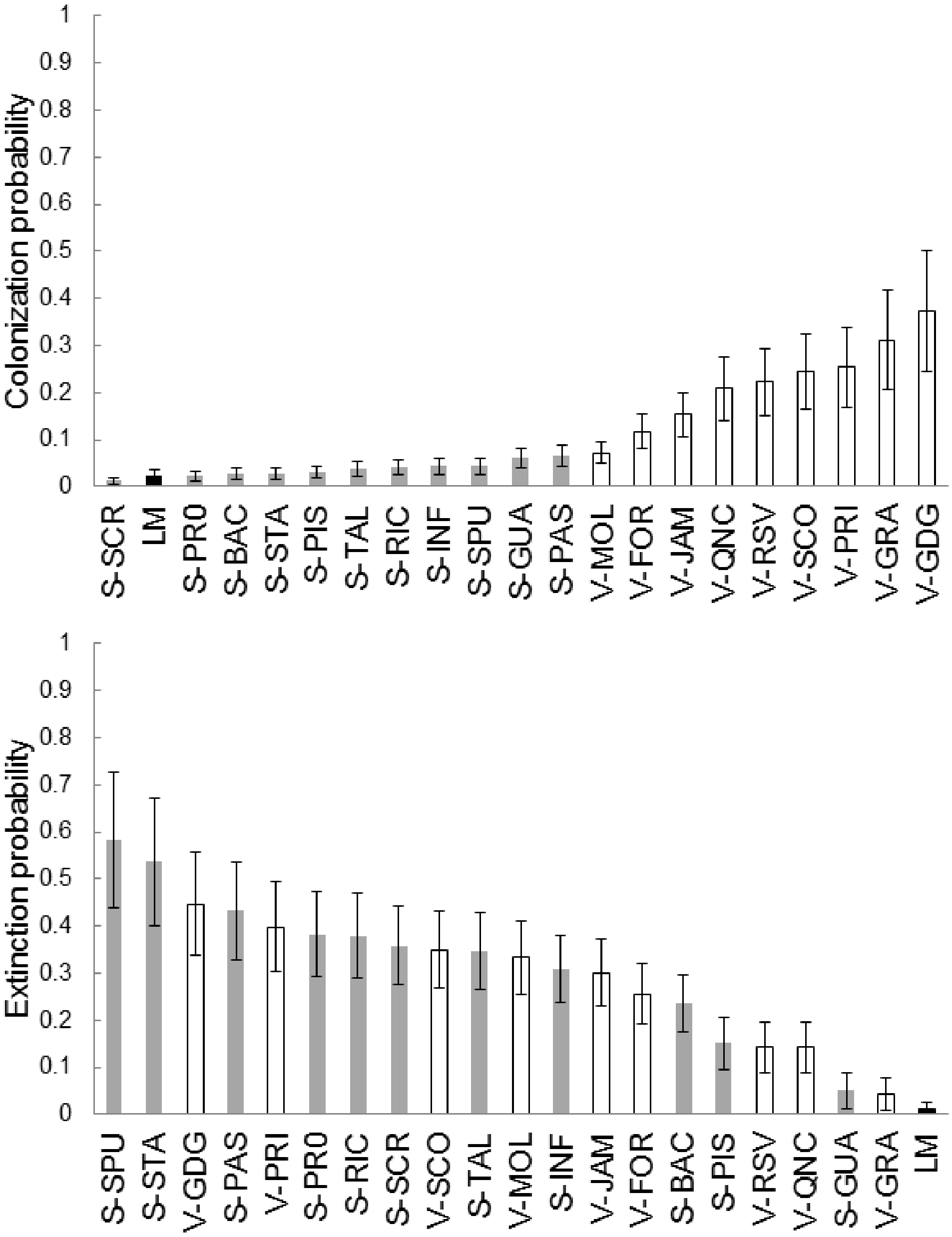


Figure 8. Colonization and extinction probability in each sampled patch as predicted by the top ranked occupancy model (the graph includes model predictions and standard errors). Patches are sorted by shrubs (shrub_sel, colonization) and size (logHA, extinction); the three landscapes are represented with different colors (grey: S, black: L, white: V).

3.1.2. 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 compared to summer) and in sites with higher resource abundance (Table 12). I found that dormice density was significantly lower in the Sabina and Viterbo landscapes when compared to Lamone (Table 12). Finally, I detected a negative temporal trend, with the population density across all landscapes significantly decreasing throughout the study period (months since beginning of the study, Table 12).

Table 12. 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. shrub_sel = abundance index of selected shrubs (see Table 3 for a checklist),; T_ave= mean temperature during sampling. SA=Sabina landscape, VT=Viterbo landscape.

Term			Wald's test	significance
Random effects	Variance	Standard Deviation		
Observation	1.11	1.05		
Grid	0.43	0.66		
Fixed effects	β	SE	*Z*	*p*
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

3.1.3. 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 13, 14). In addition, survival probability was different in the three landscapes, being higher in the Lamone landscape and lower in the Viterbo landscape; the Sabina landscape had intermediate survival values (Table 13, 14).

Table 13. Final set of Cormack-Jolly-Seber models ranked according to QAICc (only models with 4 $\Delta QAIC_C$ are shown). Covariates are represented in brackets (see Table 2 for details on the covariates). Phi = survival probability, p = recapture probability, QAICc = 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.

Model	$QAIC_C$	$\Delta QAIC_C$	$QAIC_C$ 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*simps+body mass), p(season)	280.24	2.05	0.05	7
phi(body mass+simps*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

Table 14. β averaged estimates of the final Cormack-Jolly-Seber model, obtained from models within 2 $\Delta QAIC_C$. Estimate and standard error (SE) are reported for intercept and covariate parameters (see Table 2 for details on the covariates). Phi = survival probability, p = recapture probability.

β	estimate	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

3.1.4. Litter size

I 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 Table A 2). The only predictor variable affecting litter size was landscape, with females bearing significantly larger litters in the Lamone landscape (Wald test: χ= -2.1; $\beta_{\text{intercept}}$= 1.51 (0.07); $\beta_{\text{landscape}}$= -0.3 (0.14), p=0.03).

3.2. The role of interspecific interactions

3.2.1. Population dynamics

A total of 8109 captures out of 47718 trap-nights were obtained. 2056 individuals of *A. flavicollis*, 1568 *A. sylvaticus*, and 1121 *M. glareolus* were marked. Molecular analyses were performed on 2008 individuals. *Apodemus* spp. were detected at least once in all fragments, while *M. glareolus* was detected in 27 fragments. Local population densities varied markedly among fragments (observed number of individuals/hectare: *A. sylvaticus*, range = 0 - 128, mean = 17; *A. flavicollis*, range = 0 - 159, mean = 24; *M. glareolus*, range = 0 - 173, mean = 15) and the dynamics of the three species all showed strong fluctuations including local extinctions (Figure 9, 10, 11).

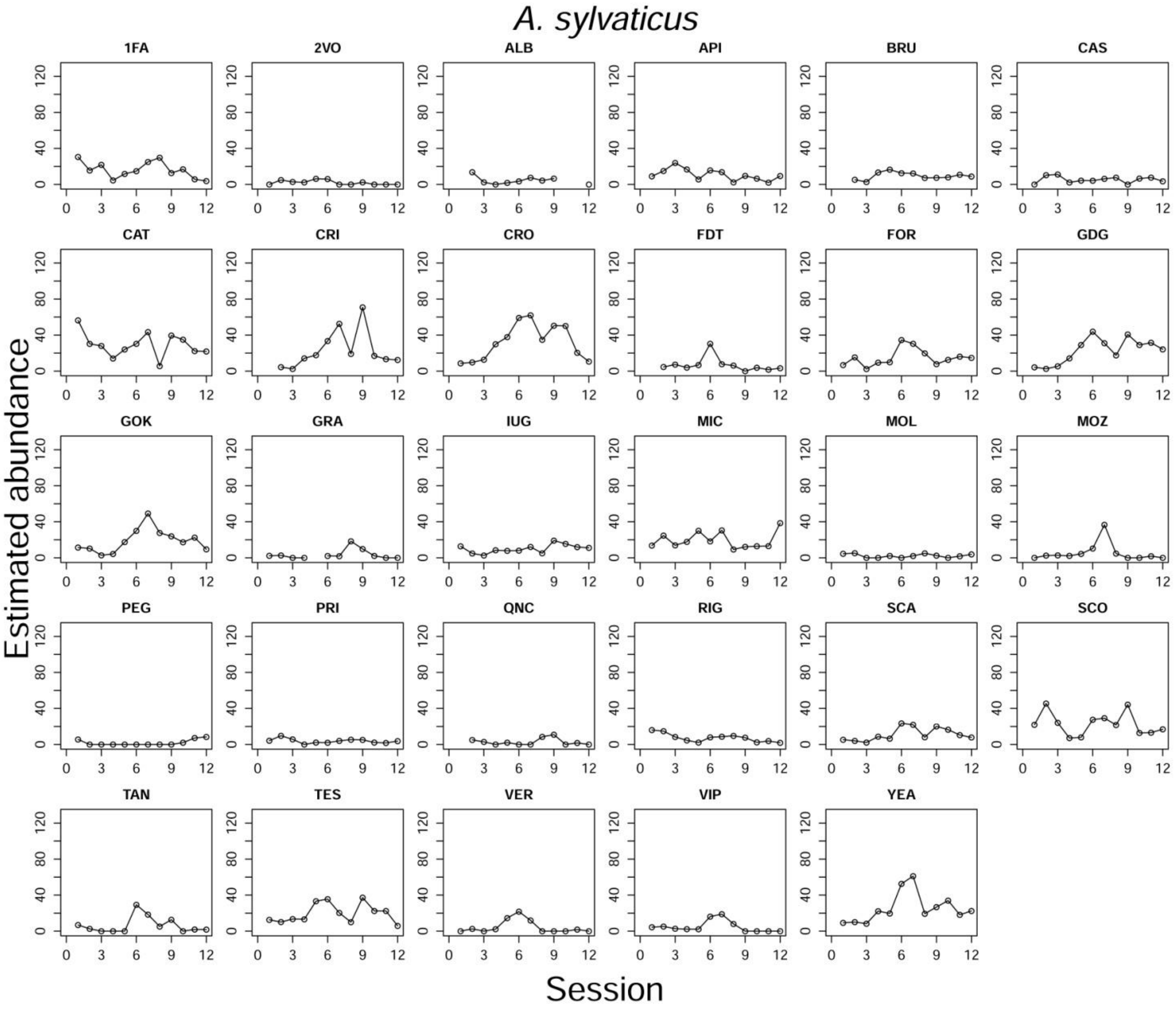


Figure 9. Estimated abundance of *A. sylvaticus* individuals in each grid (labeled by an alpha-numeric code, e.g. 1FA) from sampling session 1 (April 2011) to 12 (February 2013).

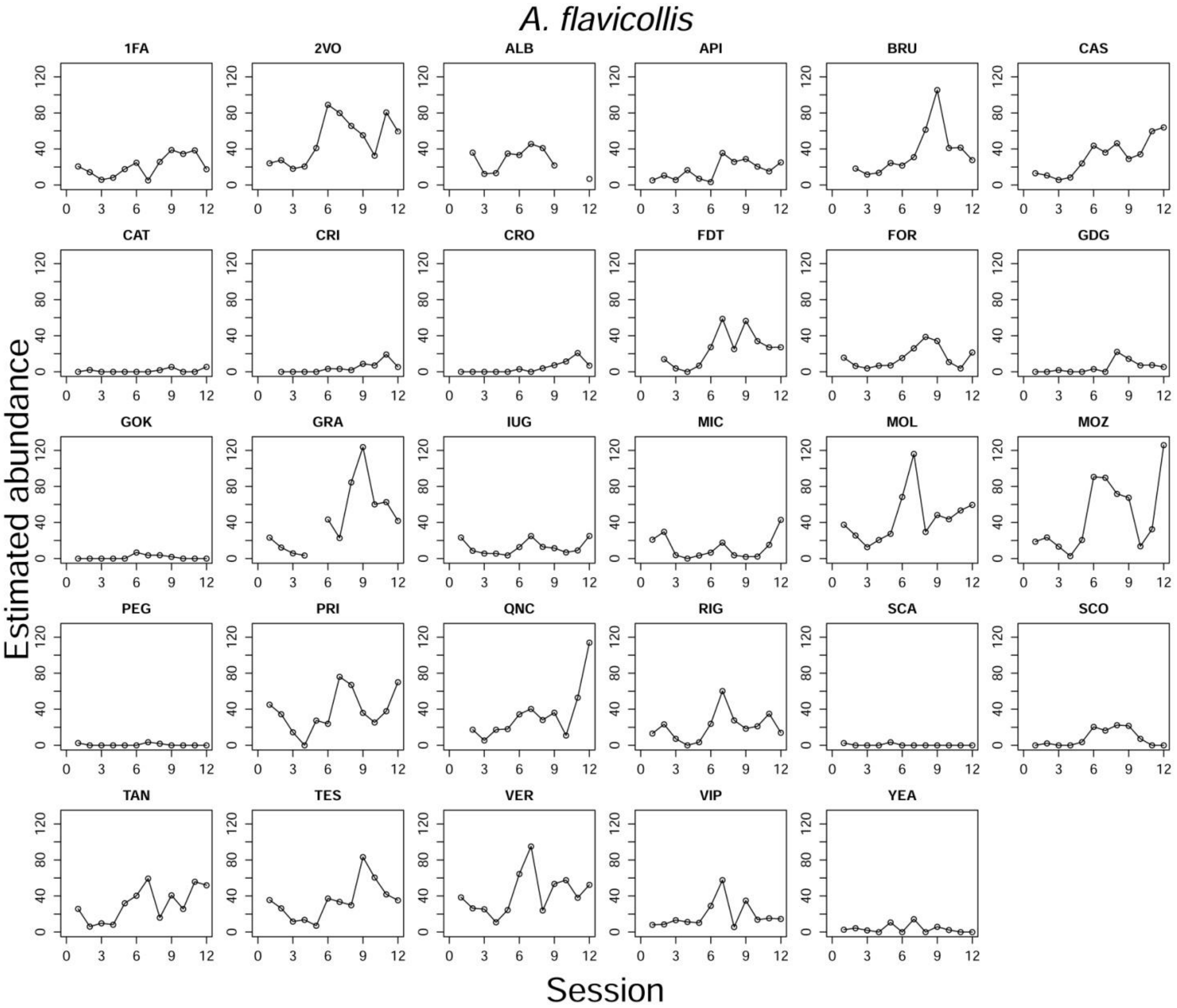


Figure 10. Estimated abundance of *A. flavicollis* individuals in each grid (labeled by an alpha-numeric code, e.g. 1FA) from sampling session 1 (April 2011) to 12 (February 2013).

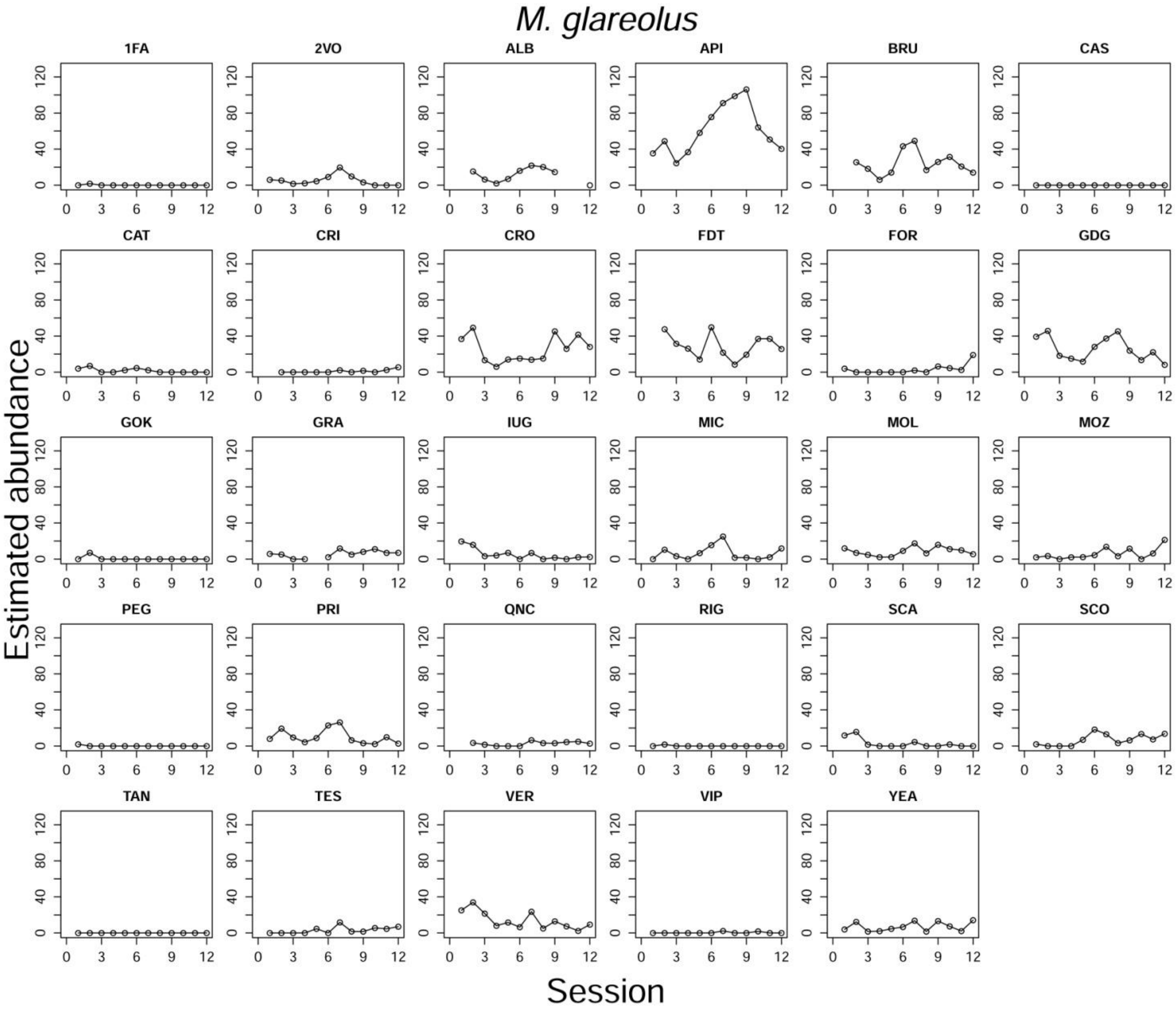


Figure 11. Estimated abundance of *M. glareolus* individuals in each grid (labeled by an alpha-numeric code, e.g. 1FA) from sampling session 1 (April 2011) to 12 (February 2013).

3.2.2. Landscape and habitat factors

I selected different species-specific spatial scales for habitat amount (1000 m, 100 m and 100 m respectively for *A. sylvaticus*, *A. flavicollis* and *M. glareolus*) and connectivity (1000 m, 900 m and 100 m respectively for *A. sylvaticus, A. flavicollis* and *M. glareolus*) variables (Table 7, 8). The three species were distributed according to different factors both at landscape and habitat level. The abundance of *A. sylvaticus* responded negatively to woodland cover, while the abundance of *A. flavicollis* and *M. glareolus* increased in well-connected patches, irrespectively of woodland cover (Table 15, 16, Figure 12). Different habitat and food resource factors influenced the distribution of the species, with *A. sylvaticus* being associated with low shrub diversity, *A. flavicollis* with a high amount of acorn resources and *M. glareolus* with a complex vertical structure of shrubs (Table 15, 16, Figure 12).

Table 15. Ranking of GLMMs (Poisson) on individual abundance as a function of habitat and landscape variables. K = number of parameters; AICc = Akaike's Information Criterion; AICc Wgt = Akaike's weight; LL = log-likelihood. Habitat 1000 and Habitat 100 = wood cover (hectares) in a 1000 or 100 m buffer around the grid; Simpson = shrubs diversity index; Acorns Qc = biomass of *Q. cerris* acorns (g/m2); Acorns Qp = biomass of *Q. pubescens* acorns (g/m2); Hedgerows 900 and Hedgerows 100 = total length of hedgerows (m) in a 900 or 100 m buffer around the grid; Shrub structure = index of vertical complexity of shrubs. Models > 10 delta AICc are not shown.

Model	K	AICc	Delta AICc	AICc Wgt	LL
A. sylvaticus					
Habitat 1000* + Simpson	5	2660.51	0.00	0.45	-1323.95
Habitat 1000* + Simpson + Acorns Qp*	6	2662.40	1.89	0.17	-1323.29
Habitat 1000* + Acorns Qp* + Simpson	6	2662.98	2.46	0.13	-1323.58
Habitat 1000* + Acorns Qp*	5	2664.06	3.55	0.08	-1325.73
Habitat 1000* + Simpson + Acorns Qc* + Acorns Qp*	7	2665.25	4.74	0.04	-1322.96
Habitat 1000*	4	2665.91	5.39	0.03	-1328.12
Habitat 1000* + Acorns Qc* + Acorns Qp*	6	2666.07	5.55	0.03	-1325.12
Acorns Qc* + Simpson	5	2666.70	6.19	0.02	-1327.05
Habitat 1000* + Acorns Qc*	5	2667.10	6.59	0.02	-1327.25
Simpson	4	2668.46	7.95	0.01	-1329.40
Simpson + Acorns Qc* + Acorns Qp*	6	2668.89	8.37	0.01	-1326.53
Acorns Qc* + Acorns Qp*	5	2669.13	8.62	0.01	-1328.26
Acorns Qc*	4	2669.77	9.26	0.00	-1330.05
Simpson + Acorns Qp*	5	2670.22	9.71	0.00	-1328.81
A. flavicollis					
Acorns Qc* + Hedgerows 900	5	3249.59	0.00	0.38	-1618.49
Simpson + Acorns Qc* + Hedgerows 900	6	3250.35	0.76	0.26	-1617.27
Habitat 100* + Acorns Qc* + Hedgerows 900	6	3251.49	1.90	0.15	-1617.83
Habitat 100* + Simpson + Acorns Qc* + Hedgerows 900	7	3253.19	3.60	0.06	-1616.93
Acorns Qc* + Simpson	5	3253.40	3.82	0.06	-1620.40
Acorns Qc*	4	3253.86	4.27	0.04	-1622.09
Habitat 100* + Acorns Qc*	5	3254.70	5.12	0.03	-1621.05
Habitat 100* + Acorns Qc* + Simpson	6	3255.50	5.92	0.02	-1619.84
M. glareolus					
Shrub structure + Hedgerows 100	5	2044.59	0.00	0.91	-1015.86
Shrub structure	4	2049.67	5.08	0.07	-1019.93
Hedgerows 100	4	2053.86	9.28	0.01	-1022.02

*$\log_{10}$-transformed

Table 16. Parameter estimates of the top-ranked GLMM models (Poisson distribution, log link) on individual abundances (12 sampling sessions in 29 sampling grids) of the three species as functions of habitat characteristics, landscape variables and competitors density (individuals/hectare). Habitat 1000 = wood cover (hectares) in a 1000 m buffer around the grid; Simpson = shrubs diversity index; Acorns Qc = biomass of *Q. cerris* acorns (g/m2); Shrub structure = index of vertical complexity of shrubs; Hedgerows 900 and Hedgerows 100 = total length of hedgerows (m) in a 900 or 100 m buffer around the grid; As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*.

A. sylvaticus		
Random effects:		
Groups	Variance	Std. Dev.
grid	0.4362	0.6605
session	0.1235	0.3514
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	15.1700	4.3710
Habitat 1000*	-1.0560	0.2922
Simpson	-13.7200	5.0000
Mg density	-0.0051	0.0007
A. flavicollis		
Random effects:		
Groups	Variance	Std. Dev.
grid	0.5568	0.7462
session	0.3597	0.5997
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	-0.6723	0.4706
Acorns Qc*	1.1290	0.1621
Hedgerows 900	0.0001	0.0000
As density	0.0028	0.0006
M. glareolus		
Random effects:		
Groups	Variance	Std. Dev.
grid	1.9320	1.3898
session	0.1470	0.3835
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	-3.0569	0.8934
Shrub structure	0.3503	0.0870
Hedgerows 100	0.0128	0.0042
As density	-0.0029	0.0007
Af density	0.0015	0.0005

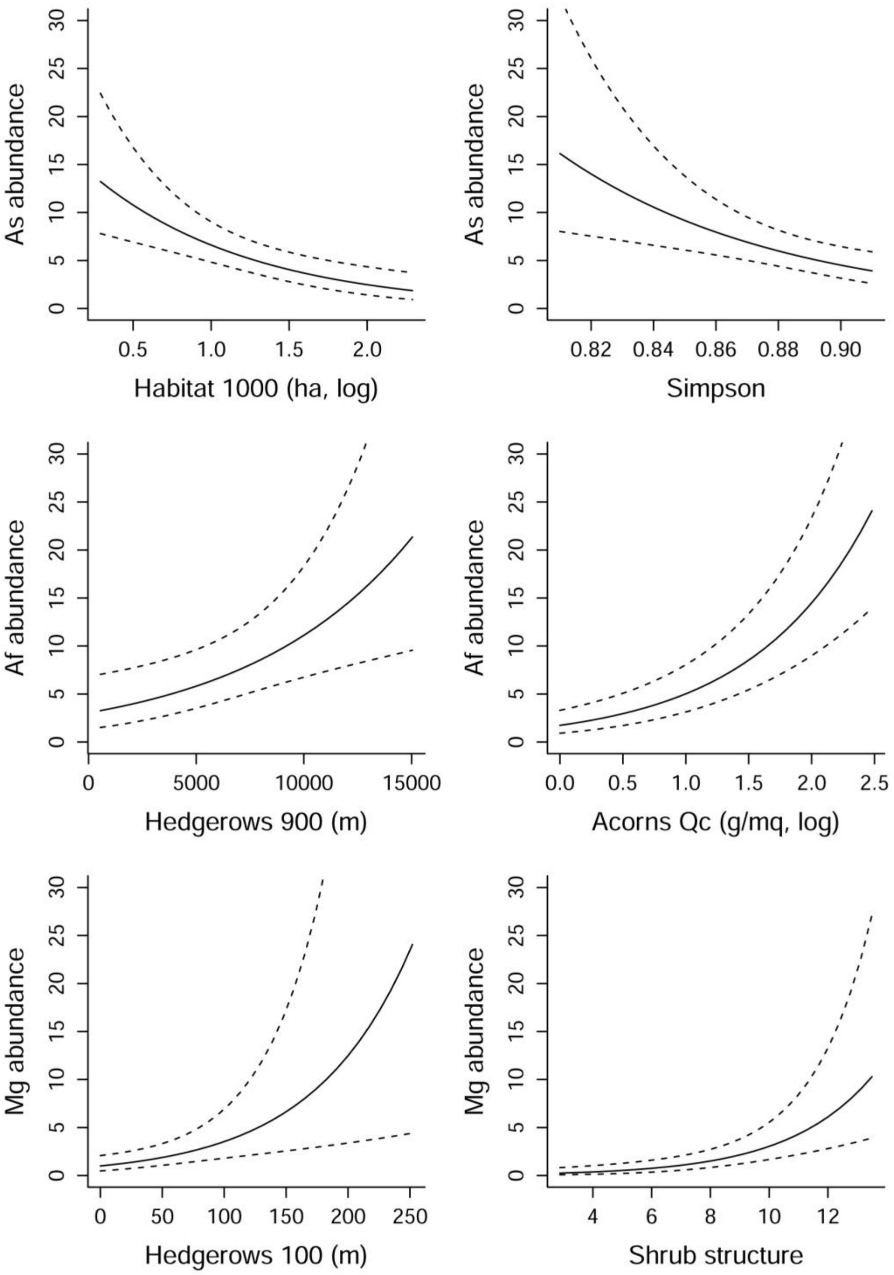


Figure 12. Effect of habitat variables (acorns, shrubs) and landscape variable (wood cover, hedgerows) on the abundance of *A. sylvaticus* (As), *A. flavicollis* (Af) and *M. glareolus* (Mg) as predicted by the top-ranked GLMM models. Habitat 1000 = cover of woods (hectares) in a 1000 m buffer around the grid; Simpson = index of shrub diversity; Acorns Qc = biomass (g/m2) of *Q. cerris* acorns; Hedgerows 900 and Hedgerows 100 = total length of hedgerows (m) in a 900 or 100 m buffer around the grid; Shrub structure = index of shrub vertical complexity. Dashed lines represent 95% confidence intervals.

3.2.3. Effect of competitors

I found an effect of the abundance of competitor species on several individual and population parameters. Nevertheless, these effects were relatively weak in most cases.

For each significant negative interaction between species I report the effect size, here calculated as the magnitude of the effect corresponding to an increase of competitors of 100 individuals/hectare.

A. sylvaticus was negatively influenced by the co-generic *A. flavicollis*. High densities of *A. flavicollis* determined a slight decrease in the survival probability (effect size: 0.049) and recruitment (effect size: 0.039) of *A. sylvaticus* (Table 17, Figure 13). High densities of *M. glareolus,* instead, determined a decrease in the mean body mass of *A. sylvaticus* (effect size: 0.708), but without other effects on vital rates (Table 17, Figure 13). Despite the detection of individual-scale negative effects of competitors, I did not observe a corresponding effect on population density, except for a weak effect of *M. glareolus* (effect size: 1.66 individuals) (Table 17, Figure 13).

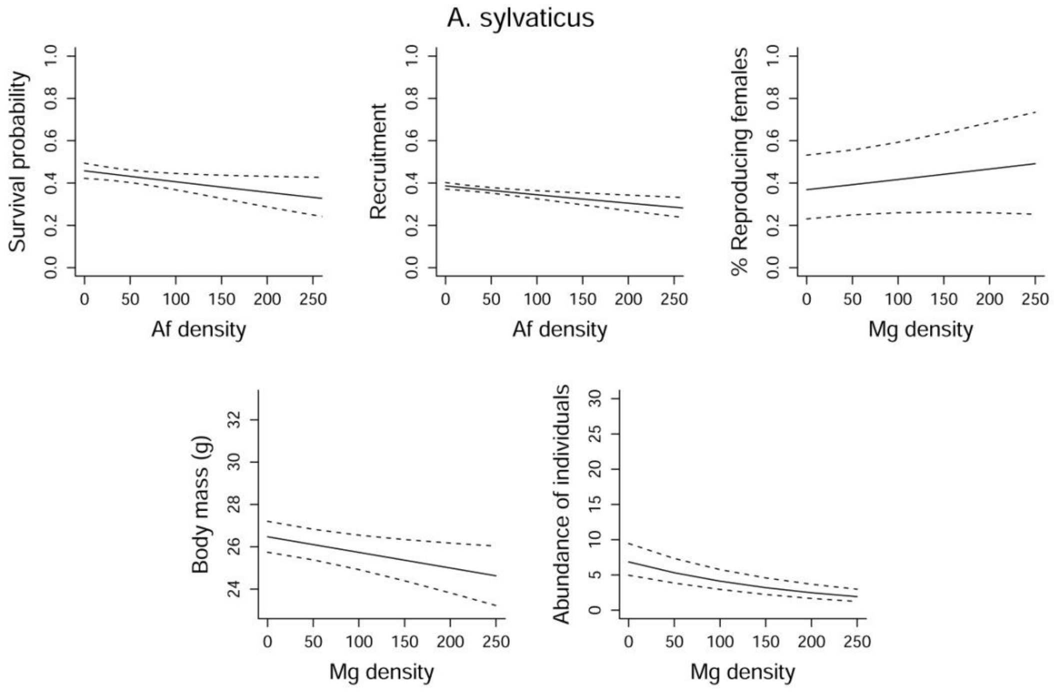


Figure 13. Partial plots with the effect of competitor density (Af = *A. flavicollis* and Mg = *M. glareolus*) on survival, recruitment, % of reproducing females, body mass (g) and abundance of *A. sylvaticus*. Dashed lines represent 95% confidence intervals.

A. flavicollis was negatively influenced by the co-generic *A. sylvaticus* at several levels, including survival (effect size: 0.180), reproduction (effect size: 0.117) and body mass (effect size: 1.288) (Table 17, Figure 14). *M. glareolus* had negative effects on *A. flavicollis* as well, on survival (effect size: 0.025) and body mass (effect size: 0.461) (Table 17, Figure 14). These effects were lower than the effects of *A. sylvaticus.* These individual-scale effects were translated into population-level effects only in the case of *A. sylvaticus*, which determined a slight decrease in the density of *A. flavicollis* (effect size: 4.0 individuals) (Table 17, Figure 14).

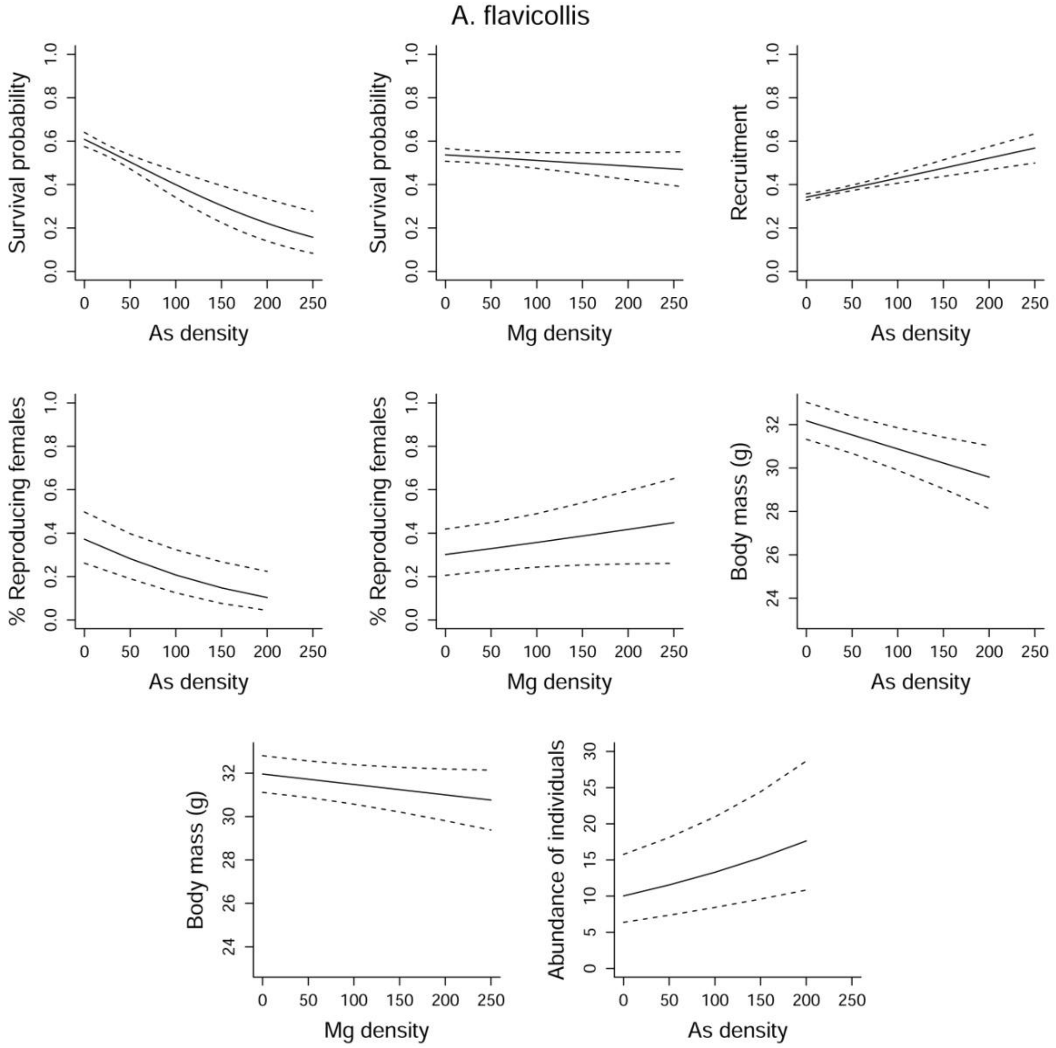


Figure 14. Partial plots with the effect of competitor density (As = *A. sylvaticus* and Mg = *M. glareolus*) on survival, recruitment, % of reproducing females, body mass (g) and abundance of *A. flavicollis*. Dashed lines represent 95% confidence intervals.

M. glareolus was only scarcely influenced by the two competitors, with *A. sylvaticus* having an effect on its body mass (effect size: 1.944), without significant effects on vital rates, and with *A. flavicollis* slightly reducing its survival probability (effect size: 0.084) (Table 17, Figure 15). I observed significant but extremely weak effects of the two competitors on population density (Table 17, Figure 15). Dashed lines represent 95% confidence intervals.

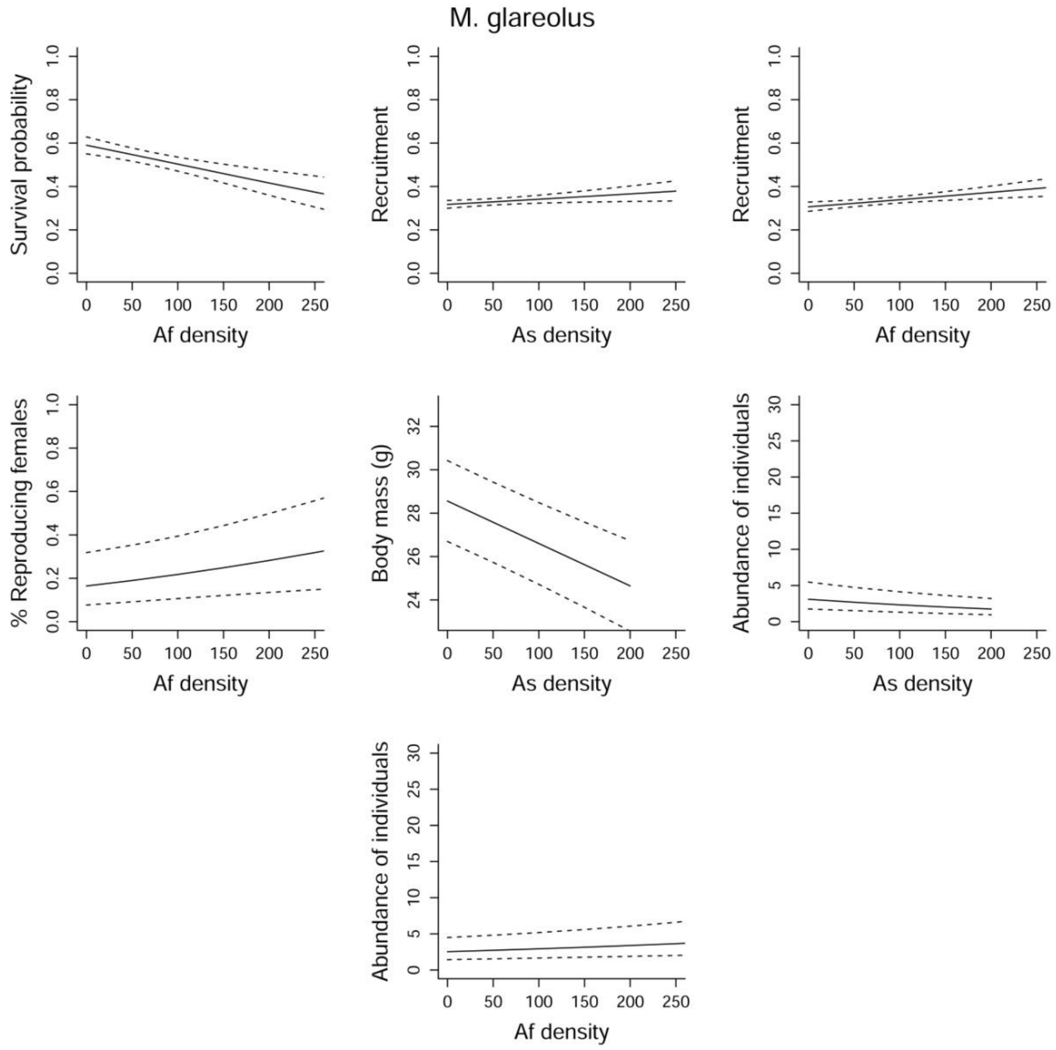


Figure 15. Partial plots with the effect of competitor density (As = *A. sylvaticus* and Af = *A. flavicollis*) on survival, recruitment, % of reproducing females, body mass (g) and abundance of *M. glareolus*.

Table 17. Ranking of models on a) survival (phi) and recruitment (f), b) body mass, c) reproduction probability of females (repr) and d) individual density (n) of each species as function of competitors. Individual densities were modeled also as functions of habitat and landscape variables (details on variables in Table 9). As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*. K = number of parameters; AICc = Akaike's Information Criterion; AIC Wgt = Akaike's weight; LL = log-likelihood. Models > 10 delta AICc are not shown.

a) Survival and recruitment

Model		K	AICc	Delta AICc	AIC Wgt	Deviance
A. sylvaticus						
phi (Af)	f (Af)	12	16306.76	0.00	0.53	16282.64
phi (Mg+Af)	f (Af)	13	16308.34	1.57	0.24	16282.19
phi (Af)	f (Mg+Af)	13	16308.42	1.66	0.23	16282.27
A. flavicollis						
phi (As+Mg)	f (As)	13	23245.23	0.00	0.40	23219.12
phi (As)	f (As)	12	23245.48	0.25	0.36	23221.39
phi (As)	f (As+Mg)	13	23246.24	1.02	0.24	23220.14
M. glareolus						
phi (Af)	f (As+Af)	13	12826.89	0.00	0.60	12800.69
phi (As+Af)	f (As+Af)	14	12827.67	0.78	0.40	12799.43

b) Body mass

Model	K	AICc	delta AICc	AIC Wgt	LL
A. sylvaticus					
mass (Mg)	5	8052.46	0.00	0.60	-4021.21
mass (Af+Mg)	6	8053.26	0.81	0.40	-4020.60
A. flavicollis					
mass (As+Mg)	6	12147.49	0.00	0.69	-6067.73
mass (As)	5	12149.09	1.60	0.31	-6069.53
M. glareolus					
mass (As)	5	7528.99	0.00	0.50	-3759.47
mass (As+Af)	6	7529.00	0.01	0.50	-3758.47

(continued on the next page)

Table 17 (continued)

c) Reproduction probability of females

Model	K	AICc	delta AICc	AIC Wgt	LL
A. sylvaticus					
repr (Mg)	4	1234.90	0.00	0.40	-613.43
repr (Af)	4	1235.08	0.18	0.37	-613.52
repr (Af+Mg)	5	1235.97	1.07	0.23	-612.95
A. flavicollis					
repr (As+Mg)	5	1469.51	0.00	0.56	-729.73
repr (As)	4	1469.95	0.44	0.44	-730.96
M. glareolus					
repr (Af)	4	822.29	0.00	0.43	-407.12
repr (As+Af)	5	822.75	0.46	0.34	-406.34
repr (As)	4	823.46	1.17	0.23	-407.71

d) Population density

Model	K	AICc	Delta AICc	AICc Wgt	LL
A. sylvaticus					
n (Habitat 1000* + Simpson + Mg)	6	2529.02	0.00	0.62	-1258.37
n (Habitat 1000* + Simpson + Af + Mg)	7	2530.01	0.99	0.38	-1257.82
A. flavicollis					
n (Acorns Qc* + Hedgerows 900 + As)	6	3129.47	0.00	0.69	-1558.60
n (Acorns Qc* + Hedgerows 900 + As + Mg)	7	3131.09	1.62	0.31	-1558.36
M. glareolus					
n (Shrub structure + Hedgerows 100 + As + Af)	7	1959.89	0.00	0.96	-972.76
n (Shrub structure + Hedgerows 100 + Af)	6	1966.40	6.51	0.04	-977.06

Beyond the negative effects reported above, I also observed a few positive responses between species (Figure 13, 14, 15), such as a weak positive effect of *A. sylvaticus* on recruitment and population abundance of *A. flavicollis*. Detailed results on positive and negative effects including parameter estimates are reported in Tables 18, 19, 20.

Table 18. Parameter estimates of the top-ranked Pradel capture-mark-recapture models on individual survival (phi) and recruitment (f) of the three species as functions of competitors density (individuals/hectare). As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*.

A. sylvaticus		
Parameter	Estimate	SE
phi (Intercept)	-0.1696	0.0740
phi - Af density	-0.0021	0.0010
f (Intercept)	-0.4621	0.0338
f - Af density	-0.0018	0.0005
A. flavicollis		
Parameter	Estimate	SE
phi (Intercept)	0.4705	0.0734
phi - As density	-0.0085	0.0016
phi - Mg density	-0.0010	0.0007
f (Intercept)	-0.6539	0.0340
f - As density	0.0037	0.0006
M. glareolus		
Parameter	Estimate	SE
phi (Intercept)	0.3644	0.0826
phi - Af density	-0.0035	0.0008
f (Intercept)	-0.8584	0.0600
f - As density	0.0011	0.0005
f - Af density	0.0015	0.0005

Table 19. Parameter estimates of the top-ranked GLMM models (binomial distribution, logit link) on the probability of reproduction of females (12 sampling sessions; mark = individual ID) of the three species as a function of competitors density (individuals/hectare). As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*.

A. sylvaticus		
Random effects:		
Groups	Variance	Std. Dev.
mark	0.3190	0.5648
session	1.1560	1.0754
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	-0.5386	0.3401
Mg density	0.0020	0.0019
A. flavicollis		
Random effects:		
Groups	Variance	Std. Dev.
mark	0.4232	0.6506
session	0.6507	0.8067
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	-0.6037	0.2650
As density	-0.0082	0.0022
Mg density	0.0025	0.0015
M. glareolus		
Random effects:		
Groups	Variance	Std. Dev.
mark	0.0543	0.2331
session	1.8812	1.3716
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	-1.6255	0.4402
Af density	0.0035	0.0014

Table 20. Parameter estimates of the top-ranked LMM models on the body mass of adult individuals (12 sampling sessions; mark = individual ID) of the three species as a function of competitors density (individuals/hectare). As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*.

A. sylvaticus		
Random effects:		
Groups	Variance	Std. Dev.
mark	4.7450	2.1780
session	1.2700	1.1270
Residual	14.1940	3.7680
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	26.4716	0.3732
Mg density	-0.0074	0.0028
A. flavicollis		
Random effects:		
Groups	Variance	Std. Dev.
mark	9.6160	3.1010
session	1.7820	1.3350
Residual	14.0900	3.7540
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	32.3271	0.4395
As density	-0.0130	0.0035
Mg density	-0.0048	0.0025
M. glareolus		
Random effects:		
Groups	Variance	Std. Dev.
mark	5.0520	2.2480
session	9.5170	3.0850
Residual	16.6920	4.0860
Fixed effects:		
Parameter	Estimate	SE
(Intercept)	28.5600	0.9500
As density	-0.0196	0.0031

3.3. Perceptual range and movement ability

119 individuals were captured and released (59 *A. flavicollis*, 18 *A. sylvaticus* and 42 *M. glareolus*; Table 21). Due to the low number of individuals of the two sexes I could not perform statistical tests separately for males and females. However, I did not observe any apparent difference in movement behavior between sexes, so I pooled males and females data in order to increase sample size.

Tracks were followed for a maximum of 294 m (mean length 43 m, standard deviation 44 m). Maximum length of tracks was higher in the less obstructed matrices (294, 171 and 161 m respectively in the bare, the low and the intermediate wheat fields) than in the more obstructed ones (69 and 61 m in the grass and high wheat fields).

3.3.1. Orientation in the bare field

In the bare field individuals of *A. flavicollis* oriented directly toward the wood at the distance of 20 m and 40 m, but not at 100 m, suggesting a perceptual range of at least 40 m (Table 21, Figure 16a, Figure A 8). The orientation of *A. sylvaticus* individuals suggested a perceptual range of at least 100 m (Figure 16b). However, the low sample size for *A. sylvaticus* (due to difficulty in capturing individuals of this species, as resulted after molecular confirmation of the species), did not allow robust statistical inference for any of the three release distances. On the contrary, individuals of *M. glareolus* were not significantly oriented towards the wood at any distance, suggesting a perceptual range of less than 20 m (Table 21, Figure 16c, Figure A 9).

Table 21. Results of the V-tests performed on weighted mean vectors of individual movements, with the expected mean toward the wood and along the plantation rows (axial data). N = sample size (number of individuals); u = V-test statistic. Statistical significance ($p < 0.05$) is in bold.

Matrix type	Distance from the wood (m)	N	towards the wood		along the rows	
			U	p	u	p
A. flavicollis						
bare field	20	7	1.95	**0.025**	-	-
bare field	40	7	2.42	**0.006**	-	-
bare field	100	6	-0.40	0.65	-	-
grass field	10	5	-1.04	0.844	-	-
grass field	20	6	-0.67	0.743	-	-
wheat field - low	40	7	1.17	0.125	2.24	**0.011**
wheat field - intermediate	10	5	-0.58	0.711	1.84	**0.032**
wheat field - intermediate	20	11	-0.89	0.81	2.11	**0.017**
wheat field - high	20	5	0.53	0.305	2.74	**0.001**
A. sylvaticus						
bare field	20	2	-	-	-	-
bare field	40	2	-	-	-	-
bare field	100	3	-	-	-	-
grass field	20	4	-	-	-	-
wheat field - low	40	3	-	-	-	-
wheat field - intermediate	20	2	-	-	-	-
wheat field - high	20	2	-	-	-	-
wheat field - pooled	20, 40	7	-	-	2.57	**0.004**
M. glareolus						
bare field	20	6	-1.02	0.84	-	-
bare field	40	6	0.93	0.181	-	-
bare field	100	8	0.06	0.478	-	-
grass field	20	6	0.16	0.437	-	-
wheat field - low	40	6	0.15	0.444	3.37	**0.000**
wheat field - intermediate	20	5	-0.51	0.689	2.59	**0.003**
wheat field - high	20	5	0.32	0.379	2.67	**0.002**

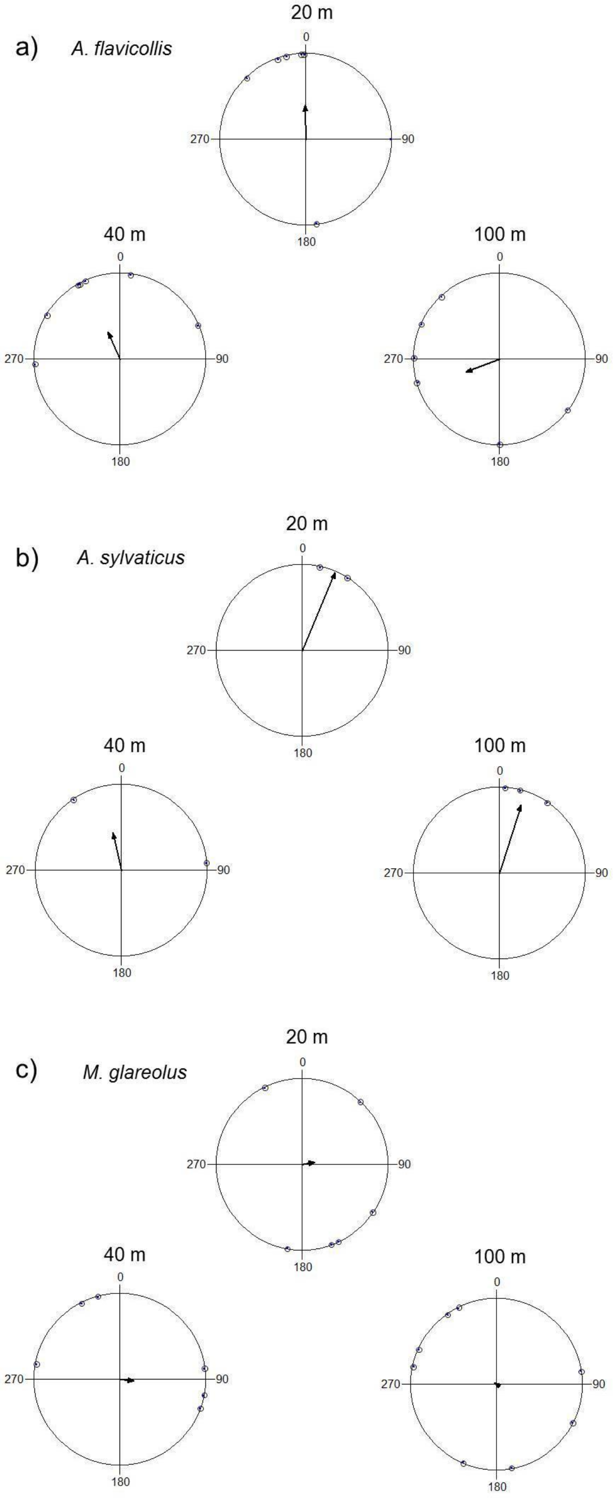


Figure 16 (a, b, c). Angular orientations of *A. flavicollis* (a), *A. sylvaticus* (b) and *M. glareolus* (c) released in the bare field at 20 m, 40 m and 100 m from the wood. Each point around the circle represents the mean direction of an individual path; arrows represent the mean vector of each group of individuals; central point represents the release point; the zero represents the wood direction. *A. flavicollis* and *A. sylvaticus* oriented towards the wood (respectively at 20-40 m and 20-100 m), while *M. glareolus* did not orient toward the wood at any distance.

3.3.2. Orientation in the wheat field

In the wheat field *A. flavicollis* and *M. glareolus* moved along wheat plantation rows at all the stages of growth (Table 21, Figure 17a,b,c, Figure A 10). Due to low sample size I pooled all available data for *A. sylvaticus* (all stages of growth and distances). Also for this species I found that individuals moved parallel to plantation rows (Table 21; Figure A17d).

In the wheat field neither *A. flavicollis* nor *M. glareolus* oriented towards the wood at any maturation stages (Table 21). For *A. sylvaticus* the low sample size did not allow performing statistical tests.

3.3.3. Orientation in the grass field

The control tests in the grass field showed that none of the species was oriented either towards the wood (Table 21), or towards any direction (Hotelling's test; at 20 m: *A. flavicollis*, F = 0.018, p = 0.983; *A. sylvaticus*, F = 0.494, p = 0.669; *M. glareolus*, F = 1.329, p = 0.361; at 10 m: *A. flavicollis*, F = 0.163, p = 0.857): in the absence of environmental cues these rodents appeared to move randomly (Figure 18; Figure A 11).

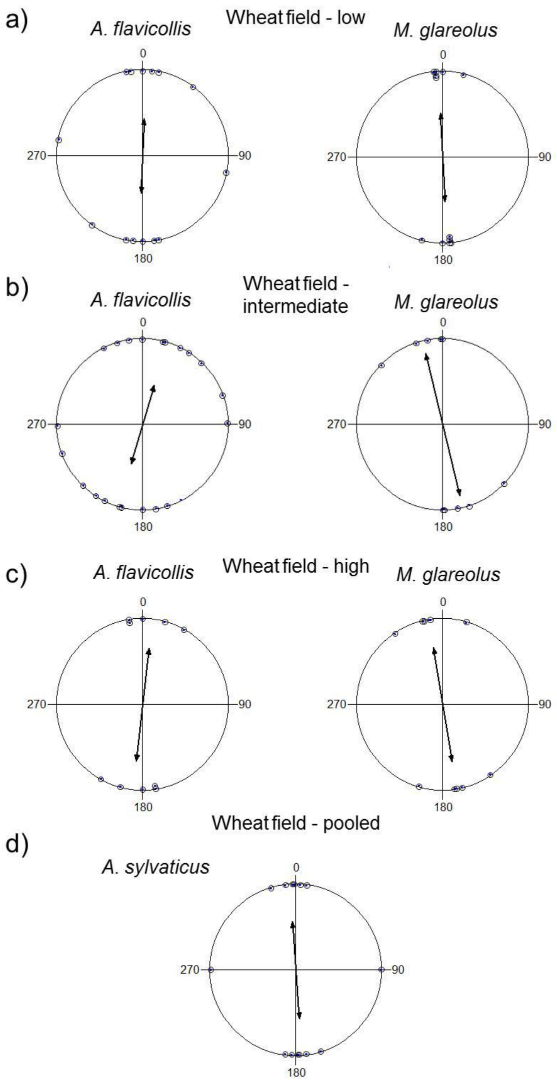


Figure 17 (a, b, c, d). Angular orientations of *A. flavicollis*, *A. sylvaticus* and *M. glareolus* released in the wheat field. Each pair of opposite points around the circle represents the mean axial direction of an individual path; arrows represent the mean axial vector of each group of individuals; central point represents the release point; the 0-180° axis represents the plantation rows direction. All species moved along plantation rows.

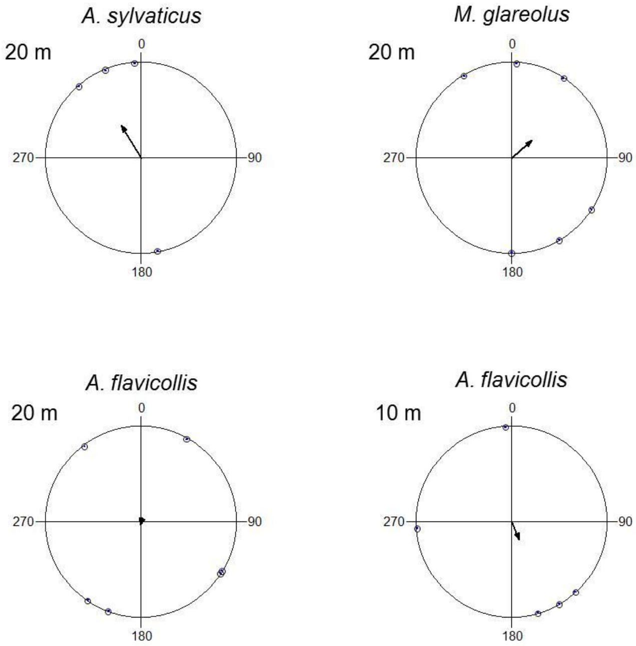


Figure 18. Angular orientations of *A. flavicollis*, *A. sylvaticus* and *M. glareolus* released in the grass field at 10 and 20 m from the wood. Each point around the circle represents the mean direction of an individual path; arrows represent the mean vector of each group of individuals; central point represents the release point; the zero represents the wood direction. None of the species oriented towards the wood or towards any particular direction.

4. DISCUSSION

4.1. Population and individual-scale responses to patch size, isolation and quality.

4.1.1. 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. 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). These findings are also consistent with the 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 agricultural matrix (Mortelliti et al. 2013) and this may explain why target populations showed no effect of isolation on colonization/extinction. Further studies should evaluate the response of the species in more fragmented landscapes to test if with higher levels of patch isolation populations are more dispersal-limited. The findings of this study 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, which is in accordance with the basic biology of this species (Amori et al. 2008, Juškaitis 2008). As previously highlighted, habitat quality directly influenced individual parameters. 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). I stress that I have focused on the most relevant food resources for this species, which are flowers and fruits (Bright and Morris 1996, Juškaitis 2008). I acknowledge, however, that this species also may occasionally consume small invertebrates and bird eggs. I suggest that future studies focusing on habitat quality include an assessment of the availability of other food resources.

4.1.2. Comparison among the studied landscapes

Survival was higher in the Lamone landscape, which may suggest that individuals survive more in non-fragmented landscapes. However, I 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 may also suggest higher level of emigration occurring in the patches nested in these two landscapes (Schtickzelle and Baguette 2003).

Large litters were recorded in the non-fragmented area (Lamone). I 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.

4.1.3. The extinction process

Local extinction was due mainly to patch size. 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 extent of available habitat. I found no evidence that habitat quality (at least in the way I 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 the amount of habitat was probably linked to absolute population size, which, in the landscapes I investigated, was low in small patches (tens of individuals, as inferred from the abundance index), 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 effect (a reduction in the individual fitness associated to low population abundance or density; Stephens et al. 1999). 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.

I 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.

4.2. The role of interspecific interactions

4.2.1. Determinants of species' distribution

Populations were distributed according to species-specific habitat and landscape factors and findings are consistent with knowledge on the basic ecology of these species. The two habitat specialists (*A. flavicollis* and *M. glareolus*) were favored by high connectivity and high quality sites (in terms of food resources and vertical structure of the vegetation), while the generalist *A. sylvaticus* was associated with (but not limited to) isolated and low-quality sites. The latter species is known to exploit the agricultural matrix, being able to easily move across it, at least in certain periods of the year (Tattersal et al. 2001). The higher ability to move between forest fragments, therefore, can explain its presence in highly fragmented contexts. On the contrary, the two specialists are less prone to move out of forested areas, occasionally using hedgerows for long-distance movements between fragments (Zhang and Usher 1991, Kotzageorgis and Mason 1997, Mortelliti et al. 2009). *A. flavicollis* was also favored by a high biomass of acorns, consistently with its granivorous habits, strictly relying on acorn production in oak-dominated forests. *M. glareolus* responded to shrubs (such as hawthorn, *Crataegus monogyna*, or blackthorn, *Prunus spinosa*), probably related to the availability of leaves, flowers and fruits which are an important component of its diet (Abt and Bock 1998). Furthermore, *M. glareolus* is known to rely on a developed shrub structure as a protection from predators, compared to the more agile and faster *Apodemus* spp. which are more capable to escape from them (Buesching et al. 2008). The negative response of *A. sylvaticus* to shrubs can be interpreted as an indirect effect of its higher flexibility to exploit degraded sites compared to the two habitat specialists.

4.2.2. Spatial segregation of species

Relative distribution of the three species, showing a spatial segregation of generalists and specialists according to habitat quality, isolation and connectivity, suggests that interspecific interactions may have an important role in their response to habitat loss and fragmentation. The pattern I have observed in this empirical study is consistent with predictions of theoretical studies (Amarasekare 2003). Results are also in accordance with pattern-based empirical studies that have showed that habitat fragmentation favors generalist species which tend to predominate in fragmented and degraded areas, while specialists are favored in large, connected, high-quality areas (e.g. Nupp and Swihart 2001, Braschler and Baur 2005, Youngentob et al. 2012). The observed pattern, however, may be determined by two underlying mechanisms. The first mechanisms is that the generalist species (*A. sylvaticus*) is able to exploit fragmented contexts better than specialists (as expected in a heterogeneous competitive environment; Amarasekare 2003). The specialist species would be eventually excluded in more fragmented sites through interference/exploitation competition. The second possible mechanism is that habitat specialists are intrinsically more prone to extinction in fragmented and degraded contexts (e.g. due to the disruption of their dispersal ability or demography), so that generalists would be able to exploit vacant habitats where competitive pressure has been released (e.g. Nupp and Swihart 2001). They would be favored in this by their higher colonization ability (as predicted by the competition-colonization trade-off hypothesis in a homogeneous competitive environment; Amarasekare 2003). The demographic approach that I followed allowed me to look more deeply into the mechanisms leading to the observed patterns of spatial segregation, as I discuss in the remainder of the subchapter.

4.2.3. Effect of competitors

By surveying several generations of these short-life and fast-breeding rodents (Amori et al. 2008), I observed the response of species to a variation in the abundance of competitors and directly quantified the actual degree of interspecific interference (Figure 19).

Survival of *A. sylvaticus* was poorly influenced by the co-generic *A. flavicollis*, even at very high densities (e.g. 250 estimated individuals/hectare). On the contrary, the effect of *A. sylvaticus* on the survival of *A. flavicolli*s was much higher and determined a decrease from 0.6 to less than 0.2 in presence of high densities of competitors. This change may reflect higher mortality and/or induced emigration due to competition for resources (e.g. overexploitation by *A. sylvaticus*) or direct interference (e.g. behavioral mechanisms). This result is not consistent with what expected based on the knowledge on these species, which describes *A. flavicollis* as being dominant over *A. sylvaticus* (Hoffmeyer 1973, Hoffmeyer and Hansson 1974, Montgomery 1978). The inverted competitive hierarchy I observed between these two co-generic species confirms that in highly fragmented landscapes competitive relationships may be strongly modified in favor of generalists (e.g. Youngentob et al. 2012).

Also for recruitment I did not detect any strong negative effect on *A. sylvaticus*, instead I found a positive effect on *A. flavicollis* in response to *A. sylvaticus* density. Such positive effect is likely an indirect response of both species to common favorable environmental (local or temporal) conditions, suggesting that in certain contexts they may be both favored at the same time. Furthermore, the increase in recruitment of *A. flavicollis* may help to balance the reduction in survival so that the individual-scale effects do not translate into an overall effect at population level (i.e. abundance of individuals). In fact, I did not observe any negative effect on the abundance of individuals of this species. Therefore, *A. flavicollis* may have compensated the increased mortality/emigration either through an increased production or immigration of individuals (or a combination of both). With the methods I used I could not distinguish production of juveniles from immigration. However, I measured a reduction in reproduction rate (% of reproducing females) of *A. flavicollis* in response to *A. sylvaticus*, which dropped from about 0.4 to almost 0. This effect indicates a possible inhibition of reproduction by competitors (e.g. due to the depletion of resources), therefore it is likely that the increased recruitment observed for *A. flavicollis* was due to immigration (from not-sampled areas within the same patch or from not-sampled neighboring patches) rather than intra-grid production of new individuals.

Body mass showed similar results: as a measure of individual conditions (I stress that to control for age-effects I excluded juveniles and sub-adults from this analysis) mass can reflect the degree to which individuals manage to exploit resources in a site (e.g. Montgomery 1981, Fasola and Canova 2000). I found only negative relationships for this parameter, showing that all the three species compete with each other for resources into a certain extent. The two strongest effects, however, were exerted by *A. sylvaticus* which determined a decrease in the mean body mass of *A. flavicollis* and *M. glareolus* of about 10 % and 15 % respectively, again confirming the potential impact of this species on the performance of habitat specialists.

The effect on body mass, however, was the only negative inter-specific effect that I detected on *M. glareolus*, except for a weak effect on survival rate exerted by *A. flavicollis*, and it did not reflect any other vital rates. As for the effects exerted by *M. glareolus* towards the other two species, I observed a weak reduction in the body mass and survival of *A. flavicollis*. I observed an effect on body mass of *A. sylvaticus* too, which also experienced an overall decrease in the abundance of individuals. It should be noted, however, that these effects were actually weak, confirming the scarce interference that *M. glareolus* had with coexisting *Apodemus* populations (Lambin and Bauchau 1989, Abt and Bock 1998).

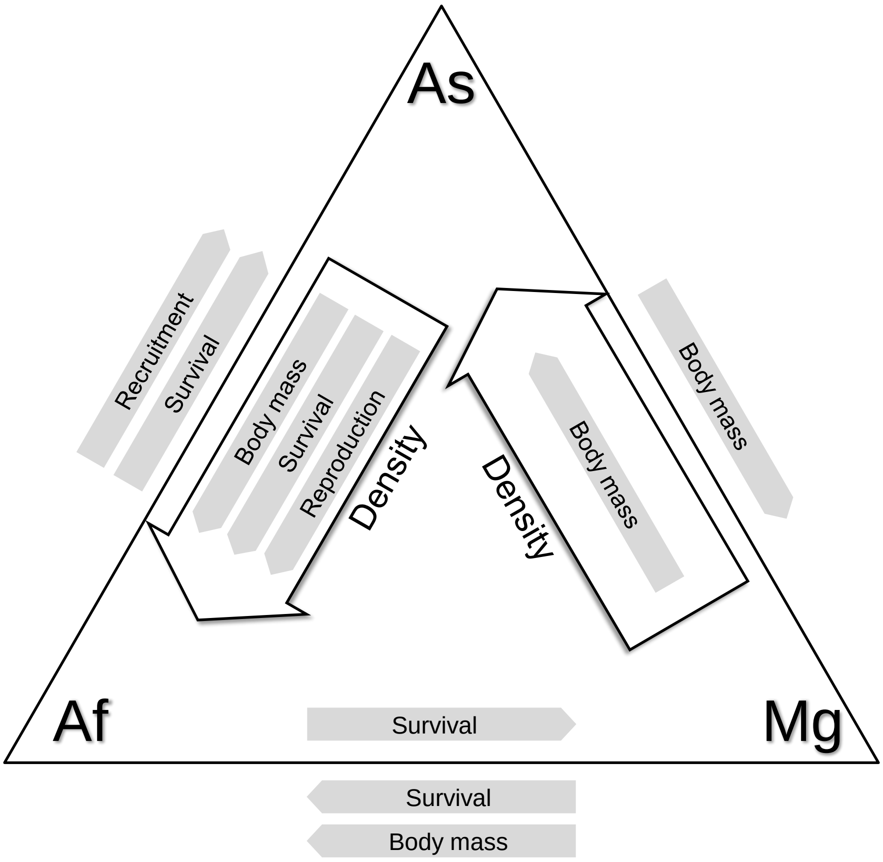


Figure 19. Summary of the reciprocal competitive (negative) effects between *A. sylvaticus* (As), *A. flavicollis* (Af) and *M. glareolus* (Mg). Grey arrows represent significant effects on survival, recruitment, reproduction, body mass; large arrows represent significant effects on population density; the direction of the arrows represents the direction of the effects. Positive effects are not shown.

4.2.4. The role of competition

Empirical results provide stronger support for the heterogeneous competitive environment hypothesis (Amarasekare 2003), predicting generalist species to be competitively superior and to actively exclude specialists in fragmented contexts. Nevertheless I acknowledge that I detected a relatively weak interference between species, acting on a few vital rates, and I could not find strong evidence for an upscale of these individual-scale effects at the level of population abundance. Furthermore, even if a spatial segregation was actually observed, species showed to be able to coexist into a certain extent. Where one species dominated, the other two were almost always able to coexist at low densities, without being completely excluded. These results indicate that interspecific interactions may not be the major force leading to the observed segregation. The scarce competitive effects that I detected suggest that populations were mainly distributed according to their ecological requirements. Competitive exclusion of specialists from isolated and degraded fragments was still acting but was likely to play a minor role in determining the observed pattern of distribution.

A possible explanation of these results is an actual absence of potential competition between these species. However, given the high niche overlapping between these forest-dwelling ground rodents (especially between *Apodemus* spp.), I consider an actual absence of competition and interference as not likely. It is possible that other mechanisms, acting at a biological scale not detectable with my methods, are used by populations to enhance coexistence while avoiding interference. As an example, microhabitat or temporal segregation (e.g. St-Pierre et al. 2006, Buesching et al. 2008, Darmon et al. 2012, 2014, Abu Baker and Brown 2014) may be used by individuals as a response to competitors to reduce negative competitive effects before they are expressed.

4.3. Perceptual range and movement ability

Experiments showed that (a) perceptual ranges were species-specific, (b) individuals followed plantation rows when moving through the matrix at any stage of wheat growth, (c) in grass fields individuals did not follow any preferential direction.

4.3.1. Perceptual ranges

In accordance with Prevedello et al. (2011), the matrix type influenced perceptual ranges of the target species. Individuals were able to perceive the wood only in the bare fields, where the three species showed different perceptual ranges, possibly reflecting their different dispersal capabilities and habitat specialization. *A. sylvaticus* is the most generalist species, it can occasionally be found in the matrix and it is characterized by very high dispersal abilities (Marsh and Harris 2000), so it is supposed to have a higher ability to navigate in the fields; *A. flavicollis* has also high dispersal ability but it is more dependent on forest habitat than *A. sylvaticus* (Marsh and Harris 2000); *M. glareolus* is the most strictly forest species, with very limited dispersal abilities (Harris and Yalden 2008), as confirmed by the fact that it failed to perceive the forest even at 20 m. This result is probably due to the fact that these strictly forest species are not adapted to disperse through open areas and they do not have wood fragments as a search image.

In the other matrix types none of the species perceived the wood: the presence of vegetation, even if very low (only 20 cm), was probably high enough to obstruct their perception. This results may suggest sight as the main navigation system of these species, at least in their initial movements. It is possible that other orienting systems are used (e.g. olfactory cues) to find habitat patches that are not immediately detected by sight.

4.3.2. Movements in wheat fields

In the wheat fields individuals of the three species moved mainly along plantation rows. Wheat fields are an obstructed matrix type in which plantation rows create less obstructed corridors along which animals are facilitated in their movement. Wheat rows were perceived as corridors at any stage of growth, even in the initial phase (low wheat) during which the growing leaves might obstruct the path, compared to the subsequent stages with higher, naked stems. However, they chose to follow them, probably (1) because they were facilitated in moving and (2) to keep a straight direction. The use of environmental cues to keep a straight direction when searching for a new habitat in a hostile matrix has proved to be an efficient strategy compared to random walking, because it minimizes time spent in the matrix (Zollner and Lima 1999).

These results confirm that the orientation of plantation rows in the agricultural matrix influences animals' movement, possibly facilitating or hampering the reaching of a wood.

4.3.3. Methodological considerations

I did not observe any visible negative effects of fluorescent marking on the health and behavior of individuals of the three species that I kept in captivity; furthermore, the fluorescent powder was completely removed from the fur within a day from the marking. I cannot exclude, however, a species-specific effect of disturbance on individuals (handling, marking and translocation) which could differently influence the behavior of the three species. The efficiency of fluorescent powder is limited to its duration, which depends on environmental conditions, such as moisture of vegetation and soil, wind, and presence of vegetation which facilitates dropping of powder. I found that this method was more efficient (in terms of length of detected paths) in the less obstructed matrices possibly because with denser vegetation the powder was lost faster and detected less easily. However, results suggest that this distance was sufficient to determine the perceptual ability of the individuals; furthermore, maximum tracked distance in each matrix type was always sufficient to reach the next forest fragment.

4.3.4. Implications for conservation

These findings have clear implications for the conservation of mammalian species in agricultural cereal-dominated landscapes providing empirical evidence that wheat plantation rows should be planted orientated between habitat patches and should be considered as a complementary conservation strategy to increase connectivity in agricultural landscapes.

I emphasize that an extremely large portion of emerged land is covered by wheat plantations. The potential practical implications of these results are therefore remarkable. Orientation of plantation rows usually follows logistical constraints, e.g. minimizing fuel consumption of tractors for planting/harvesting or suppressing weeds. If compared to expensive conservation initiatives such as creation of hedgerows, however, modifying the directionality of agricultural fields will surely prove to be both feasible and affordable. Landowners should be encouraged to orient plantation rows so as to maximize the connection between habitat fragments (e.g. avoiding to plant wheat rows parallel to woods). I stress that even small scale initiatives may prove significant (see Figure A12 for a relevant example).

Since I worked on three ecologically different species, findings may well extend to a wide range of small and medium-sized terrestrial vertebrates with limited orientation abilities. In order to further generalize these management directives, future studies should investigate (a) the effects of other environmental and landscape factors, i.e. by replicating experiments in additional fields to reduce possible effect of local factors, or by considering additional experimental factors such as microhabitat, slope of terrain, weather, patch size, hedgerows, etc. and (b) the relation between the size of the species and that of the linear structures: do larger animals perceive wheat lines in the same way? Answering to such questions may contribute to a better understanding of the effectiveness of the orientation of plantation rows as a possible strategy to increase landscape connectivity.

4.4. Conclusions

4.4.1. The importance of a multiple-scale approach to understand the effects of habitat fragmentation

This is one of the few studies investigating in detail the demographic mechanisms of response of species to habitat fragmentation. Furthermore, results not only apply to landscapes subject to anthropic disturbance, but they can also be extended to naturally heterogeneous landscapes.

From this point of view, the fragmented landscapes investigated in this work can be seen as "natural experiments", created by human action, where it is possible to study ecological processes that may have a much wider validity, contributing to important advances in the field of landscape and animal ecology, as well as conservation biology. The holistic approach that I followed (Lidicker 1988) allowed me to provide an overview on the process by which factors such as landscape features, habitat characteristics and co-occurring species interact to affect the performance of populations in fragmented landscapes. My results provide insights on the ecological scale (i.e. individuals, populations, systems of populations) where the effects are most relevant. Furthermore, I contributed to understand how individual-scale effects translate into population-scale effects, which is one of the main current ecological question (Sutherland and Freckleton 2013). Unlike occupancy studies, detailed large scale demographic studies 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 such as litter size or survival rates, particularly time- and resource-consuming for mammal species. Even if logistically challenging, demographic studies represent a means to investigate processes leading to population extinction or persistence (Holland and Bennett 2010). The analysis of population occurrence or density alone may lead to erroneous conclusions, as these parameters are not always good proxies for population performance (Van Horne 1983) and in some cases they can mask the real vulnerability of species to habitat fragmentation (Holland and Bennett 2010).

I found that interspecific interactions play a minor role in shaping the community of small mammals in the studied system, influencing vital rates of competitors into a certain extent but without translating into strong effects on population densities. This was not consistent with the results of other studies, showing that in some cases the detrimental effect of fragmentation on species is driven by the alteration of the natural equilibria between species (e.g. Youngentob et al. 2012). I found, instead, that landscape characteristics (habitat cover and connectivity) and local features (habitat quality, in terms of food resources and habitat structure) play a major role for all the investigated species.

The importance of habitat quality, as expected, depends on species-specific life history traits; quality is a key factor for habitat specialists, whereas for habitat generalists it plays a minor role. Such species are more flexible in using different types of habitats, thus being able to exploit even degraded contexts. The demographic approach allowed me to show how the effects of habitat quality translate from the individual level to the level of single populations and systems of populations through concatenated mechanisms. I found that habitat quality enhances individuals' survival and it consequently sustains higher population densities. By increasing survival, it also facilitates the establishment of populations in vacant habitats and helps to increase the persistence of extinction-prone systems of populations.

I also found that an increase of survival did not correspond to a consequent decrease in populations' extinction risk, showing that individual-scale processes are not necessarily linearly transferred from one biological scale to another. This also occurred in the system of competitors that I investigated, where individual level competitive effects did not translate into population level effects, confirming the importance of a demographic approach in dissecting ecological processes. Higher levels of biological organization, in fact, have emergent properties which cannot be deduced by the sum of lower scales' properties (Bennett et al. 2006). Even if habitat quality (in terms of vegetation, food resources or competitive pressure) increases the performance of individuals, animals resulted to be constrained by the physical structure of the landscape where they live, as density and extinction probability of local populations showed to be ultimately determined by landscape features.

The response of species to landscape structure was species-specific, with habitat specialists strictly relying on landscape features which increase the available local habitat (large patches or sites with a large amount of surrounding habitat) or facilitate individuals in their movements (well-connected habitat fragments). Habitat generalists are less influenced by landscape properties and prove to be able to exploit small and isolated fragments, likely due to their higher ability to cross open matrix areas compared to habitat specialists. The importance of landscape properties is also showed by perceptual range experiments, which again highlight the higher ability of generalists in moving through open areas compared to specialists. Crossing the matrix to move between habitat patches in a fragmented landscape proved to be a crucial step, which can drastically hamper the survival of individuals and can thus impede the connectivity between populations, increasing their chance of extinction. A role of fine-scale matrix characteristics (i.e. vegetation patterns, wheat cultivation rows) in facilitating animal movements also emerges, showing the importance of small-scale initiatives to increase functionality of fragmented landscapes.

4.4.2. Implications for conservation

Results of this study suggest that in order to increase the viability of animal systems in fragmented landscapes there is the need to properly manage the quality of habitat, which proved to be a major determinant of animal populations' performance. Nevertheless, findings also strongly suggest not to ignore the overall landscape context where populations are embedded. It appears, in fact, that populations are ultimately constrained by the physical structure of their habitat. For this reason, results of this work suggest that in landscapes that have been extensively cleared, restoration aimed to increase the amount of habitat, as well as the management of outside-patch landscape elements (hedgerows, agricultural fields) might be the most effective way to invest money in order to ensure the persistence of animal communities. Results also suggest that small scale initiatives may be crucial to determine the success of interventions aimed toward the conservation of fragmentation-sensitive species. As an example, increasing the level of connectivity by building a system of hedgerows aimed to help dispersal-limited species may not give the expected results. If hedgerows are not completely connected to woodland fragments there is in fact the risk of favoring more generalist species which are more able to face gaps and move between patches compared to habitat specialist. Intrinsic species-specific characteristics should be never ignored while defining conservation interventions.

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APPENDICES

Table A 1. Presence/absence data used to parameterize multiple season occupancy models of *M. avellanarius* including data for the 38 visits (24 sampling sessions conducted during three years). 0=no captures of the species in the grid, 1= capture of one or more individuals, - =missing visit. In the heading of the table the sampling session is specified: e.g. 8-2 (May 2011) refers to the second visit of the 8th sampling session performed during May 2011. Sessions with more than one visit correspond to months with triple visits. In the first column abbreviations for each grid are reported; LM=Lamone, S= Sabina, V=Viterbo.

Grid	1-1 (May 2010)	2-1 (Jun 2010)	3-1 (Jul 2010)	4-1 (Aug 2010)	5-1 (Sep 2010)	6-1 (Oct 2010)	7-1 (Nov 2010)	8-1 (May 2011)	8-2 (May 2011)	8-3 (May 2011)	9-1 (Jun 2011)	10-1 (Jul 2011)	10-2 (Jul 2011)	10-3 (Jul 2011)	11-1 (Aug 2011)	12-1 (Sep 2011)	12-2 (Sep 2011)	12-3 (Sep 2011)	13-1 (Oct 2011)	14-1 (Nov 2011)	14-2 (Nov 2011)	14-3 (Nov 2011)	15-1 (Dec 2011)	16-1 (Apr 2012)	17-1 (May 2012)	17-2 (May 2012)	17-3 (May 2012)	18-1 (Jun 2012)	19-1 (Jul 2012)	19-2 (Jul 2012)	19-3 (Jul 2012)	20-1 (Aug 2012)	21-1 (Sep 2012)	21-2 (Sep 2012)	21-3 (Sep 2012)	22-1 (Oct 2012)	23-1 (Nov 2012)	24-1 (Dec 2012)
LM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
S-BCC	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-GUD	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	-	-	0	0	-	-	0	0	-	-	0	1	0
S-INF	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-PRT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-PSS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-PST	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-RCR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	-	0	0	-	-	0	0	-	-	0	0	0
S-SCR	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	0	-	-	0	0	-	-	0	0	0
S-SPT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-STL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	-	-	0	0	-	-	0	0	0
S-TLC	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	-	0	0	-	-	0	0	-	-	0	0	0
V-FOR	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
V-GDG	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0
V-GRF	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0
V-JMG	1	0	0	1	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V-MLS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
V-PRV	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1
V-QNC	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	0
V-RSV	1	1	1	1	1	1	0	0	1	1	1	0	0	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
V-SCP	1	1	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1

Table A 2. Data on litter size of *M. avellanarius* for the 62 captures of mother with pups. L=Lamone, S= Sabina, V=Viterbo.

Grid	Date of capture	Number of pups	Grid	Date of capture	Number of pups
L-CAN	20/05/2010	4	L-MAN	10/09/2011	5
L-CAN	20/05/2010	4	L-MAN	4/10/2011	4
L-CAN	31/08/2010	8	L-MAN	12/11/2011	3
L-CAN	5/10/2010	8	L-RIS	6/09/2011	1
L-CAN	5/10/2010	4	L-RIS	6/09/2011	6
L-CAN	5/10/2010	6	L-RIS	10/09/2011	6
L-CAN	4/08/2011	5	L-SUE	1/09/2010	6
L-CAN	4/08/2011	4	L-SUE	30/10/2010	5
L-CAN	10/09/2011	6	L-SUE	10/05/2011	3
L-CAN	4/10/2011	3	L-SUE	10/05/2011	3
L-CAN	28/04/2012	3	L-SUE	14/05/2011	4
L-CAV	1/09/2010	3	V-FOR	2/12/2011	2
L-CAV	2/08/2012	6	V-GRA	5/09/2011	3
L-CAV	2/10/2012	3	V-GRA	7/11/2011	2
L-CIN	29/07/2010	5	V-GRA	7/11/2011	2
L-EAS	30/10/2010	5	V-GRA	7/11/2011	2
L-EAS	30/10/2010	6	V-GRA	2/12/2011	4
L-FRS	1/09/2010	4	V-GRA	2/12/2011	2
L-FRS	30/10/2010	7	V-GRA	2/12/2011	2
L-FRS	5/08/2011	5	V-QNC	13/11/2010	3
L-FRS	9/09/2011	4	V-QNC	13/11/2010	6
L-FRS	9/09/2011	6	V-QNC	3/08/2011	4
L-MAN	18/06/2010	3	V-QNC	3/08/2011	5
L-MAN	30/07/2010	1	V-QNC	5/09/2011	3
L-MAN	5/10/2010	3	V-QNC	5/09/2011	6
L-MAN	5/10/2010	2	V-QNC	5/10/2011	7
L-MAN	5/10/2010	8	V-QNC	7/11/2011	5
L-MAN	31/10/2010	5	V-QNC	26/04/2012	3
L-MAN	31/10/2010	5	V-QNC	6/07/2012	2
L-MAN	26/11/2010	5	V-SCO	7/11/2011	2
L-MAN	5/08/2011	4	V-SCO	3/12/2011	2

Figure A 1. Scatter plots between pairs of predictors for population density of *A. sylvaticus*, *A. flavicollis*, *M. glareolus*. Simpson = shrubs diversity index; Shrub structure = index of vertical complexity of shrubs; Acorns Qc = biomass of *Q. cerris* acorns (g/m2, log10-transformed); Acorns Qp = biomass of *Q. pubescens* acorns (g/m2, log10-transformed); Patch size = size of the wood fragment (hectares, log10-transformed); Habitat 100 and 1000 = wood cover (hectares, log10-transformed) in a 100 or 1000 m buffer around the grid; Hedgerows 100, 900 and 1000 = total length of hedgerows (m) in a 100, 900 or 1000 m buffer around the grid.

Figure A 2. Example of a cereal-crops-dominated fragmented landscape in central Italy, with forest fragments embedded in the agricultural (especially wheat fields) matrix. The picture was taken after wheat harvest.

Figure A 3. Example of interface between a wheat field and a wood fragment.

Figure A 4. Example of a wheat field in early maturation stage.

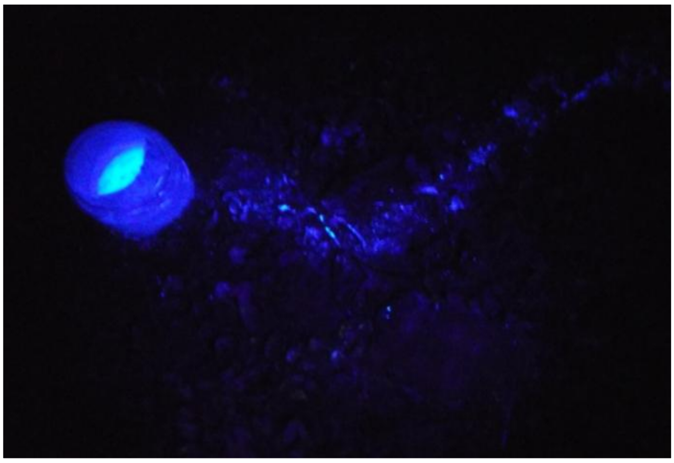

Figure A 5. Release mechanism (a glass jar) with traces of fluorescent powder, visible with ultra-violet light.

Figure A 6. *M. glareolus* marked with fluorescent powder, visible with ultra-violet light.

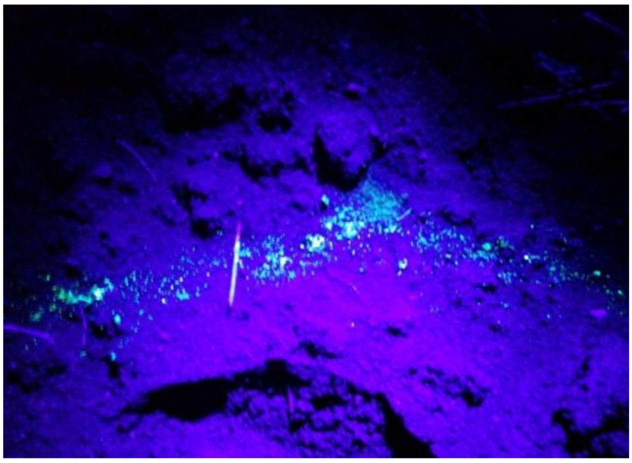

Figure A 7. Segment of the path of an individual (*M. glareolus*) released on the bare uncultivated field, visible with ultra-violet light.

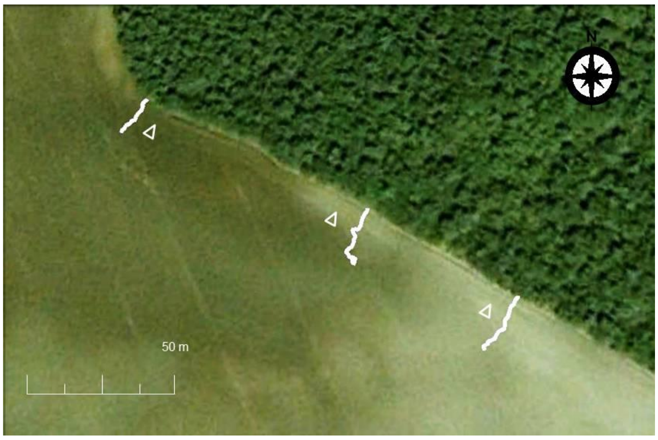

Figure A 8. Example of the paths (white lines) of individuals (*A. flavicollis*) reaching the wood in the bare field. White arrows represent path direction.

Figure A 9. Path of an individual (*M. glareolus*) released in the bare field at 100 m from the wood. White line represents individual path; white arrows represent path direction. Note that the individual did not move towards the wood.

Figure A 10. Path of an individual (*A. flavicollis*) following plantation rows in the wheat field. Black arrows represent plantation rows orientation; white line represents individual path; white arrows represent path direction. Note that the individual followed the row in the opposite direction relative to the wood.

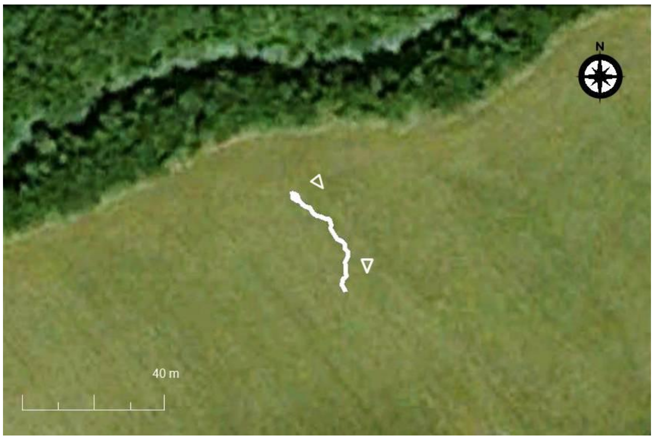

Figure A 11. Path of an individual (*A. sylvaticus*) released in the grass field at a distance of 20 m from the wood. White line represents individual path; white arrows represent path direction.

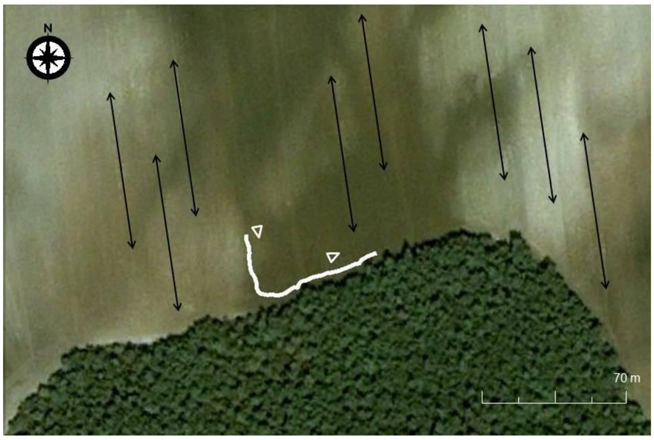

Figure A 12. Path of an individual (*A. flavicollis*) following plantation rows in the wheat field. Black arrows represent plantation rows orientation; white line represents individual path; white arrows represent path direction. In this field plantation rows were directed towards the wood, but in order to facilitate tractor movement, at approximately 2 meters from the habitat patch, the lines were bent to become parallel to the edge of the fragment. Note that, as expected, the individual continued to follow the row without reaching the wood, showing that even small scale field management may prove significant.

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SUPPLEMENTARY PICTURES

Pictures of the study area showing woodland patches, agricultural matrix and hedgerows.

Pictures showing the internal vegetation structure of woodland patches, examples of trap grids (red dots), Sherman traps, Longworth traps and nest-boxes.

Pictures showing individuals of *M. avellanarius* (a, c, e, h, i), *A. sylvaticus* (b), *A. flavicollis* (d), *M. glareolus* (g) during data collection (h, l).