

Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes

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Date of the manuscript draft: September 1, 2015

Manuscript word count: 7330

## Abstract

**Context.** Theory predicts that habitat loss and fragmentation may have drastic consequences on species' interactions. To date, however, little empirical evidence exists on the strength of interspecific competition in shaping animal communities in fragmented landscapes.

5 **Objectives.** Our aim was to measure the degree of ongoing competitive interference between species in fragmented landscapes. Our model system was the community of ground-dwelling rodents of deciduous woodlands in central Italy, composed of a habitat generalist species (*Apodemus sylvaticus*) and two forest specialists (*A. flavicollis* and *Myodes glareolus*). Our objectives were to test whether species were segregated among patches and whether the spatial  
10 segregation was determined by interspecific competition.

**Methods.** We surveyed the populations inhabiting 29 woodland patches in a highly fragmented landscape by means of a capture-mark-recapture protocol, capturing >4500 individuals. First we modelled species' distribution as a function of habitat, resource availability and landscape variables. The second stage of our analyses involved measuring the response of vital rate  
15 parameters (body mass, reproduction, survival, recruitment, population density) to the density of competitors.

**Results.** Species' relative distribution reflected a spatial segregation of habitat generalists and specialists according to habitat quality, cover and connectivity. However, the interspecific effects on vital parameters mainly affected individual level parameters, whereas we found no  
20 substantial effects at the population level.

**Conclusions.** A mechanism of competitive exclusion of generalist species affecting specialist species was occurring. However, if compared to other factors such as habitat connectivity and resources, interspecific competition played a minor role in shaping the studied community.

25 **Key-words.** Agricultural matrix, colonization, emigration, habitat degradation, hedgerows, immigration, landscape mosaic, oak forest, patch size, rodents.

## Introduction

Habitat loss and fragmentation are amongst the major processes threatening the viability of wildlife populations worldwide (Fahrig 2003; Fischer and Lindenmayer 2007). Animal species  
30 are impacted by habitat loss and fragmentation according to their natural history traits (Henle et al. 2004): generalist, edge, or highly mobile species are expected to be scarcely impacted or even advantaged by fragmentation-induced landscape modifications, whereas specialists or less mobile species are expected to decline (e.g. Gibb and Hochuli 2002; Ripperger et al. 2014).

The uneven response of species to landscape change may thus lead to a modification in  
35 the structure of natural communities (e.g. Gibb and Hochuli 2002; Robertson et al. 2013b; Mortelliti and Lindenmayer 2015). As a consequence, fragmentation-sensitive species have to face a landscape with less and more scattered habitat resources, but they may also have to face a new competitive environment (e.g. due to an increase in the abundance of generalist competitors or new invading species) (e.g. Braschler and Baur 2005; Youngtob et al. 2012,  
40 Montgomery et al. 2012). Generalist competitors may deplete a limiting resource for a habitat specialist (exploitation competition) which in turn would be less vital and more prone to decline. Alternatively, interspecific competition may involve direct interference (interference competition), including aggressive behaviour or physical limitation of a species by another one, e.g. by occupying all available nesting sites in a small habitat fragment and thus reducing  
45 the fitness of the other species.

Despite the extensive scientific literature measuring fragmentation-induced effects on species and communities (Fahrig 2003; Lindenmayer and Fischer 2006), the role of interspecific interactions in shaping fragmented populations is still far from being clear (Amarasekare 2003; Magrach et al. 2014). Several theoretical studies describe possible  
50 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).

The best way to study competition in fragmented landscapes would be to use removal experiments (e.g. Ginger et al. 2003; Brunner et al. 2013; but see Dugger et al. 2011). Removal  
55 experiments, however, are hard to conduct at the large scale required to investigate fragmentation-related processes. For this reason, the few studies that have examined interspecific interactions in fragmented landscapes have done so by looking at distribution patterns (Nupp and Swihart 2001; Brown 2007; Kath et al. 2009; Youngentob et al. 2012; Fisher et al. 2013; Robertson et al. 2013a). Nevertheless, inferring competition processes from  
60 pattern-based studies can lead to misleading conclusions. It is particularly difficult, in fact, to understand whether what looks as an apparent competitive response is instead 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 be able to make strong inference on the role of interspecific competition in fragmented landscapes we need to detect  
65 competition in action, which requires a demographic approach. By focusing on the effect of competitors on the vital rates of a target species, researchers can quantify the immediate response of species to competitors and thus partition its effect from the effect of the surrounding landscape characteristics. To the best of our knowledge, there are no large-scale empirical studies directly measuring the effect of competitor species on the demographic  
70 performance of populations in fragmented landscapes.

To contribute in filling the critical knowledge gap on the role of interspecific interactions in shaping animal communities in fragmented landscapes we conducted a large-scale demographic study specifically designed to measure the degree of ongoing competitive interference between species. We used as a model system the guild of forest- and ground-  
75 dwelling rodents of central Italy, which is composed of three species: the wood mouse (*Apodemus sylvaticus*), the yellow-necked mouse (*A. flavicollis*) and the bank vole (*Myodes glareolus*). The wood mouse is a generalist species known to inhabit a wide range of different habitats including forests, hedgerows and agricultural fields, being therefore the least sensitive

to land-use change (Montgomery and Dowie 1993, Marsh and Harris 2000; Mortelliti et al.  
80 2009; Mortelliti et al. 2010b). The bank vole and the yellow-necked mouse, instead, are more  
strictly associated to forest habitats (from mature stands to recently coppiced woodlands, e.g.  
Capizzi and Luiselli 1996; Ecker et al. 2002) and are for this reason here considered as "forest  
specialists". These three species have been extensively studied in the past and several studies  
have provided empirical evidence of potential competition between them (e.g. Montgomery  
85 1980; Montgomery 1981; Buesching et al. 2008; Amori et al. 2010). *A. sylvaticus* and *A.*  
*flavicollis* have highly overlapping trophic niches and daily activity rhythms, whereas  
overlapping with *M. glareolus* is less pronounced (e.g. Canova 1993; Abt and Bock 1998). *A.*  
*flavicollis* is known to behaviourally dominate *A. sylvaticus* and *M. glareolus* both in field and  
experimental conditions, whereas there is no clear dominance hierarchy between *A. sylvaticus*  
90 and *M. glareolus* (e.g. Andrzejewski and Olszewski 1963; Hoffmeyer 1973; Montgomery  
1978; Lambin and Bauchau 1989).

We surveyed the populations inhabiting 29 woodland patches in a fragmented landscape of  
central Italy every other month for two years. This frequent sampling interval allowed us to  
measure the response of one species to a variation in the density of the other two species. We  
95 focused on a set of key ecological parameters (Dooley and Bowers 1998; Bowers and Dooley  
1999; Holland and Bennett 2010) that would allow us to measure the response of individuals  
and populations: body mass, survival, reproduction, recruitment and population density.

We hypothesized species to segregate according to their competitive strength and  
specialization to forest habitat (Tilman 1994; Amarasekare 2003). First, we hypothesized a  
100 spatial segregation between species with habitat specialists being confined in large, well-  
connected, high quality patches, and generalists to exploit small, isolated, low-quality patches  
(e.g. Nupp and Swihart 2001; Braschler and Baur 2005; Youngentob et al. 2012). We tested  
this hypothesis by modelling species' distribution as a function of habitat cover, habitat quality  
and connectivity provided by hedgerows.

105 Second, we hypothesized that the observed distributions were due to a mechanism of  
competitive segregation rather than being a species-specific response to habitat characteristics.  
In order to test this hypothesis we measured the response of the target vital rate parameters of  
each species (body mass, survival, reproduction, recruitment, population density) to the  
increase or reduction in the density of competitors.

110

## Methods

### *Study species*

We focused on the guild of forest- and ground-dwelling rodents in central Italy which is  
115 composed of three species: *A. sylvaticus*, *A. flavicollis* and *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 to land-use change (Marsh and Harris  
100 2000; Mortelliti et al. 2009; Mortelliti et al. 2010b).

Several studies have provided empirical evidence of potential competition between them (e.g.  
120 Montgomery 1980; Montgomery 1981; Buesching et al. 2008; Amori et al. 2010). *A. sylvaticus*  
and *A. flavicollis* have highly overlapping trophic niches, mainly constituted by tree and shrub  
seeds and invertebrate preys (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  
125 behaviourally dominate *A. sylvaticus* both in field and experimental conditions (Hoffmeyer  
1973; Hoffmeyer and Hansson 1974; Montgomery 1978; Cihakova and Frynta 1996). A  
behavioural 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  
130 1989). Niche overlapping between *M. glareolus* and *Apodemus* spp. is less pronounced as *M.*

*glareolus* is more herbivorous, preferring items such as leaves and fruits, but also consuming insects, seeds and fungi into a smaller extent (Gębczyńska 1983; 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 135 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), which makes our study system particularly suited to our scope, as it allows us to focus on competitive effects. We emphasise 140 that our model system includes all the species that compose the community of forest- and ground-dwelling rodents.

### *Study area*

The study was conducted in a fragmented landscape (< 20% of residual woodland cover) 145 located in central Italy (coordinates: 42°30'50", 12°4'40"; elevation: 350 m; Fig. 1). Woodland patches, constituted by mixed deciduous forest dominated by *Quercus pubescens* (downy oak) and *Q. cerris* (turkey oak), were embedded in an agricultural matrix (mainly wheat fields) crossed by a network of hedgerows providing structural connectivity to habitat patches (Fig. 1).

150 #Fig. 1 approximately here#

### *Experimental design and site selection*

Twenty-nine woodland patches were selected following a gradient in patch size and habitat structure (range 0.56 ha to 234 ha). Patch size was measured from aerial photographs through 155 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 and food resource variables). We focused on the structure of the shrub component of vegetation which is known to be very important for small mammals both as a source of food (fruits, leaves, seeds) and as protection from predators (Amori et al. 2008; Buesching et al. 160 2008). Following this approach we managed to obtain a gradient in structure which was not-correlated with patch size.

In each habitat patch a squared trapping grid was set up (7x7 with 10 m of distance between traps). Where the size or shape of the patch did not allow us to build a regular 7x7 grid, the sampled area was modified accordingly maintaining the same trap density (100 165 traps/hectare) and, if applicable, number (49 traps or less, if the patch was not large enough) as regular grids. Grid size ranged from 14 to 49 trap points.

### *Sampling protocol*

Demographic data were collected following a capture-mark-recapture (hereafter CMR) 170 protocol. Twelve trapping sessions were conducted over a two year period, with trapping taking place 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. 175 During the three consecutive nights within a session, instead, populations were considered closed. Closure assumption in each session was confirmed applying closure test ( $p > 0.05$ ) implemented in CloseTest software (Stanley and Richards 2004).

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 180 homogeneous sampling effort per area unit. Traps were baited with a mix of sunflower seeds, peanut butter and apple; bedding was provided for thermoregulation; traps were checked daily early in the morning. Trapped individuals were identified to species level, sexed, assigned to an

age class, 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; several studies found that its effects on vital parameters (such as body weight, survival, etc.) or recapture rate was negligible (Ambrose 1972; Fairley 1982; Montgomery 1985; 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 relatively 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* sp. which was obtained through the protocol by Michaux et al. (2001). Individuals were disinfected with 0.05% sodium hypochlorite solution and released at the capture site. All trapping was conducted in accordance with Italian legislation (Legge 157/92, Articolo 2).

#### 200 *Habitat and food resource variables*

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

Habitat features were sampled in 8 squared plots sized 100m<sup>2</sup> (hereafter quadrats) systematically located within each grid. In each quadrat the cover of each shrub species was

measured through a modified Braun-Blanquet scale (cover classes: 0%, 0.1-25%, 25-50%,  
210 50%-75%, 75-100%). The cover of all species was then summarized through the Simpson's  
Index of diversity to obtain a measure of shrubs abundance-diversity in each grid. The vertical  
structure of shrubs was also measured by visual quantification through an index ranging from 0  
(absence of shrubs in all vertical layers) to 16 (maximum vertical complexity). Vegetation  
measurements were conducted in spring 2012.

215 Further, the productivity of oaks was measured by quantifying the biomass of acorns  
fallen on the ground. Within each quadrat, we located under each productive oak (*Q. pubescens*  
and *Q. cerris*) two circular sub-plots (0.5 m of radius); here we collected, counted and weighed  
all acorns found on the ground. 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  
220 then used to obtain an estimate of the total dry acorns biomass in the grids. Acorn sampling  
was conducted in Autumn 2011 and 2012 in the period immediately following the fall of  
acorns. We sampled acorns twice because 2011 corresponded to a year of high production,  
whereas 2012 was characterized by a much scarcer acorn production. Acorns sampled during  
the high-production year (Autumn 2011) were used as predictor variables for the subsequent  
225 months (i.e. October and December 2011, February, April, June, August 2012), whereas acorns  
sampled during the second year were used as predictors for the period encompassing October,  
December 2012 and February 2012.

### *Landscape variables*

230 Previous studies have shown how different species respond to the amount and configuration of  
habitat at different scales (Wiens 1989; Fahrig 2013).

A series of preliminary analyses was conducted to select the spatial scales with the  
strongest effect on the abundance of each of our target species, following the approach  
suggested by Fahrig (2013). Habitat amount and connectivity were measured in ten concentric

235 buffers around the grids, with radius ranging from 100 m to 1000 m with an increment of 100  
m between buffers. In each buffer, habitat amount was measured as the total cover of  
woodland, 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). We fitted generalized linear mixed models (Poisson  
240 distribution, log link) to model the series of estimated individual abundances of *A. sylvaticus*,  
*A. flavicollis* and *M. glareolus* as functions of habitat amount and connectivity in the ten  
different buffers. We used grid size as an offset variable, and grid ID and sampling session as  
random factors.

For each variable (Habitat or Hedgerows) we selected the spatial scale corresponding to the  
245 model with the lowest AICc (Akaike's Information Criterion). Selected scales were retained for  
all of the following analyses.

### *Data analysis*

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

The goal of the first analysis was to test for spatial segregation between species.  
Species' distribution was modelled by testing 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) on the population abundance of each  
255 species. Predictors were not correlated between each other. A summary of all tested predictors  
is provided in Table S1.

The goal of the subsequent analyses was to measure the effects of competitors on vital  
rates. The effect of interspecific competitors' density (estimated number of individuals/grid  
area) was tested on a set of key parameters representative of the performance of individuals  
260 and populations (survival, recruitment, reproduction, body mass, population density). To take

into account a possible time-lag in the response to competitors, following preliminary analyses, we used the response to competitors with a lag of one session (two months). Furthermore, to take into account possible intra-specific factors in addition to competitors, we also tested the effect of conspecifics' density on survival, recruitment, reproduction and body mass.

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### *Population abundance*

Population size in each grid and session was estimated by fitting CMR models (robust design Pradel models with Huggin's parameterization). Capture and recapture probabilities were modelled as a function of the number of active traps in the grids and season variables (temperature and mm of rain during sampling). In this way we could take into account possible variation in trapping efficiency during the year and between sites.

Generalized linear mixed models (hereafter GLMM) with Poisson distribution (log link) were fitted to model the time-series of estimated abundances of individuals (29 sites and 12 sampling sessions) as a function of local habitat characteristics, food resources and landscape variables (Table S1) or competitors' density. As we did not have data on acorn availability for the period before October 2011, we removed the first three sessions of data from the relative analyses. Grid size was used 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). Grid and sampling session were also used as random factors to account for the non-independence of data from the same site and during the same period of the year.

### *Survival and recruitment*

CMR models (robust design Pradel models with Huggin's parameterization) were fitted to test the effect of intra- and interspecific 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  
290 individuals at time t per individuals at t-1) and it includes individuals actually born in the study area and immigrated individuals (Amstrup et al. 2006).

### *Body mass*

Linear mixed models (hereafter LMM) were fitted to test the effect of intra- and interspecific  
295 competitors' density on individual body mass, an index of body condition (e.g. Montgomery 1981; Fasola and Canova 2000). In order to exclude age-effects on body mass, only adult individuals were used for the analysis; we also excluded pregnant females because of the higher body mass associated to pregnancy. Session and individual ID were used to control for non-independence of multiple data from single individuals. Sampling grid was not used as a  
300 random factor as preliminary analyses showed that it was redundant with individual ID (explained variance ~ zero).

### *Reproduction*

GLMMs with binomial distribution (logit link) were fitted to test the effect of intra- and  
305 interspecific 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. The 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, session and individual ID were used as random  
310 factors.

### *Model selection and effect size*

In each analysis (population density, survival, recruitment, body mass and reproduction) models were ranked according to the Akaike's information criterion corrected for finite samples (AICc). Among each set of hypotheses, top-ranked models (< 2 delta AICc) were used to obtain model-averaged parameter estimates (Burnham and Anderson 2002). Based on these estimates we computed the effect size of each competitor on each target parameter. Effect size was quantified as the increment or decrement of each parameter following an increase in competitors' density from 0 to 100 individuals/hectare. This approach allowed us to quantify the strength of the effect of each variable and to compare it to the relative strength of other predictor variables. CMR analyses were conducted with program MARK (White and Burnham 1999); for all other analyses we used software R (R Core Team 2013).

## 325 **Results**

### *Population dynamics*

We obtained a total of 8109 captures out of 47718 trap-nights. We marked 2056 *A. flavicollis*, 1568 *A. sylvaticus*, and 1121 individuals of *M. glareolus*. Furthermore, we obtained a total of 95 simultaneous captures of two individuals (1.2 % of the total number of captures) both in Longworth and Sherman traps. Seventy-six of these were pairs of individuals of the same species (9 As-As, 59 Af-Af, 8 Mg-Mg), whereas 19 were pairs of different species (11 Af-As, 7 Af-Mg, 1 As-Mg).

Both *Apodemus* species were detected at least once in all woodland patches, while *M. glareolus* was detected at least once in 27 patches. Local population densities varied markedly among patches (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 disappearance.

### *Landscape and habitat factors*

340 Different species-specific spatial scales were selected 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.

The abundance of *A. flavicollis* was positively affected by woodland cover (more cover led to higher abundance), conversely, the abundance of *A. sylvaticus* was negatively affected  
345 by tree cover. *A. flavicollis* was also positively affected by connectivity, as well as *M. glareolus* which increased in well-connected patches, irrespective of woodland cover (Table 1, Table S2). Different habitat and food resources influenced the distribution of our target species. *A. sylvaticus* was associated with low shrub diversity but preferred sites with higher acorn production (both downy and turkey oak). *A. flavicollis* was also associated with a high amount  
350 of acorn (turkey oak) but contrarily to *A. sylvaticus* it preferred sites with high shrub diversity. *M. glareolus* was favoured by a complex vertical structure of shrubs and was negatively associated to sites with high biomass of acorns (downy oak) (Table 1, Table S2).

#Table 1 approximately here#

355

### *Effect of competitors*

Significant effects of intra- and interspecific competitors were found on several individual and population parameters.

*A. sylvaticus* was negatively influenced by the congeneric *A. flavicollis*. High densities  
360 of *A. flavicollis* determined a decrease in survival probability, recruitment and reproduction of *A. sylvaticus* (Table 2, Table S3). High densities of *M. glareolus*, instead, determined a decrease in the mean body mass of *A. sylvaticus*, but without other effects on vital rates. We also observed negative effects on population density, due both to *A. flavicollis* and *M. glareolus* (Table 2, Table S3). We detected significant negative intra-specific effects on

365 survival, recruitment and body mass, as well as a positive intra-specific effect on reproduction probability (Table 2, Table S3).

*A. flavicollis* was negatively influenced by the congeneric *A. sylvaticus* at several levels, including survival, reproduction and body mass (Table 2, Table S3, Fig. 2). *M. glareolus* had significant negative effects on *A. flavicollis* as well, and these effects were exerted on survival, 370 recruitment and body mass (Table 2, Table S3). These effects were lower than the effects exerted by *A. sylvaticus* and did not correspond to population-level effects (Table 2, Table S3, Fig. 2). We also detected significant negative intra-specific effects on all individual level parameters (survival, recruitment, body mass, reproduction).

375 #Fig. 2 approximately here#

*M. glareolus* was negatively influenced by *A. sylvaticus* at the level of survival, body mass and reproduction, whereas *A. flavicollis* only affected its survival probability (Table 2, Table S3). A significant effect of *A. sylvaticus* was also observed on population density. As for 380 the other two species, we detected significant negative intra-specific effects on survival, recruitment and body mass, as well as a positive effect on reproduction probability.

Beyond the negative effects reported above, a few positive responses were also observed between species. Detailed results on positive and negative effects including parameter estimates and effect sizes are reported in Table 2.

385

#Table 2 approximately here#

## Discussion

Our results provide one of the few empirical evaluations of the strength of interspecific 390 interactions in shaping animal communities in fragmented landscapes. A key novelty of our

study is that we followed a demographic approach, which allowed us to quantify the strength of the ongoing competitive interference and thus helped us to dissect the underlying ecological mechanisms. Unlike occupancy studies, detailed large scale demographic studies are not common in the fragmentation literature. This is because of the intensity of sampling required (e.g. monthly surveys repeated over two years) and the difficulty of estimating multiple demographic parameters. Our detailed analyses were possible because of the large sample of individuals captured (more than 4000 marked animals) and because of the strong fluctuations in the abundance of individuals, which provided an ideal experimental context for evaluating the response of the demographic parameters of our target species to an increase/decrease in the abundance of competitors.

The relative distribution of the three target species reflected a spatial segregation of habitat generalists and specialists according to habitat quality, habitat cover and habitat connectivity. Interspecific responses were found but, as we discuss below, they appeared to be relatively weak and acting on parameters at the individual level (e.g. individuals' body mass, survival probability), without substantial effects at the level of population (abundance of individuals). Such interspecific effects, however, were significant and stronger than the corresponding effect of intra-specific factors. Our results showed that a mechanism of competitive exclusion of specialists by generalist was occurring, but, when compared to other factors such as habitat connectivity and resources, it appeared to play a minor role in shaping the studied small mammal community.

#### *Determinants of species' distribution*

Populations were distributed according to species-specific habitat and landscape factors and our findings are consistent with knowledge on the basic ecology of these species, even though a certain degree of regional variation can be observed between different European countries and between different altitudes (e.g. Fitzgibbon 1997).

The two habitat specialists (*A. flavicollis* and *M. glareolus*) were favoured by high connectivity, and high quality sites (in terms of food resources and vertical structure of the vegetation). *A. flavicollis* was also associated to high habitat cover. On the contrary, the  
420 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 for foraging, being able to easily move across it (Sozio et al. 2013), at least in certain periods of the year (Tattersal et al. 2001). The higher ability to move between woodland patches, therefore, can explain its presence in highly fragmented contexts. On the contrary, the two specialist species are less prone to move  
425 out of forest areas (Sozio et al. 2013), occasionally using hedgerows for long-distance movements between patches (Zhang and Usher 1991; Kotzageorgis and Mason 1997; Mortelliti et al. 2009; Mortelliti et al. 2010b). *A. flavicollis* and *A. sylvaticus* were also both favoured by a high biomass of acorns. This finding is consistent with their granivorous habits and confirms the fact that this genus strictly relies on acorn production in oak-dominated  
430 forests (Margaletic and Glavas 2002). On the contrary *M. glareolus* responded negatively to acorns, and its positive response to shrubs (such as hawthorn, *Crataegus monogyna*, or blackthorn, *Prunus spinosa*) is 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  
435 more agile and faster *Apodemus* spp. which are more capable of escaping from predators (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, in terms of shrub diversity, compared to the two habitat specialists (Harris and Yalden 2008).

#### 440 *Spatial segregation of species*

The relative distribution of the three species (i.e. a certain degree of spatial segregation of generalists and specialists according to habitat quality, isolation and connectivity) suggests that

interspecific interactions may have a role in determining their response to habitat loss and fragmentation. The pattern we have observed in our empirical study is consistent with  
445 predictions of theoretical studies, such as a spatial segregation of species based on the trade-off between their competitive strength and colonization ability (Tilman 1994; Amarasekare 2003). Our results are also in accordance with pattern-based empirical studies that have shown how habitat fragmentation favours generalist species which tend to predominate in fragmented and degraded areas, while specialists are favoured in large, connected, high-quality areas (e.g.  
450 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 mechanism is that the generalist species (*A. sylvaticus*) is able to exploit fragmented contexts better than specialists, being a stronger competitor in those contexts (as expected in a heterogeneous competitive environment; Amarasekare 2003). Thus the specialist species would  
455 eventually be 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). As a consequence, generalists are able to exploit vacant habitats where competitive pressure has been released (e.g. Nupp and Swihart 2001). Generalists would be  
460 favoured 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 we followed allowed us to look more deeply into the mechanisms leading to the observed patterns of spatial segregation. Our findings suggest that  
465 the distribution patterns that we have observed are a result of the first mechanism (generalists dominate in the more fragmented contexts and consequently specialists are reduced in numbers), as we discuss in the remainder of our paper.

### *Effect of competitors*

470 By surveying several generations of these short-lived and fast-breeding rodents (Amori et al. 2008; Harris and Yalden 2008), we observed the response of species to a variation in the abundance of intra- and interspecific competitors and directly quantified the degree of ongoing interference.

As expected, the two *Apodemus* species had negative effect on each other's survival, but  
475 the effect of *A. sylvaticus* on *A. flavicollis* was much higher (more than two times higher by comparing effect sizes). The effect of *A. sylvaticus* on *A. flavicollis* was one of the strongest effects we were able to detect: an effect size of -0.2 means that in presence of high densities of *A. sylvaticus*, an *A. flavicollis* individual has 20% less chance of remaining in the population due to competitive effects. This change may reflect higher mortality and/or induced emigration,  
480 e.g. due to competition for resources (overexploitation by *A. sylvaticus*). Other parameters confirmed this result: body mass and reproduction of *A. flavicollis* were reduced in presence of high densities of *A. sylvaticus*, respectively by 1.3 grams and 16% of reproducing individuals. Furthermore, by comparing effect size of inter and intra-specific factors, we found that *A. flavicollis* individuals were much more negatively influenced by *A. sylvaticus* than by  
485 conspecifics (at the level of survival, body mass and reproduction probability). These results are not consistent with previous studies conducted in non-fragmented areas, which describe *A. flavicollis* as being dominant over *A. sylvaticus* (Hoffmeyer 1973; Hoffmeyer and Hansson 1974; Montgomery 1978). The inverted competitive hierarchy that we observed between these two congeneric species strongly suggests that in highly fragmented landscapes competitive  
490 relationships may be strongly modified in favour of generalists (as suggested by Youngentob et al. 2012).

Despite the detection of significant inter-specific competitive effects between the two *Apodemus* species, such effects did not upscale into an effect at the level of population density. In fact, we did not detect a negative effect of *A. sylvaticus* on *A. flavicollis* populations, while

495 the effect of *A. flavicollis* on *A. sylvaticus* was only slightly negative (a reduction of just 0.2 individuals/hectare in presence of high densities of competitors).

We found a positive effect on the recruitment of *A. flavicollis* in response to an increase in the density of *A. sylvaticus*. Such positive effect may be an indirect response of both species to common favourable environmental (local or temporal) conditions, and suggests that in  
500 certain contexts both species may have been favoured at the same time. Furthermore, the increase in recruitment of *A. flavicollis* may help to balance the reduction in survival and may be the explanation of why individual-scale effects do not translate into an overall effect at population level (i.e. abundance of individuals). Therefore, *A. flavicollis* may have compensated the increased mortality/emigration in response to *A. sylvaticus* either through an  
505 increased production of juveniles or through immigration of individuals (or a combination of both). Our analyses did not allow us to distinguish the production of juveniles from immigration. However, the reduction in reproduction rate of *A. flavicollis* in response to *A. sylvaticus* may indicate a possible inhibition of reproduction by competitors (e.g. due to the depletion of resources), therefore we conclude that it is likely that the increased recruitment  
510 observed for *A. flavicollis* was due to immigration rather than intra-patch production of new individuals.

We found that *A. sylvaticus* also had negative effects on the other forest specialist, *M. glareolus*, even though the strongest manifestation of this effect was detected at body mass level (determining a reduction of 2 grams in presence of high density of competitors), whereas  
515 no other strong effects were detected at the individual and population level (e.g. a reduction of just 0.48 individuals/hectare in presence of high density of competitors). As a measure of individual conditions (we stress that to control for age-effects we excluded juveniles and sub-adults from this analysis) body mass can reflect the degree to which individuals manage to exploit resources in a site (e.g. Montgomery 1981; Fasola and Canova 2000). Our results show  
520 that, to a certain extent, all three species compete with each other for resources. This is also

confirmed by the fact that, as observed for the other species, intra-specific effects in *M. glareolus* were much lower than inter-specific effects, showing at least a certain degree of competition between species. The strongest effects at the level of body mass, however, were exerted by *A. sylvaticus*, again suggesting the impact of this generalist species on the performance of habitat specialists.

As for the effects exerted by *M. glareolus* towards the other two species, we observed few negative effects which, however, were weaker than the effect between the two *Apodemus* species (e.g. body mass of *A. sylvaticus* decreased by just 0.72 grams in presence of high density of bank voles), confirming the limited interference that *M. glareolus* has with coexisting *Apodemus* populations (Lambin and Bauchau 1989; Abt and Bock 1998).

We acknowledge that our study lies on the assumption that the three species are, potentially, active competitors. The patterns we have observed could also be interpreted as the result of minimal or reduced potential competition between these species. However, given that several studies provided support for their potential competition, and given the high niche overlapping between these rodents (especially between *Apodemus* spp.), also confirmed by the negative effects on body mass that we detected, we consider this event as unlikely. Other mechanisms, acting at a biological scale not detectable with our methods, may be used by populations to enhance coexistence while avoiding interference. As an example, microhabitat or temporal segregation (e.g. Buesching et al. 2008; Darmon et al. 2012; Abu Baker and Brown 2014) may be used by individuals as a response to competitors to minimize the amount of interspecific interference. As a support to this, we found that multiple simultaneous captures in a same trap were much more frequent between individuals of the same species than between individuals of different species, possibly indicating their propensity to avoid direct interspecific contacts.

545

## Conclusions

Our empirical results suggest generalist species to be competitively superior and to actively limit specialists in fragmented contexts (in partial accordance with an heterogeneous competitive environment, Amarasekare 2003). However, such interspecific limitation appeared  
550 to be exerted mainly on individual vital rates (e.g. survival), without corresponding effects on population abundance.

Even if a certain degree of spatial segregation was actually observed (in terms of contrasting abundance values as function of opposite landscape features), species showed to be able to coexist to a certain extent. In fact, where one species dominated, the other two were almost  
555 always occurring at low densities, without being completely excluded. These results indicate that interspecific interactions may not be the major force shaping the structure of the community. Habitat segregation mainly driven by the natural history traits (i.e. generalist versus specialist), in addition to other mechanisms (e.g. microhabitat and/or temporal segregation) may facilitate the coexistence of these species in the landscapes. An ongoing weak  
560 interference, mainly taking place at the individual scale, appears to act as a further mechanism of continuous adjustment between the coexisting populations of these species.

## Tables

565

Table 1. Model-averaged (based on models within 2 delta AICc) parameter estimates ( $\beta$ ) and standard errors (SE) for the abundance of individuals (12 sampling sessions in 29 sampling grids) of the three species as functions of habitat characteristics and landscape variables.

Variables were standardized before analyses. Habitat 100 and Habitat 1000 = woodland cover (hectares) in a 100 or 1000 m buffer around the grid; Simpson = shrubs diversity index; Acorns Qp = biomass of *Q. pubescens* acorns ( $\text{g/m}^2$ ); Acorns Qc = biomass of *Q. cerris* acorns ( $\text{g/m}^2$ ); 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.

Parameter	$\beta$	SE
<i>A. sylvaticus</i>		
(Intercept)	1.79	0.16
Habitat 1000	-0.48	0.13
Simpson	-0.38	0.13
Acorns Qp	0.15	0.04
Acorns Qc	0.14	0.04
<i>A. flavicollis</i>		
(Intercept)	2.23	0.27
Habitat 100	0.64	0.21
Acorns Qc	0.08	0.06
Hedgerows 900	0.17	0.22
Simpson	0.07	0.13
<i>M. glareolus</i>		
(Intercept)	0.45	0.35

Hedgerows 100	1.00	0.32
Acorn Qp	-0.20	0.04
Shrub structure	1.19	0.32

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575 Table 2. Model-averaged (based on models within 2 delta AICc) parameter estimates ( $\beta$ ), standard errors (SE) and effect sizes for a) survival, b) recruitment, c) body mass, d) reproduction probability of females and e) population density for each species as functions of intra- and interspecific competitors' density (individuals/hectare). As = *A. sylvaticus*; Af = *A. flavicollis*; Mg = *M. glareolus*.

Intra- and interspecific factors:	Effects on <i>A. sylvaticus</i>			Effects on <i>A. flavicollis</i>			Effects on <i>M. glareolus</i>		
	$\beta$	SE	Effect size	$\beta$	SE	Effect size	$\beta$	SE	Effect size
a) Survival									
(Intercept)	0.20	0.13		0.88	0.11		0.39	0.10	
As density	-0.004	0.001	-0.11	-0.009	0.002	-0.22	-0.0004	0.0007	-0.009
Af density	-0.004	0.001	-0.09	-0.003	0.0006	-0.08	-0.004	0.0008	-0.09
Mg density	0.0002	0.0004	0.01	-0.0004	0.0006	-0.01	-0.00007	0.0002	-0.002
b) Recruitment									
(Intercept)	-0.43	0.07		-0.52	0.06		-0.85	0.07	
As density	-0.0006	0.0007	-0.04	0.002	0.0007	0.15	0.001	0.0006	0.05
Af density	-0.002	0.0006	-0.13	-0.001	0.0004	-0.12	0.001	0.0005	0.07
Mg density	0.0001	0.0002	0.01	-0.00008	0.0002	-0.004	-0.00003	0.00008	-0.001
c) Body mass									
(Intercept)	26.50	0.41		32.30	0.45		28.92	0.96	
As density	-0.001	0.002	-0.12	-0.013	0.003	-1.3	-0.02	0.003	-2.0
Af density	0.001	0.002	0.10	-0.00006	0.0004	-0.006	0.0005	0.001	0.05
Mg density	-0.007	0.003	-0.72	-0.004	0.003	-0.36	-0.004	0.002	-0.41
d) Reproduction probability of females									
(Intercept)	-0.49	0.34		-0.52	0.28		-1.50	0.48	

As density	0.00004	0.0003	0.001	-0.008	0.002	-0.16	-0.002	0.002	-0.02
Af density	-0.0007	0.001	-0.02	-0.0005	0.0008	-0.01	0.003	0.002	0.04
Mg density	0.001	0.002	0.02	0.001	0.002	0.03	-	-	-

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e) Population density

(Intercept)	1.93	0.20		1.97	0.32		0.67	0.39	
As density	-	-	-	0.003	0.0006	2.2	-0.003	0.0007	-0.48
Af density	-0.0002	0.0004	-0.2	-	-	-	0.001	0.0005	0.31
Mg density	-0.005	0.0007	-2.8	0.0001	0.0003	0.08	-	-	-

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580

## Figure captions

Fig 1. Study area located in the Viterbo Province, central Italy. Black shapes = sampled  
585 woodland patches; grey shapes = woodland patches that were not sampled; white areas =  
agricultural matrix; lines = hedgerows.

Fig 2. Partial plots with the effect of intra-and interspecific competitors' density ( $A_s = A.$   
*sylvaticus*,  $A_f = A. flavicollis$ ,  $M_g = M. glareolus$ ) on survival probability, recruitment (number  
590 of new individuals at time  $t+1$  for each individual at time  $t$ ), % of reproducing females and  
body mass (g) of *A. flavicollis*.

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## Online Supplementary Material

- 770 Table S1. Summary of habitat, food resources and landscape variables used as predictors.
- Table S2. Ranking of GLMMs on individual abundance as a function of habitat and landscape variables.
- Table S3. Ranking of models on survival, recruitment, body mass, reproduction probability of females and individual density of each species as functions of conspecifics and interspecific
- 775 competitors.