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Hierarchical spatial segregation of two Mediterranean vole species: the role of patch-network structure and matrix composition

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Abstract According to ecological theory, the coexistence of competitors in patchy environments may be facilitated by hierarchical spatial segregation along axes of environmental variation, but empirical evidence is limited. Cabrera and water voles show a metapopulation-like structure in Mediterranean farmland, where they are known to segregate along space, habitat, and time axes within habitat patches. Here, we assess whether segregation also occurs among and within landscapes, and how this is influenced by patch-network and matrix composition. We surveyed 75 landscapes, each covering 78 ha, where we mapped all habitat patches potentially suitable for Cabrera and water voles, and the area effectively occupied by each species (extent of occupancy). The relatively large water vole tended to be the sole occupant of landscapes with high habitat amount but relatively low patch density (i.e., with a few large patches), and with a predominantly agricultural matrix, whereas landscapes with high patch density (i.e., many small patches) and low agricultural cover, tended to be occupied exclusively by the small Cabrera vole. The two species tended to co-occur in landscapes with intermediate patch-network and matrix characteristics, though their extents of occurrence were negatively correlated after controlling for environmental effects. In combination with our previous studies on the Cabrera-water vole system, these findings illustrated empirically the occurrence of hierarchical spatial segregation, ranging from within-patches to among-landscapes. Overall, our study suggests that recognizing the hierarchical nature of spatial segregation patterns and their major environmental drivers should enhance our understanding of species coexistence in patchy environments.

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Introduction

Understanding the mechanisms facilitating the coexistence of potential competitors in patchy environments is a long-standing topic in ecology (Hanski 1983; Chesson 2000; Amarasekare 2003; Valladares et al. 2015). Most studies have addressed this problem by evaluating how species segregate along patch-level niche axes, such as food, microhabitat or time of activity (Holt 2001; Jorgenson 2004; Leibold and McPeek 2006). However, it is possible that coexistence may also be facilitated by niche partitioning

beyond local habitat patches, with, for instance, variation in patch-network structure and matrix composition contributing to determine whether two competitors can coexist at the local and regional levels (Hanski and Ranta 1983; Yu et al. 2001; Nowakowski et al. 2013). Although this idea has been widely addressed theoretically, empirical investigation of landscape-level niche partitioning remains relatively scarce (Amarasekare 2003; Boeye et al. 2014).

In a system with two asymmetric competitors, the most extreme case of landscape-level segregation may occur when the dominant competitor occupies all landscapes meeting its requirements in terms of, for instance, patch-network and matrix characteristics, while the subordinate competitor is forced into landscapes unsuitable for the dominant competitor (Schippers et al. 2015). In this case, coexistence would only be possible at the regional scale, because the two competitors would be unable to share the same landscapes. At the other extreme, the two species may always be able to coexist at the landscape level, which is often judged to result from the interplay between species' limiting factors, competitive and colonization abilities, and the spatial distribution of shared resources (Amarasekare and Nisbet 2001; Amarasekare 2003; Hanski 2008). A situation intermediate between these two extremes may also occur, with some landscape features leading to occupation by either only the dominant or only the subordinate competitor, and others favoring the coexistence of the two species. For instance, the subordinate competitor may be totally absent from landscapes that are optimal for the dominant competitor, but be able to coexist or even be the sole occupant in less favorable landscapes (Durant 1998). However, even in landscapes where both species coexist, the dominant may still influence the subordinate competitor by constraining its distribution or abundance at smaller spatial scales (Amarasekare 2003; Schippers et al. 2015). Overall, therefore, it is possible that segregation may occur over a hierarchy of scales depending on environmental circumstances, with potential competitors using, for instance, different landscape types, different patch types within landscapes where they coexist, and different space, time, and food resources within those patches that are used simultaneously. At present, little information is available to test these ideas, probably because this would require detailed data on species distribution and co-occurrence patterns across landscapes with different properties (e.g., Yu et al. 2001; Richter-Boix et al. 2007; Schmidt et al. 2008), which are often costly to collect and difficult to replicate in natural systems, particularly for vertebrate species.

In this study, we used a system of two vole species that share similar resources in Mediterranean farmland landscapes, to evaluate whether segregation occurs at more than one spatial scale, and whether segregation at different scales is associated with pa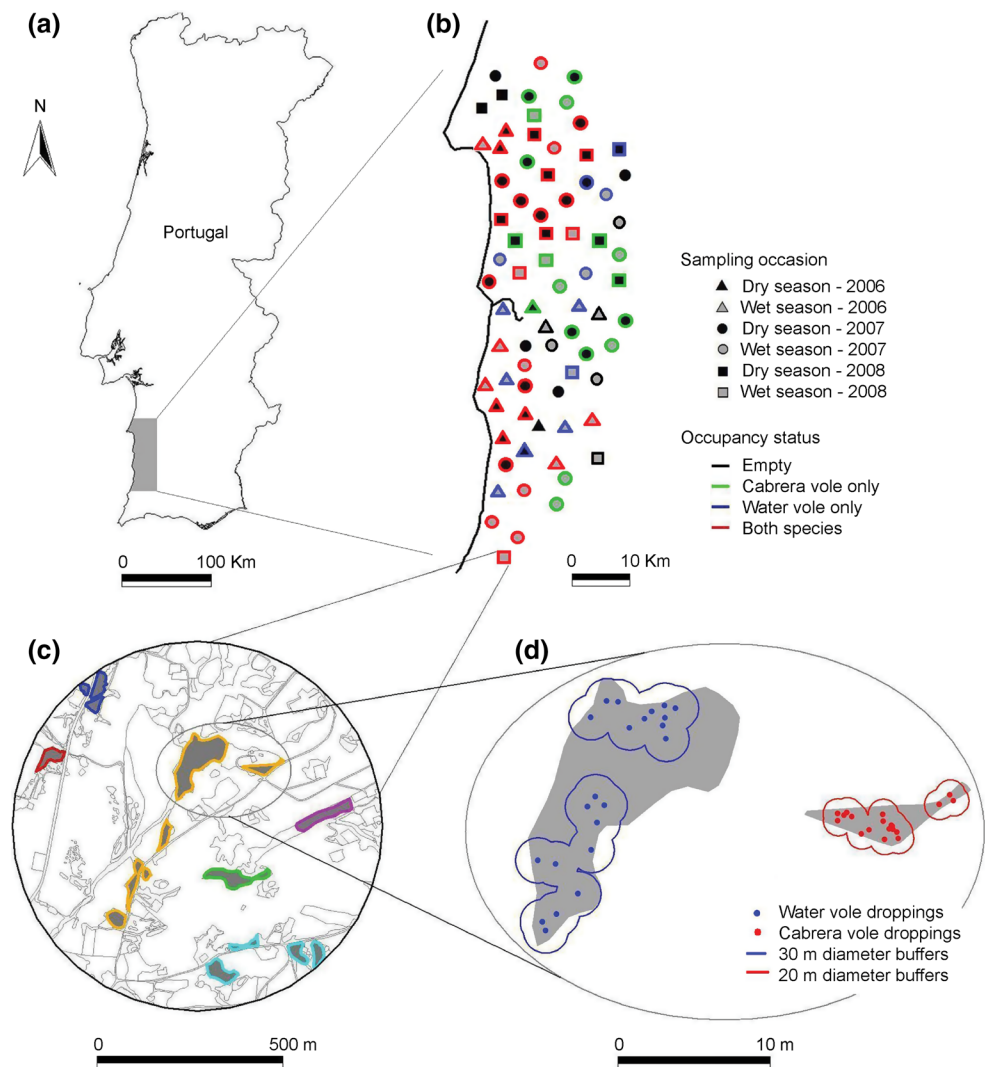rticular environmental conditions. We focused on two species of conservation concern (Palomo et al. 2007), the Cabrera vole (*Microtus cabrerae*) and the southern water vole (*Arvicola sapidus*, hereafter water vole), which in agricultural landscapes exhibit a metapopulation-like spatial structure, occupying similar patches dominated by wet and tall herbaceous vegetation, imbedded within matrices of varying land use types (Pita et al. 2007, 2013). Previous studies have shown that Cabrera and water voles share much the same food preferences, grazing mostly on evergreen annual and perennial monocotyledons, such as grasses, sedges, and rushes (Soriguer and Amat, 1988; Román 2007; Rosário et al. 2008). However, the species tend to segregate at the patch-level, along axes of space, microhabitat, and time of activity (Pita et al. 2010, 2011a, b). In the case of time, for instance, there was some evidence that the dominant competitor (water vole) excludes the subordinate competitor (Cabrera vole) from its preferred time of activity (Pita et al. 2011b). Segregation beyond the patch-scale has never been assessed, but this may occur, because each species is strongly affected by landscape features such as patch-network structure and matrix composition (Pita et al. 2007, 2013). Therefore, to test whether segregation occurs over a hierarchy of spatial scales, we examined the distribution and co-occurrence patterns of the two species across replicate landscapes with variable habitat amount, patch density, and matrix composition, assessing: (1) whether the two species coexist in some landscapes but not in others; (2) how shared and exclusive use by each species are shaped by landscape features; and (3) whether the area used by each species within shared landscapes (extent of occurrence) is consistent with a negative impact of the dominant competitor on the subordinate competitor (Guillaumet and Leotard 2015). Results are used to discuss the implications of hierarchical spatial segregation for understanding the coexistence of potential competitors in fragmented landscapes.

Methods

Study system

The study was conducted in south west Portugal (37°21′–38°04′N, 08°51′–08°30′W, Fig. 1a), which is characterized by Mediterranean climate with oceanic influence, with mean monthly temperatures about 16 °C, and average annual rainfall around 650 mm, of which >80 % falls between October and March (wet season) (Pita et al. 2009; Beja et al. 2014). During our study, the mean monthly temperature ranged from 11.2 °C (wet season, 2007) to 21.0 °C (dry season, 2006), and mean monthly precipitation ranged from 28.1 mm (dry season, 2008) to 101.0 mm (wet season, 2006) (Table SM1 in Supplementary information). The

region is mainly devoted to mixed annual crop–livestock farming (>65 % of the study area), while woody cover is restricted to a few woodlots (mean ± SE = 3.54 ± 0.34 ha) and hedges with planted trees (mainly pines and eucalyptus) delimiting irrigated fields (Pita et al. 2009; Beja et al. 2014). Semi-natural habitats occur in dunes, stream valleys, and cork oak woodlands surrounding the farmed area. Despite the overall trend for agricultural intensification since the early 1990s, some areas have been abandoned or maintain extensive agriculture, resulting in many landscape types and ecological gradients that reflect different management options (Pita et al. 2009; Beja et al. 2014).

Cabrera and water voles occur in the study area as spatially structured populations, and they are both largely restricted to of wet and tall (≈>30 cm) herbaceous vegetation dominated by grasses, sedges, rushes, and reeds, typically along small streams, temporary ponds, field margins, and road verges (Pita et al. 2007, 2013). Within habitat patches, individuals of both species tend to show strong

site-fidelity, with mean ± SE (range) home-range sizes of 946.3 ± 126.3 m² (198.2–2600.2 m²) for the larger-sized water vole, and 418.2 ± 56.3 m² (39.3–1075.6 m²) for the smaller-sized Cabrera vole (Pita et al. 2010).

Sampling design

The study was conducted between 2006 and 2008, and was based on 75 landscapes selected across the study area. Each landscape corresponded to a circular area with ≈78 ha, encompassing vole habitat patches and the surrounding matrix occupied by a variety of land uses. The mean ± SE (range) nearest neighbor distance between centers of landscapes was 3.6 ± 0.07 km (2.5–5.8 km) (see Fig. 1b). Landscape size was set to be much larger than the area used by adult breeding voles (i.e., >800 times larger than their mean home-ranges; Román 2007; Pita et al. 2010), while allowing replication across the region, such that a wide range of landscape types could be sampled (as in Bennett

et al. 2006). A total of 20, 37, and 18 landscapes were surveyed in 2006, 2007, and 2008, respectively, with a total of 38, and 37 surveyed during the wet (October–March) and dry (April–September) seasons, respectively (Fig. 1b). In each landscape, a single snapshot survey was conducted to characterize the patch-network structure and matrix composition, and to assess the (1) presence/absence of each species in the landscape, (2) and the extent of occupancy of each species within each landscape (see below).

Landscape variables

Suitable vole habitats were visually identified through systematic field surveys and mapped from GPS recordings made along their borders, considering a minimum polygon area of 50 m^2, and a minimum distance between polygons (ground resolvable distance) of 5 m (Pita et al. 2013). Information was then incorporated in a geographical information system (GIS, ArcView 3.2, Redlands, CA, 1999). Patch networks were described by estimating the total area (ha) covered by suitable habitat for voles (hereafter referred to as habitat amount), and the number of potential breeding habitat patches (i.e., patches larger than the minimum area required for a breeding pair and respective progeny) per square km (hereafter referred to as patch density) (Fig. 1c).

Information on the minimum areas required by breeding pairs of Cabrera and water voles was unavailable, thus, we set the threshold based on the minimum home-range sizes for resident adults of each species observed in our study area (Pita et al. 2010), though excluding a few very small outliers. We considered that the minimum breeding patch for Cabrera voles corresponded to one or more habitat polygons distanced from each other by less than 50 m and covering a total habitat area of at least 250 m^2. Breeding habitat patches for water voles were estimated likewise, by setting the thresholds at 100 m and 500 m^2, respectively. After computing patch density estimates for the two species using these thresholds, we found that they were strongly correlated (Pearson's $r = 0.88$, 95 %CI = 0.81– 0.92, $P < 0.001$). Therefore, in subsequent analysis for both Cabrera and water voles, we estimated patch densities based on the threshold for the later species. This was a simplification, because the perceptual range of patchiness is species-specific (Swihart et al. 2003), but we believe it provides a reasonable basis to assess potential spatial segregation along patch density gradients (as in Basset 1995; Basset and de Angelis 2007). The rationale is that breeding area requirements of the smaller species are nested in those of the larger one (Basset and de Angelis 2007), and that occupied patches we treat as distinct units actually function as independent local breeding populations for both species. This assumption would have been difficult to accept for water voles if we had defined patches based on

Table 1 Summary statistics of landscape variables recorded per landscape ($n = 75$) sampled for Cabrera and water voles in SW Portugal (2006–2008)

Set/variables	Units	Code	Mean ± SE	Range
Patch network				
Habitat amount	ha	HA	1.90 ± 0.26	0–12.91
Breeding habitat patch density*	*Patches/km^2	PD	3.15 ± 0.23	0–8.97
Matrix				
Cover agricultural land	ha	AGRIC	10.10 ± 1.68	0–65.69
Cover extensive pastures	ha	EPAST	16.28 ± 1.85	0–59.42
Cover intensive pastures	ha	IPAST	12.49 ± 2.13	0–63.77
Density of irrigation structures	km/km^2	IRRIG	0.34 ± 0.11	0–4.78

* Based on the perceptual ranges of the larger species, the water vole (see "Landscape variables" for details)

the threshold for the Cabrera vole. Some caution is needed when interpreting the results, however, as small patches potentially providing breeding areas for Cabrera voles (i.e., those between 250 and 500 m^2) are necessarily overlooked. These small patches represented only <5 % of the overall patch number, thus excluding them was unlikely to have had major impacts on our results.

The main types of land uses in the matrix expected to affect the species were also mapped in the GIS, based on high resolution (0.5 m/pixel) aerial photographs from 2005, and ground validation. These included the cover (ha) by agricultural fields (AGRO, land used for the production of cereals, vegetables, and other crops), extensive pastures (EPAST, semi-natural pastures, and fallows lightly grazed by cattle), improved pastures (IPAST, sown and irrigated pastures for cattle grazing), and the density (km/km^2) of irrigation structures (IRRIG, irrigation channels and drainage ditches) (Pita et al. 2007, 2013; see Table 1 for summary statistics).

Vole surveys

Cabrera and water vole surveys were based on systematic searches for their typical presence signs, in particular, fresh latrines or scattered droppings along runways, which are easily recognizable in the field (Fedriani et al. 2002; Pita et al. 2007, 2013). Searches at each landscape lasted in average (±SE, range) 4.1 ± 2.2 days (0.5–8 days), with more effort devoted to landscapes with larger amounts of potential habitat. Within each landscape, longer surveys were made in larger patches, with a minimum of about half an hour per patch. This sampling effort was judged to

have minimized the likelihood of false negatives, as recent studies on the water vole suggest that occupancy may be detected in 80–100 % of cases during 30-min surveys, even in large patches (Fernández et al. 2016; Peralta et al. 2016). Considerable care was also taken to accurately distinguish the dropping of both species, which was mainly based on their sizes: length × width in mm of 4.8–9.6 × 1.8–3.2 in Cabrera voles versus 7.0–16.0 × 3.0–6.9 in water voles (Garrido-García and Soriguer 2014; Román 2014). Reliability in the identification of vole droppings was validated using molecular methods (Barbosa et al. 2013; Mira et al. unpublished data).

Sign surveys were always conducted in periods with no precipitation during at least the previous 2 days, to avoid flattening and wetting of feces. Searches consisted in scanning the whole surface of suitable habitats mapped, starting in preferred microhabitats (i.e., relatively taller and denser vegetation sites) and then expanding to other less suitable locations, so as to maximize the likelihood of detecting the target species (MacKenzie and Royle 2005; Peralta et al. 2016), which are often clustered on a particular portion of the patches. Searches often implied lifting the vegetation, though minimizing disturbance as much as possible. When vegetation density in one particular site was too high to walk through (e.g., bramble *Rubus* thickets), we searched around the edges enclosing that site. The locations of all vole droppings detected were recorded with a GPS with 5 m precision.

Surveys were used to estimate the occupancy of each landscape (hereafter landscape occupancy) considering four possible categories: empty, occupied by either cabrera or water voles, and occupied by both species. We also estimated the extent of the area occupied by each species within each landscape (hereafter extent of occupancy), based on the spatial distribution of droppings. This was done by creating and merging buffers of 20 and 30 m diameters centered on each GPS location of Cabrera and water voles droppings, respectively (as in Pocock et al. 2003; see Fig. 1d). These buffer lengths were defined to provide a circle with an area close to the mean home-range estimated in the study area for each species (Pita et al. 2010).

Data analysis

Multinomial logit (unordered) generalized mixed effect modeling (Multinomial GLMM) with Bayesian Markov chain Monte Carlo (MCMC) simulation was used to model the probability of landscape occupancy by each species alone and by both species together in relation to patch-network and matrix covariates, using empty landscapes as a baseline category. Landscapes without suitable vole habitats (i.e., patches dominated by wet and tall herbaceous vegetation) were dropped to avoid trivial results. We used

the maximal random intercept structure effects justified by our experimental design, so as to better control variation, increase the power of the analyses, and optimize generalization of the findings (e.g., Gillies et al. 2006; Barr et al. 2013). Therefore, we included in the random component four categorical variables reflecting potential effects of sampling year (three levels), sampling season (two levels), and spatial contagion in the distribution of Cabrera and water voles (four levels each, based on equal class intervals of the proportion of occupied landscapes in a 5-km buffer of each focal landscape). The buffer radius corresponded to the maximum dispersal distance recorded for the larger species, the water vole (Román 2007). Before analysis, covariates were scaled and log-transformed, to reduce the influence of extreme values and improve model convergence. Colinearity among all covariates was tested using variance inflation factors (VIF), and considering VIFs <2 as indicating acceptable levels of colinearity (Zuur et al. 2010).

In multinomial model building, we first assessed the effect of each covariate alone on landscape occupancy, and then selected as candidate those covariates which yielded deviance information criterion (DIC) values lower than that of the null model (including random effects only). This allowed reducing the number of possible covariates, and avoided the examination of candidate models with too many parameters relative to the number of observations (e.g., Kleinbaum et al. 1998). Candidate models including multiple covariates were then built using all possible subsets of influential variables. Due to limited sample size, only main effects were considered in model building. The best candidate model had the lowest DIC, but we also retained as equally supported all models at <5 DIC units from the best (ΔDIC). For each model, we estimated the 95 % credible intervals (CI) and pMCMC-values (significant pMCMC < 0.05) of each covariate. Model fit was estimated using pseudo-R^2 (Johnson 2014). A similar MCMC-GLMM modeling approach based on bivariate Gaussian distribution error was used to relate the extent of occupancy of each species to patch-network and matrix covariates. Empty landscapes were excluded from this analysis. Model posterior distributions were used to estimate the correlation between the two dependent variables; given as $\mathrm{Corr}_{\mathrm{Mc,As}} = \mathrm{Cov}_{\mathrm{Mc,As}} / \sqrt{V_{\mathrm{Mc}} \cdot V_{\mathrm{As}}}$, where $\mathrm{Cov}_{\mathrm{Mc,As}}$ is the covariance between the extents of occupancy of the Cabrera (Mc) and the water vole (As), and V_{Mc} and V_{As} represent the respective variances (e.g., Hadfield 2010; Wilson et al. 2010). Significant correlations were determined by the 95 % credible intervals not overlapping with zero. For simplicity, we present, here, the results of the model yielding lowest DIC values in each set of analysis. Results regarding alternative models are presented in Supplementary material (Tables SM1–SM6).

Table 2 Candidate models to explain landscape occupancy by Cabrera and water voles, and their respective DIC values, ΔDIC, and adjusted pseudo-R^2

Fixed effects	DIC	ΔDIC	Adjusted pseudo-R^2
HA + PD + AGRIC*	128.04	0.00	0.47
HA + PD + AGRIC + EPAST*	130.79	2.75	0.45
HA + PD*	130.96	2.92	0.43
HA + AGRIC	133.22	5.18	0.41
HA + PD + EPAST	134.47	6.43	0.41
HA + AGRIC + EPAST	134.78	6.74	0.41
HA	135.69	7.65	0.37
HA + EPAST	137.71	9.67	0.37
PD + AGRIC + EPAST	141.71	13.67	0.34
PD + AGRIC	142.32	14.28	0.32
PD + EPAST	144.72	16.68	0.30
PD	147.05	19.01	0.25
AGRIC + EPAST	150.10	22.06	0.24
EPAST	154.28	26.24	0.18
AGRIC	158.60	30.56	0.12
NULL	164.93	36.89	

* Indicates most supported models (ΔAIC ≤ 5). See Table 1 for variable codes

GLMMs were run in the package 'MCMCglmm' version 2.19 (Hadfield 2010) using R 3.0.2 (R Development Core Team 2014), keeping >1000 posterior samples (Hadfield 2012). Models were run until they reached acceptable low levels of first-order autocorrelation (generally <0.08 for successive iterations) for both fixed and variance components (Plummer et al. 2006; Hadfield 2010), and until they reached convergence, as assessed visually using trace plots for both fixed effects and variance components, and computationally using Geweke's convergence diagnostic (Plummer et al. 2006). For multinomial models, we used 1×10^8 iterations, burn-in size of 1×10^5, and sampling every 5×10^4 iterations, whereas for Gaussian models, we used 3×10^4 iterations, burn-in size of 3×10^3, and thinning interval of 10 iterations. Prior specification in multinomial models followed Hadfield (2012), setting variance at one for all diagonal terms (variances) and 0.5 for all off-diagonal terms (covariances) in the residual structure. For random effects, we specified priors to have a variance equal to one, with a degree of belief (nu) equal to one. We screened multiple alternative priors and selected those producing the best trace plots of the variance components, though model results were largely insensitive to changes in the prior specification. For Gaussian models, we used default uninformative flat priors for the residual structure, while for the random component, we set the variance at one, and the nu at 0.002 (Gelman 2006; Hadfield 2012). Adjusted pseudo-R^2 were estimated with 'MuMIn' (Barton 2014).

Results

A total of 142.7 ha of suitable habitat for voles was found in 69 of the 75 landscapes surveyed, corresponding to ca. 3 % of the surveyed area. Overall, 184 patches > 500 m² were identified in 68 landscapes, of which 51 and 42 % were occupied by Cabrera and water voles, respectively, and 18 % were occupied by both. Also, 17 small (<500 m²), isolated (>100 m from the nearest patch) habitats were identified in 14 landscapes. From these, eight patches in seven landscapes could be considered as potentially providing exclusive breeding patches for Cabrera voles (i.e., those between 250 and 500 m²). Presence signs of Cabrera and water voles were found in three and one of these habitats, respectively, with no evidence for local co-occurrence. Overall, 62 landscapes were occupied by at least one species, of which 26 % were occupied exclusively by Cabrera voles, 17 % were occupied by water voles alone, and 46 % were occupied by both species (Fig. 1b).

Colinearity among covariates was low (VIFs <2, see Supplementary material, Table SM2), and thus, they were all considered in the analyses. Multinomial MCMC-GLMM regressions with single covariates provided support for the influence of patch density, habitat amount, and proportional cover by agricultural land and extensive pastures on landscape occupancy status (Supplementary material, Table SM3). These variables were used to build 16 candidates models, three of which were roughly equally supported (ΔDIC < 5; Table 2). Among these, the model including habitat amount, patch density, and cover by agricultural
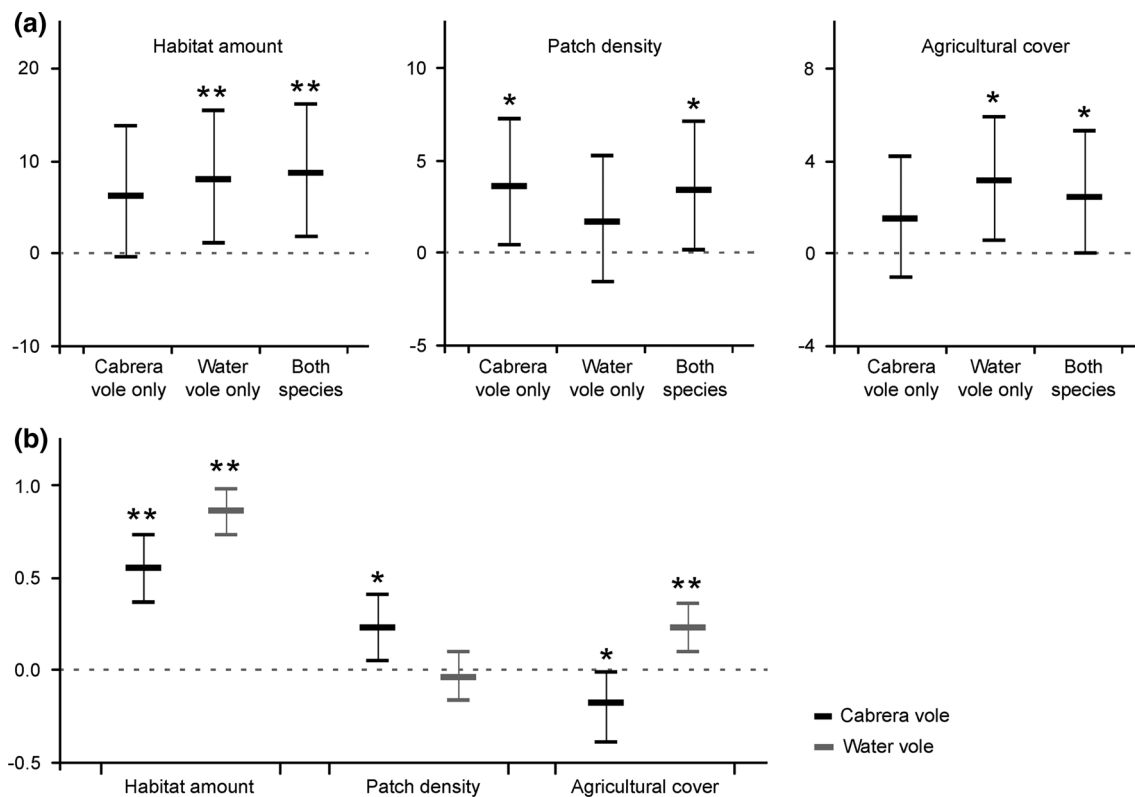
Fig. 2 **a** Posterior estimates of model coefficients and 95 % CI for the first ranked multinomial MCMC-GLMM logit model relating landscape occupancy to habitat amount, patch density, and cover by agricultural land. Empty landscapes were the baseline category (location of the effects = 0) (see Supplementary material, Table SM3). **b** Posterior estimates of model coefficients and 95 % CI for the first ranked bivariate Gaussian MCMC-GLMM models relating the extent of area occupied by Cabrera and water voles to habitat amount, patch density, and agricultural cover (see Supplementary material, Table SM6). Effective sample size was >1000 for all fixed effects in all models run. *Asterisks* indicate that coefficients are significantly different from zero: *$P < 0.05$; **$P < 0.001$

land had the lowest DIC and an adjusted pseudo-R^2 of 0.47 (Table 2). Results were largely consistent among the three best supported models (Supplementary material, Table SM4), indicating that landscape occupancy by water voles alone or by both vole species together was very significantly favored by higher amounts of habitat (pMCMC <0.001), while exclusive landscape occupancy by the Cabrera vole was significantly (pMCMC <0.05) favored by higher patch density. Also, landscapes with increased cover by agricultural land showed significantly higher probability of being occupied exclusively by water voles (Fig. 2a).

The mean ± SE (range) extent of occupancy per landscape was 0.72 ± 0.11 ha (0–3.98) for Cabrera voles and 1.80 ± 0.26 ha (0–9.29) for water voles. Models including each single covariate alone provided support for the influence of habitat amount, patch density, cover by agricultural land, and matrix cover by extensive pastures (Supplementary material, Table SM5). Three of the 16 candidate models built with these variables were equally supported (ΔDIC < 5; Table 3). The model including habitat amount, patch density, and cover by agricultural land yielded the lowest DIC and an adjusted pseudo-R^2 of 0.88 (Table 3). This model indicated that the extents of occupancy of both Cabrera and water voles increased very significantly with the amount of habitat (Fig. 2b). For the Cabrera vole, there was also a significant positive effect of patch density and a significant negative effect of agriculture cover, while for water voles, there was a very significant positive effect of agricultural land cover (Fig. 2b). These results were consistent among the best supported models (Supplementary material, Table SM6). There was a significant negative correlation between the extents of occupancy of Cabrera and water voles after controlling for the effect of environmental variables (Corr$_{Mc,As}$; posterior mode = −0.39; 95 %CI −0.61 to −0.16).

Discussion

This study, together with previous research on the Cabrera-water vole system (Pita et al. 2010, 2011a, b), is consistent with the idea that segregation between the two species

Table 3 Candidate models to explain the extent of occupancy of Cabrera and water voles within landscapes, and their respective DIC values, ∆DIC, and adjusted pseudo-R^2

Fixed effects	DIC	∆DIC	Adjusted pseudo-R^2
HA + PD + AGRIC*	219.69	0	0.88
HA + AGRIC*	222.72	3.03	0.87
HA + PD + AGRIC + EPAST*	223.37	3.68	0.88
HA + AGRIC + EPAST	226.55	6.86	0.86
HA + PD	227.02	7.33	0.86
HA	229.74	10.05	0.85
HA + PD + EPAST	230.17	10.48	0.86
HA + EPAST	232.87	13.18	0.83
PD + AGRIC + EPAST	330.66	110.97	0.26
PD + EPAST	333.34	113.65	0.21
AGRIC + EPAST	333.52	113.83	0.19
EPAST	335.43	115.74	0.15
PD + AGRIC	336.94	117.25	0.14
PD	339.47	119.78	0.08
AGRIC	340.19	120.5	0.06
NULL	341.65	121.96	

* Indicates most supported models (∆AIC ≤ 2). See Table 1 for variable codes

probably occurs at more than one spatial scale, and that segregation at different scales is associated with particular environmental conditions. Specifically, we found that the two species coexisted in some landscapes but not in others, and that shared and exclusive use by each species were associated with total habitat amount, the density of habitat patches, and matrix composition. Also, we found evidence for a negative correlation between each species extent of occupancy within shared landscapes after controlling for patch-network and matrix variation. Overall, therefore, our study concurs to a growing body of evidence suggesting that segregation between competitors may occur at multiple hierarchical spatial scales, from within-patch to among-landscapes (e.g., Inouye 1999; Gilbert et al. 2008; Laporta and Sallum 2014), thus underlining the importance of considering processes operating over a range of spatial scales to understand how competitors coexist in real landscapes (Whittaker et al. 2001; Kneitel and Chase 2004).

Vole segregation among landscapes

Segregation patterns of water and Cabrera voles among landscapes were partly consistent with the idea that the large and putatively dominant competitor tended to occupy all landscapes meeting its requirements in terms of patch-network and matrix characteristics, while the smaller and putative subordinate competitor seemed to be partly forced into landscapes unsuitable for the dominant competitor. This was supported by the observation that water voles tended to be the sole occupants of landscapes with large habitat patches (i.e., landscapes with high habitat amount but relatively low patch density) and high matrix cover by

agricultural land, which were shown previously to benefit this species (Pita et al. 2013). Because water voles are relatively large, large patches may provide conditions for a large number of individuals, and thus, reduce the probability of local extinction (Pita et al. 2013; Sutherland et al. 2014). Agricultural land may be beneficial to water voles, because the wet margins that typically appear along irrigated fields are likely to offer habitat and dispersal opportunities across the dry farmland (Telfer et al. 2003; Centeno-Cuadros et al. 2011; Pita et al. 2013). Reasons for the absence of Cabrera voles in landscapes with these characteristics are uncertain, but this may result, to at least some extent, from competitive exclusion by water voles. In fact, previous studies have shown that the probability of patch occupancy by Cabrera voles increases with patch size (Pita et al. 2007), and so, they would be expected to occur in landscapes dominated by large patches, such as those used exclusively by water voles. It is noteworthy, therefore, that exclusive occupancy by Cabrera voles was associated with landscapes with many small patches (i.e., landscapes with high patch density), which were probably unsuitable for water voles, because most patches were too small for sustaining local populations (Pita et al. 2013).

Although these observations provide support for competitive exclusion of Cabrera voles in some landscape types, we cannot rule out the possibility of the patterns observed resulting at least partly from independent and species-specific responses to patch-network, matrix or other habitat characteristics. For instance, the negative association of Cabrera vole to landscapes with high amount of agricultural land may be related to reduced dispersal ability, and thus, reduced capacity to colonize empty habitat patches

(Pita et al. 2007), rather than a negative response to water voles per second. Elucidating this would require experimental studies, manipulating, for instance, the presence of water voles or the cues of its presence (e.g., droppings) in landscapes occupied by Cabrera voles, or the density and size of patches at the landscape scale (e.g., Ginger et al. 2003; Brunner et al. 2013). Future studies should also consider the role of other competitors and shared predators, as these have not been examined so far but they can strongly affect the interactions between potential competitors (e.g., Oliver et al. 2009).

Vole coexistence within landscapes

Although we found Cabrera and water vole segregation among some landscapes types, the two species actually co-occurred in most of the surveyed landscapes. This was in line with previous observations indicating that both species can coexist within the same patches (Pita et al. 2010, 2011a, b), and suggest that coexistence may be further facilitated by some patch-network and matrix characteristics. Specifically, we found that coexistence was most likely where the habitat amount was high, but where patch density was also much higher than in landscapes occupied exclusively by water voles, which may reflect landscapes with a diversity of large and small patches. In these landscapes, small patches unsuitable for water voles may serve as refuges for Cabrera voles, and they may provide sources of individuals colonizing larger patches temporarily left vacant or only partly occupied by water voles. High patch density may also be related to small inter-patch distance, which may favor dispersal, and thus increase colonization ability by the Cabrera vole, which seems to have much lower dispersal ranges than water voles (Pita et al. 2007, 2013). We also found that landscapes occupied by both Cabrera and water voles had an intermediate cover by agricultural land uses, in relation to those occupied solely by either species. This may be due to the contrasting response of the two species to this variable, with the colonization ability of Cabrera voles declining with increasing cover by agricultural land (Pita et al. 2007), and the opposite presumably occurring for water voles (Pita et al. 2013). Overall, therefore, it seemed that coexistence was favored in landscapes that were suboptimal for water voles (relatively small patches and intermediate cover by agricultural land), and that at the same time provided refuges (small patches) and dispersal opportunities (non-agricultural land, short inter-patch distance) for Cabrera voles.

As for the segregation among landscapes, it was difficult to assess whether the observed patterns of within-landscape coexistence resulted from independent, species-specific responses to environmental factors, or whether it also involved some kind of competitive interference between species. However, we found that the extent of occurrence of water and Cabrera voles within shared landscapes was negatively correlated after controlling for potentially confounding environmental effects, which is compatible with a negative effect of the putative dominant on the putative subordinate competitor. These results suggest that in the absence of water voles and for constant environmental conditions, the area occupied by Cabrera voles would be larger than that observed in our study. This might be a consequence, for instance, of water voles displacing Cabrera voles from some suitable patches (i.e., segregation among patches), or by limiting the extent of occupancy of Cabrera voles in patches occupied by both species (i.e., within-patch segregation). Testing these hypotheses should be the subject of future research.

Implications for the coexistence of competitors

The coexistence of competitors occupying habitat patches in fragmented landscapes is generally interpreted as resulting from the partitioning of resources at local scales (classical niche-based mechanisms; e.g., Chase and Liebold 2003; Jorgenson 2004; Leibold and McPeek 2006), or from life-history tradeoffs, for instance, in competitive and colonization abilities (e.g., Amarasekare 2003; Hanski 1983, 2008). The observational studies carried out so far on the Cabrera-water vole system are insufficient to fully support or contradict either of these hypotheses, but they suggest that the mechanisms facilitating coexistence may be more complex than previously envisaged, because different processes may operate simultaneously, though their relative importance may vary across spatial scales (Kneitel and Chase 2004). On the one hand, our previous studies suggest that coexistence within local patches may be facilitated by segregation along time and habitat axis (Pita et al. 2010, 2011a, b), which is consistent with niche-based mechanisms (Chase and Liebold 2003). However, the present study suggests that niche-based mechanisms may also operate at the landscape level, as segregation versus coexistence appeared to be influenced by species habitat preferences in terms of patch-network and matrix characteristics (Morris 1987; Yu et al. 2001; Westphal et al. 2006). On the other hand, however, our study also pointed out the possibility of life-history trade-offs facilitating coexistence within landscapes, with the smaller species offsetting its lower competitive ability by occupying small habitat patches that are hardly occupied by the larger competitor, thereby enabling a fugitive-like coexistence (Amarasekare 2003; Hanski 1983, 2008). Whatever the mechanism or combination of mechanisms at play here, our results support the need to account for the hierarchical nature of species spatial segregation patterns to generate robust hypotheses about the processes that allow their

coexistence (Kneitel and Chase 2004; Szabó and Meszéna 2006; Kneitel 2012). In particular, because habitat patch-network structure and matrix composition are key landscape properties in determining scales at which segregation takes place, we suggest that spatial heterogeneity at the landscape scale should be routinely considered in both theoretical and empirical studies aiming to understand species coexistence in patchy environments (e.g., Gilbert et al. 2008; Biswas and Wagner 2012; László and Tóthmérész 2013) This, in turn, will provide invaluable information to support inferences on possible mechanisms facilitating coexistence across multiple scales, and for improving conservation actions targeting multiple interacting species (Poiani et al. 2000; Tscharntke et al. 2012).

Authors contribution statement RP, AM, PB conceived and designed the experiments. RP performed the experiments. RP, XL, AM, and PB analyzed the data. RP, XL, AM and PB wrote the manuscript.

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