

Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France

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Abstract In this study, we investigated the environmental factors driving small mammal (rodents and shrews) assemblages in permanent habitat patches in response to a gradient of agricultural intensification. Small mammals were sampled using a trapping standard method in the hedgerow networks of three contrasted landscapes differing by their level of land-use intensity and hedgerow network density (BOC1: slightly intensified; BOC2: moderately intensified and POL: highly intensified). We hypothesized that habitat and landscape characteristics have to be considered to understand the structure of local community. In that way, we carried out a multi-scale study using environmental variables ranging from local habitat (structure and composition of the hedgerows) to hedgerows neighbourhoods in a radius of 300 m (land cover and connectivity around hedges)

and to landscape units (three sites). During 1 year, 24 hedgerows were sampled seven times, representing a total of 1,379 captures (86% of rodents and 14% of shrews) and eight species, dominated by the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). Inter-site variability was significant and accounted for 18% of total variation in small mammal species abundances. But intra-site variability was also highlighted: species abundance profiles may differ greatly among hedgerows within a site. The more explanatory variables were identified at the different scales of the study: the landscape unit POL was shown to be an important factor in structuring the community, but the predominant factors explaining differences of abundances among hedgerows were about local habitat. In fact, the width of hedges and the tree species richness appeared to be significant and explaining the greatest part of the total variation of the small mammal community composition.

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Introduction

Farmland represents the major land use in Europe and France (Fitzgibbon 1997). The total area of cultivated land increased by 466% in the world from 1700 to

1980 (Meyer and Turner II 1992). While ancient agricultural systems had favourable for biodiversity in Europe over the centuries (Piorr 2003), the intensification of agricultural practices in the 20th century had been favourable to lead to a significant loss of natural and semi-natural elements of farming landscapes, inducing negative impacts on many of their floral and faunal components (Duelli and Obrist 2003).

The most important changes in agriculture have occurred since the 1950's (Burel and Baudry 1995; Turner and Meyer 1994; Robinson and Sutherland 2002). In Brittany (Western France), land-use intensification (increase in production per surface unit) and reallocation policies have produced landscape changes due to the expansion of parcel size associated with fragmentation and loss of semi-natural elements such as woodlots, hedgerows or meadows (Leonard and Cobham 1977; Agger and Brandt 1988; Meeus 1990), leading to the increase of cultivated areas. Changes were also the increase of machinery use, and the introduction of new crops, agricultural practices and farming systems (Canévet 1992; Robinson and Sutherland 2002), and finally the growing use of chemicals such as fertilizers and pesticides (McLaughlin and Mineau 1995; Stoate et al. 2001).

These changes have influenced the dynamics of biodiversity in agricultural landscapes (McLaughlin and Mineau 1995): the loss of ecological heterogeneity in agricultural landscapes induced by modern arable management has contributed to the loss of suitable habitats for many species (Legendre 1993; Wiens et al. 1993) and resulted in significant implications for farmland species of flora and fauna.

Within such a context, and with the emergence of landscape ecology, growing scientific attention has focused on the conservation and study of the different types of farmland semi-natural habitats constituting the rural landscape mosaic (Freemark et al. 2002), with a central place taken by hedgerows (Baudry et al. 2000). In fact, beside the aesthetical aspects and protection against wind and erosion, hedgerows and hedgerow networks form an essential part of rural biodiversity, carrying a broad range of different faunal and floral species (Hinsley and Bellamy 2000; Tattersall et al. 2002).

Small mammals (rodents and shrews <40 g) are a common feature of agricultural landscapes and most farming practices cause stress to them by removal of shelter, food, as well as breeding and overwintering

sites (Tew and Macdonald 1993). For several small mammals, hedgerows serve as permanent habitats (even if a use of adjacent crop fields is possible for certain species when cover is available and sufficient) (Burel 1996). Small mammals have a major role in ecosystems due to their function as prey: they provide an important food source for predatory mammals and birds (King 1985), some of which are becoming rare (e.g., *Tyto alba* in the British Isles (Fitzgibbon 1997)). With their high energy requirements and voracious feedings habits, shrews are an important component of the dynamics of terrestrial ecosystems (Churchfield et al. 2004). Rodents may also be important in promoting tree regeneration in woodland and along hedges (Hayward and Phillipson 1979). Yet they are still regarded only as major pests in agriculture causing crop damages, which have motivated numerous studies (Batzli and Pitelka 1971; Giraudoux et al. 1994). Several studies have also examined the effects of farming practices on population dynamics and demography (Jacob 2003).

Previous studies have been carried out in Brittany to correlate small mammal assemblages to landscape or local habitat characteristics in farming landscapes: Millan de la Pena et al. (2003a) studied the relationship between the small mammal community and landscape descriptors, using Barn Owl (*Tyto alba*) pellet analysis in different sites. They showed that variations in species frequency could be observed in response to agricultural intensification and that the prevalence of some species allowed to distinguish different assemblages, which were characteristics of low, medium or high intensified landscapes. Paillat (2000) and Butet et al. (2006) investigated the local factors driving diversity and abundance of small mammal species inhabiting permanent habitat patches in an intensive agricultural landscape; they showed a clear difference between communities from grassy field boundaries and hedgerows. Nevertheless those two studies were restricted to one scale, a gradient of landscape units in Millan de la Pena et al. (2003a), and local habitat patches within a single landscape unit in Paillat (2000) and Butet et al. (2006). In the present study, we wanted to integrate both scales, by comparing species abundances of the small mammal community in hedgerows belonging to three landscape units differing by their level of agricultural intensity. The main goal was to identify environmental variables that could explain the

observed differences in species assemblages abundances among the hedges. As it is known that both landscape (Hansson 1977; Barrett and Peles 1999) and habitat (Bowman et al. 2001a, b) can influence composition of small mammal assemblages, we carried out a multi-scale study using environmental variables ranging from local habitat (structure and composition of the hedgerows) to hedgerows neighbourhoods (land cover and connectivity around hedges) and to landscape units (three sites).

Material and methods

Study area and trapping sites

The study took place in Brittany (department of Ille-et-Vilaine), south of the Mont-Saint-Michel Bay (48°36' N, 1°32' W, North-Western France). Three landscape units were chosen in a study area named “Site Atelier de Pleine-Fougères” where several studies have been conducted on different biological models (Burel et al. 2003) in response to agricultural intensification. We essentially based the delimitation of the units on landscape structure drawn from aerial photographs. We took into account the grain size of the field mosaic, the density of hedgerow network, and the relative abundance of grassland vs. cropland. The three chosen sites are known to form a gradient of agricultural land-use intensity and hedgerow network density (Table 1). The first landscape unit (BOC1) is locally called “bocage” (a landscape type that is common in Brittany, characterized by a dense hedge-

row network). In BOC1, farming systems are exclusively oriented toward dairy production; 2/3 of the UAA (Used Agricultural Area) is covered by grasslands and fodder crops and milk cows predominate in the livestock. The second site, called BOC2, is also a “bocage”, but the hedgerow network density is reduced. BOC2 is more intensified than BOC1: agriculture is mainly oriented toward mixed dairy-cattle and some crop production, with 1/3 of the UAA covered by grasslands and fodder crops. Finally, the third landscape unit, called POL, is a polder, reclaimed from the sea area (“polderisation” was conducted in the site from 1851 to 1934) with a network of dykes with few hedgerows. It is highly intensified with 90% of the UAA being crop fields; agriculture is oriented toward cereals and vegetables production. The landscape unit areas are respectively 1,019 ha for BOC1, 1,659 ha for BOC2, and 2,544 ha for POL.

In each site, eight hedgerows were chosen among the network to become the sampling units for trapping small mammals. They were chosen to be as distant as possible from one another, with 600 m minimum distance between hedges in BOC1 and 700 m in BOC2 and POL.

In order to characterize the hedgerows, we extracted environmental variables at three scales (Table 2):

- (1) The first scale is that of the local habitat. We measured local variables of structure and composition. For physical structure: width of the hedges (m), average height of the canopy (m),

Table 1 Characteristics of the three landscape units : structure (mean parcel size and connectivity) and composition (proportion of the land covered by grasslands and crop fields, corn, vegetables and cereals)

	Landscape unit		
	BOC1	BOC2	POL
Mean parcel size (ha)	0.65	1.08	2.54
<i>Connectivity</i>			
Wood density (m ² /ha)	98	48	12
Hedgerow density (m/ha)	803	424	13
<i>Land-cover</i>			
% Grasslands	63.7	38.2	8.9
% Crop fields	36.3	63.8	91.1
% Corn	20.9	32.8	22.9
% Vegetables	0.2	0.6	35.6
% Cereals	15.2	30.4	32.6

Table 2 Characterization of the 24 sampled hedgerows at three scale, local habitat structure and composition, land-cover in a 300 m window and landscape unit

Scale	Local habitat						300 m window						Landscape
	Structure			Composition			wood (%)	grass (%)	corn (%)	cere (%)	veg (%)	hedge (m/ha)	Unit
	W	ACH	CTL	HR	SR	TR							
Hedges													
B1-1	2.3	5	0	11	1	0	3.12	41.66	28.36	26.86	0.00	112.79	BOC1
B1-2	5	17	5	32	1	2	21.64	64.41	11.17	2.79	0.00	85.56	
B1-3	8	16	5	17	2	2	3.33	64.83	21.03	10.82	0.00	124.71	
B1-4	3	15	4	13	0	2	6.82	50.89	22.99	19.29	0.00	113.19	
B1-5	4.5	20	4	9	8	2	7.89	59.44	15.93	16.74	0.00	80.70	
B1-6	3	18	3	15	3	3	13.49	49.93	18.32	17.51	0.75	123.77	
B1-7	4.5	15	3	19	1	2	7.44	66.55	22.00	3.56	0.44	108.16	
B1-8	4.3	15	4	15	4	1	4.73	52.51	21.60	21.16	0.00	130.43	
B2-1	2	15	2	24	2	1	9.12	34.37	22.58	33.93	0.00	71.23	BOC2
B2-2	2	12	2	15	2	1	1.09	11.60	56.36	30.94	0.00	25.08	
B2-3	5	8	4	14	5	0	2.95	36.50	34.66	25.89	0.00	60.10	
B2-4	8.5	12	5	16	7	2	0.00	23.43	27.26	49.30	0.00	39.81	
B2-5	3	12	5	48	10	3	0.33	40.05	37.14	21.85	0.62	72.61	
B2-6	2.7	12	3	16	4	2	0.34	40.51	36.30	22.52	0.34	56.57	
B2-7	9	5	3	21	3	1	0.23	22.44	27.68	49.65	0.00	38.56	
B2-8	4	20	4	24	2	1	13.23	48.20	26.47	8.36	3.73	66.01	
P-1	2.6	5	0	9	2	0	0.00	14.61	25.55	27.41	32.43	28.90	POL
P-2	20	20	5	13	2	2	0.00	0.00	33.40	25.97	40.62	27.98	
P-3	9.5	30	5	10	3	2	0.00	42.39	10.10	17.79	29.72	12.66	
P-4	2.5	15	5	17	2	2	0.00	29.20	26.00	5.72	39.07	28.98	
P-5	3.7	12	5	12	1	2	0.00	20.05	16.01	16.50	47.44	17.42	
P-6	7	12	1	16	2	1	0.00	7.51	32.68	11.29	48.51	8.16	
P-7	6	10	0	16	3	0	0.00	7.74	27.33	15.67	49.26	20.00	
P-8	22	20	5	24	1	3	1.85	3.98	36.49	14.46	43.22	34.39	

W, width (m); ACH, average height of canopy (m); CTL, cover tree layer (from 0 to 5 : 0 = 0%, 1 = 1–10%, 2 = 10–25%, 3 = 25–50%, 4 = 50–75%, 5 = >75%). HR, herbaceous species richness; SR, shrub species richness; TR, tree species richness. Wood, % of wood; grass, % of grassland; corn, % of corn; cere, % of cereals; veg, % of vegetables; hedge, hedgerow network density in the 300 m window around each hedge

and cover of the tree layer (index from 0 to 5). For vegetation composition, we made an extensive survey of the plant species present in the three layers (herbaceous, shrub and tree layer) of each sampled hedgerow. We then calculated herbaceous, shrub, and tree species richness indices.

- (2) The second scale was a land-cover neighbourhood window around each sampled hedge. The size of the window was chosen to be 300 m, which corresponds to the capacity of instantaneous movement of the most abundant species in the small mammal community, the wood mouse (*Apodemus sylvaticus*) (Szacki and Liro

1991). We used a Geographic Information System to determine the percentage of vegetables, corn, cereals, grasslands and woods, and the density of hedgerows in the 300 m windows.

- (3) The third scale is the landscape unit scale. The variables (binary) are consequently BOC1, BOC2 and POL.

Small mammal sampling method

We conducted seven trapping sessions (April, May, June–July, August, September, October and

February) in each of the 24 sampled hedgerows. For each of the seven trapping sessions, 7 days were necessary to sample all 24 hedgerows (in random order) so we can consider that the hedges were sampled simultaneously (dates of first trapping day for each session: 2003: 01/04, 13/05, 26/06, 07/08, 11/09, 21/10, 2004: 15/02).

We used a standardized method (Spitz et al. 1974) consisting of a 100 m line of 34 baited (wheat flour and margarine mixture and a piece of apple) live-traps placed every 3 m and checked at dawn twice, that is, 24 and 48 h after installation (two trap-nights). Individuals captured at 24 h were temporarily marked (colour mark on the tail) to avoid considering them twice if recaptured at 48 h. Trapping is the most common method used to study small mammals (Gurnell and Flowerdew 1990). It has been successfully used to detect patterns of richness, composition and abundance of small mammal communities through ecological gradients (Yu 1996). Live trapping is a powerful technique with which to carry out monitoring for multiple species (Flowerdew et al. 2004). We used INRA live traps, a French model of live-trap, that are known to be very efficient in catching both shrews and rodents. To fulfil our objectives, comparison of sampling units was more important than comparing species abundances. The total number of individuals trapped with this method (excluding recaptures at 48 h) was used as an index of abundance for each species (Hansson 1967).

Eight species (rodents and shrews) were captured during the whole year of trapping. There were four rodents species: *Apodemus sylvaticus* (Wood mouse, As) (Linné 1758), *Clethrionomys glareolus* (Bank vole, Cg) (Schreber 1780), *Microtus agrestis* (Field vole, Mag) (Linné 1761), *Microtus subterraneus* (Common pine vole, Ms) (de Séllys-Longchamps 1836), and four shrew species: *Crocidura russula* (White-toothed shrew, Cr) (Hermann 1780), *Neomys fodiens* (Aquatic shrew, Nf) (Pennant 1771), *Sorex coronatus* (Common shrew, Sc) (Millet 1828), *Sorex minutus* (Pigmy shrew, Sm) (Linné 1766).

Data analysis

Species richness (S) and Shannon index of diversity (H') were computed for each hedgerow and for each site (Shannon and Weiner 1949; Magurran 1988) using the Ecolostat program (Guillory 1999). Species

abundances were expressed by total capture, without any correction, because the trapping effort was strictly the same for each trapping unit.

Discriminant analysis (Rao 1948) was computed on the table of Hellinger-transformed species abundances in the 24 hedgerows to highlight inter-site variability. This was computed using ADE-4 Software™ (Thioulouse et al. 1997).

Multivariate analyses were performed using the R statistical language (R 2.0.1, R Development Core Team 2005). Species abundance data were Hellinger-transformed to make them amenable for principal component analysis (PCA) and canonical redundancy analysis (RDA) (see Legendre and Gallagher 2001). The choice of the use of PCA and RDA for analysing our data was tested using Detrended Correspondence Analysis (DCA) (see Hill and Gauch 1980), using Canoco Software (Ter Braak and Smilauer 1998). PCA and RDA were computed using the “rda” function of the “vegan” library (Oksanen et al. 2005). Variation partitioning was computed using a function written by Pierre Legendre in the R language, and now incorporated into the “vegan” library. A Venn diagram was made to present the variation partitioning. Variables used in the Variation Partitioning analysis were selected using Redundancy Analysis with forward selection for each group of variables (R statistical language).

The Minitab Software™ (version 13.31) was used to perform regression analyses in order to link the coordinates of the 24 hedgerows on the first RDA axis with the total abundance of the species (sum over the seven trapping sessions).

Results

During the 11,424 trap-nights, a total of 1,379 animals were captured during the whole year of trapping: 1,191 (86%) were rodents and 188 (14%) were shrews. Total species abundances in each hedgerow are given in Table 3.

A discriminant analysis was performed to highlight inter-site variability: inter-site inertia was significant ($P = 0.006$) and accounted for 18% of total variation in small mammal species abundances which permits us to make inter-site comparisons (Michel et al. 2006). The total and mean number of captures in hedgerows of BOC1 and BOC2 are quite similar

Table 3 Species captures (sum of the seven trapping sessions) in the 24 hedges sampled in the three sites (BOC1, BOC2 and POL). The hedges sampled at each site are numbered 1–8

Hedges	As	Cg	Ma	Ms	Cr	Nf	Sc	Sm	Total	Mean	S	H'
BOC1-1	12	0	1	13	7	0	7	4	44		6	2.313
BOC1-2	30	4	0	1	0	1	5	0	41		5	1.289
BOC1-3	10	3	1	0	0	0	1	1	16		5	1.627
BOC1-4	28	3	0	0	2	0	2	3	38		5	1.350
BOC1-5	23	8	1	0	2	0	2	5	41		6	1.854
BOC1-6	45	10	3	2	0	0	1	1	62		6	1.323
BOC1-7	60	6	0	3	2	0	3	1	75		6	1.143
BOC1-8	41	3	2	0	5	0	4	1	56		6	1.414
Site BOC1	249	37	8	19	18	1	25	16	373	46.62 (±6.28)	8	1.75
BOC2-1	11	0	0	4	0	0	4	1	21		4	1.619
BOC2-2	32	0	0	0	7	0	1	1	41		4	0.976
BOC2-3	30	3	0	1	8	2	5	2	51		7	1.916
BOC2-4	33	22	1	0	1	0	2	3	62		6	1.578
BOC2-5	49	4	0	1	0	0	9	2	65		5	1.197
BOC2-6	20	4	1	0	8	0	4	0	37		5	1.792
BOC2-7	25	23	1	2	4	0	2	2	59		7	1.914
BOC2-8	28	2	2	0	7	0	11	4	54		6	1.971
Site BOC2	228	58	5	8	35	2	38	15	389	48.62 (±5.35)	8	1.92
POL-1	30	6	0	3	4	0	7	1	50		6	1.868
POL-2	66	32	0	3	2	0	2	0	105		5	1.308
POL-3	63	22	0	5	0	0	3	0	93		4	1.259
POL-4	46	45	0	0	8	0	3	1	103		5	1.541
POL-5	32	10	0	4	1	0	1	0	43		5	1.482
POL-6	74	8	0	0	3	0	0	0	85		3	0.665
POL-7	49	3	0	0	2	0	0	0	54		3	0.535
POL-8	26	51	1	0	0	0	0	0	78		3	1.010
Site POL	386	177	1	15	20	0	16	2	617	77.12* (±8.27)	7	1.41**

Species codes (columns) are given in the Materials and methods. Total number of captures, mean number of captures, species richness (S) and Shannon's diversity (H') of the small mammal communities of the three sites are also given. * Significant difference among abundances (mean number of captures) using the Mann–Whitney U–test ($P < 0.05$). ** Significant difference among diversities (H') of the three sites using Hutcheson's test ($P < 0.01$)

whereas they are significantly higher in POL. Eight species were found in BOC1 and BOC2 but only seven in POL, due to the absence of the aquatic shrew Nf (*Neomys fodiens*). Only one individual of Nf was found in BOC1 and only two in BOC2, so the difference in total species richness is negligible among sites. The Shannon diversity index is the lowest in POL due to differences in species abundances among sites; the two main species, As (*Apodemus sylvaticus*) and Cg (*Clethrionomys glareolus*), were much more abundant in the Polder site. Whatever the sampling site, the dominant species was

the wood mouse, *Apodemus sylvaticus* (As), which represented 67% of the total number of captures in BOC1, 59% in BOC2 and 63% in POL. The bank vole, *Clethrionomys glareolus* (Cg), was also well represented, particularly in POL with 29% of the total number of captures whereas it was only 10% and 15% in BOC1 and BOC2 respectively. The six other species were much more rare, always showing abundances smaller than 10%. We can note that, using a very simple index of trophic level (Contoli 1981), the percentage of Soricidae (shrews) is 16% in BOC1, 23% in BOC2 and 6% in POL.

A principal component analysis (PCA) was performed on the Hellinger-transformed small mammal species abundances in the 24 hedgerows. The first principal component axis accounted for 42% of the variation in total species abundance. We used that axis as a global index of differentiation in community composition and plotted the values of the hedges along that axis on a map of the hedges (Fig. 1). In this representation, black squares (positive values) are opposed to white squares (negative values) in first PC axis values. The POL site (great majority of white squares) is opposed to the two bocages sites (majority of black squares). This figure especially highlights intra-site variability: species abundance profiles may differ greatly among hedgerows within a site, whereas hedgerows from different sites could exhibit close assemblages.

To identify the environmental variables that could explain the differences in species abundances among hedgerows, we performed a canonical redundancy analysis (RDA) of the Hellinger-transformed species abundance data constrained by the three groups of scale variables (habitat, land-cover and landscape

unit). The RDA biplot showing the species and the three groups of environmental variables is presented (Fig. 2). The first canonical axis shows a clear opposition between (left) hedgerows adjacent to a high proportion of grasslands and woods and surrounded by a high density of hedges (most were BOC1 and BOC2 hedgerows), and, to the right, the largest and tallest hedgerows with a greater tree species richness, and surrounded by a high proportion of vegetable crops (most of them were POL hedgerows). Individual species are also associated with particular variables: the bank vole (*Cg*, *Clethrionomys glareolus*) is associated with hedgerows of great size (wide and high) and with high tree richness and cover from the POL site. The two *Soricidae* species, the common shrew (*Sc*, *Sorex coronatus*) and the pygmy shrew (*Sm*, *Sorex minutus*) are opposite to *Cg* along the first canonical axis; they are closely associated with BOC1 and BOC2 and with a neighbourhood of grasslands, woods, and hedgerows. The abundance of the white-toothed shrew (*Cr*, *Crocidura russula*) is correlated to the proportion of corn around the hedgerows. The common pine vole

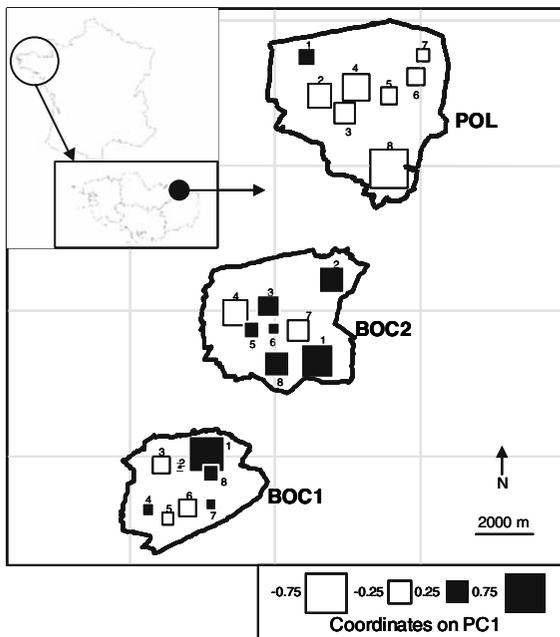


Fig. 1 Map of the 24 sampled hedgerows. The size of the squares represent their values on the first principal component (which accounts for 42% of total variation) of the Hellinger-transformed small mammal species abundance data; open squares: negative values; black squares: positive values

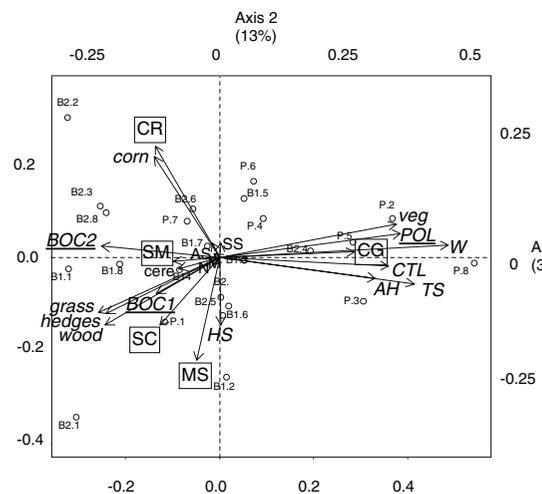


Fig. 2 Triplot of the species (squares), sites (small circles) and environmental variables on the two first canonical axis of the redundancy analysis ordination (Hellinger-transformed species abundance data constrained by the multi-scale environmental variables). Symbols of the variables: Habitat variables: W, width; AH, average height of the canopy; CTL, cover of the tree layer; TS, tree species richness; SS, shrub species richness; HS, herbaceous species richness. Land-cover variables: veg, % vegetables; corn, % corn; cere, % cereals; grass, % grasslands; wood, % woods; hedges, density of hedges. Landscape-Unit: BOC1: BOC1 site; BOC2: BOC2 site; POL: POL site

(Ms, *Microtus subterraneus*) is associated with hedgerows with high herbaceous species richness. The wood mouse (As, *Apodemus sylvaticus*, which is the dominant species at all three sites), the field vole (Mag, *Microtus agrestis*) and the aquatic shrew (Nf, *Neomys fodiens*) are not associated with any particular environmental variable.

The coordinates of the 24 sampled hedgerows along the first RDA axis can be linked to the species abundances (Fig. 3). Along the gradient defined by the first axis, we observe a significant increase of *Clethrionomys glareolus* (Cg, $P < 0.001$), and a significant decrease of *Crocidura russula* (Cr,

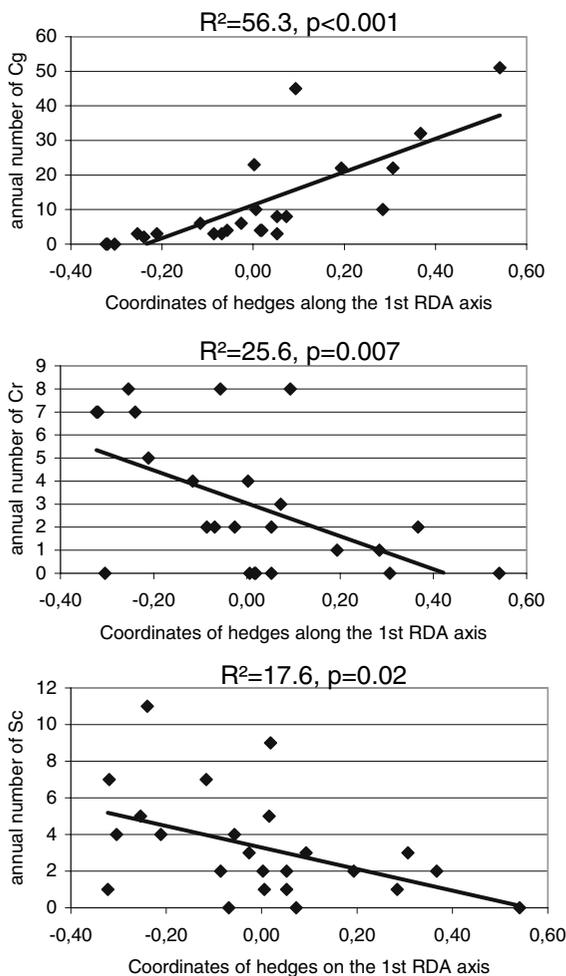


Fig. 3 Relation between the total abundances (sum over all trapping sessions) of Cg (*Clethrionomys glareolus*), Cr (*Crocidura russula*), and Sc (*Sorex coronatus*) and the coordinates of the hedgerows along the 1st axis of the canonical redundancy analysis ordination (RDA Fig. 2)

$P = 0.007$) and *Sorex coronatus* (Sc, $P = 0.02$). The dominant species, *Apodemus sylvaticus* shows no significant tendency at the 5% significance level like the other four species (not shown).

To identify the more important explanatory variables and arrange them in a hierarchy, we performed separate redundancy analyses for each group of variables (the habitat variables, then the land-cover variables, and finally the landscape unit variables) with forward selection method. This selection gave as significant variables the hedge width and tree species richness (habitat group), the percentage of vegetables (land-cover group), and the site POL (landscape unit group). Then, using only the selected variables, we performed a variation partitioning analysis (Borcard et al. 1992; Borcard and Legendre 1994). Graphical representation (Venn diagram) of the results is given in Fig. 4. The two habitat variables explain the greater part of the variation in small mammal community composition (24.7%, adjusted R-square) whereas land-cover and the landscape unit POL totally overlap and account for less variation (13.2%, adjusted R-square). 6.4% (adjusted R-square) of the variation is common to the three groups of variables.

Discussion

This study reveals that small mammal species assemblages exhibit spatial variability among hedgerows of three contrasted farming landscapes. Differences were observed on small mammal abundance

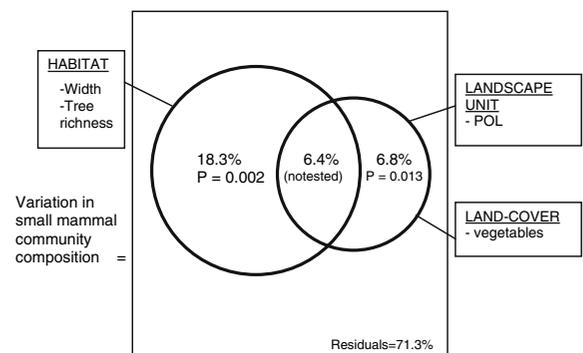


Fig. 4 Venn diagram partitioning the variation of the small mammal community composition between forward-selected environmental variables of habitat, land-cover and landscape units. The reported values are adjusted canonical R-squares. The circle for land-cover and landscape unit totally overlap

and diversity among the three sites, showing a major difference between the most intensified site, POL, and the two other sites, BOC1 (slightly intensified) and BOC2 (moderately intensified). In POL, we observed the highest local small mammal abundance and the lowest diversity. A greater simplicity in communities (low diversity) is often linked to greater abundance amplitudes (Salamolard et al. 2000). Small mammals are a group of species where landscape configuration has been thought to strongly influence population dynamics (Hansson 1977; Barrett and Peles 1999). Raoul et al. (2001) showed that the stability of small mammals could be influenced by the proportion of grasslands in the landscape. Bowman et al. (2001a, b) also found that landscape context was related to the abundance of several species. Generally, in farming landscapes, loss of diversity is observed with agricultural intensification; Millan de la Pena et al. (2003a) found similar results in a gradient of twelve sites differing by their level of agricultural intensification: species assemblages were different among sites, with a reduction of diversity with intensification. Moreover, isolated patches of habitat (this is the case in POL) usually contain fewer species than do less isolated patches because of increased extinction rates or decreased colonization rates (MacArthur and Wilson 1967; Rosenzweig 1995).

But among-site variability only accounts for 18% of the total small mammal assemblages variation. Differences among hedgerows are much more important than differences among sites. A fundamental question in population and community ecology is: what factors determine the distribution and abundance of species within local regions. Here, the question is to know which environmental variables are predominant to explain differences in species abundances among hedgerows. In a same landscape unit, we show that geographically close hedgerows may exhibit very different patterns of species abundances. This is in accordance with the findings of Bowman et al. (2000) where small mammal populations can exhibit heterogeneous densities over relatively short distances, i.e., hundreds of meters (like in our sites). This suggests the contribution of local processes in addition to landscape processes. For example, Bryja and Zúkal (2000) demonstrated in a same landscape, that the small mammal community in newly planted corridors was very different from

fully developed windbreaks. Canova and Fasola (1991) also showed that community diversity was correlated with habitat structural diversity.

Whatever the hedgerow, the two most abundant species were the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*) which are known to be associated with woodland habitat (Canova and Fasola 1991; Douglass et al. 1992). According to the RDA analysis, *Apodemus sylvaticus* seems not to be influenced by any of the environmental variables we considered. This species is very ubiquitous and eurytopic with a wide ecological plasticity (Butet 1984) and can demonstrate shifts in habitat occupancy (Ouin et al. 2000). Even if *Apodemus sylvaticus* is dependent on the hedge habitat, particularly in the autumn and winter seasons (Pollard and Relton 1970), it appears that it is free to use the whole field and thus to occupy a two-dimensional (hedgerows and agricultural mosaic) rather than an essentially one-dimensional range (hedgerows). Consequently, the generalist nature of *Apodemus sylvaticus* may enable them to adapt to changing countryside better than other species with more specialized habitat requirements (Love et al. 2000).

Contrary to *Apodemus sylvaticus*, the bank vole, *Clethrionomys glareolus* is known to be restricted to hedgerows in farming landscapes, not moving far into adjoining fields (Kosakiewicz et al. 1993). For such a habitat specialist species, abundance in a habitat patch may potentially depend on many different local or landscape factors, like the patch size, patch quality (e.g., shelter), and patch isolation, determined by characteristics of the landscape (structural connectivity), such as the amount of favourable habitat surrounding the patch. In our case, local habitat characteristics seem to have a great influence on *C. glareolus* abundance: wide and high hedgerows with a great woody character (high cover of the tree layer and high tree species richness) host high abundances of bank vole even if patch isolation is important (low connectivity); in POL, *C. glareolus* seems to be concentrated in the few hedgerows of the site, creating high population density. Nevertheless, Paillet and Butet (1996) showed that in this landscape unit, POL, *C. glareolus* were more abundant and stable in the hedges the less isolated.

The two other species of rodents were much more rare than the former. This seems to be logical because

Microtus agrestis and *Microtus subterraneus* occur primarily on grassy and open habitats such as meadows (Innes and Millar 1994) and are more seldom encountered in hedgerows.

Relatively little attention has been paid to the influence of surrounding land-use patterns on small mammal populations. Arable fields are by their nature unstable habitats for small mammals, particularly after harvesting, providing little cover from predators (Tew and Macdonald 1993), but when cover is sufficient, they could provide additional resources. Concerning shrews, the abundance of *Crocidura russula* was correlated to the abundance of corn around hedgerows. It is the commonest shrew species in Western Europe, probably due to its ability to live in open habitat and its capacity to colonize agricultural fields (Genoud and Hutterer 1990). It has been shown to be less sensitive to agricultural intensification than other shrews (Millan de la Pena et al. 2003a). Corn exhibiting a dense and high cover during part of the year could allow *Crocidura russula* to forage and exploit invertebrates resources in fields, especially since insecticide is used in corn fields (Millan de la Pena et al. 2003b). On the contrary, the two species of *Soricidae*, *Sorex coronatus* and *Sorex minutus* are much more strongly associated with undisturbed habitats around the hedgerows, such as woods, grasslands, or hedges. They are known to be dependent on preserved habitats and densely wooded landscapes (Taberlet 1986); that is possibly why they are more abundant in the hedgerows of BOC1 and BOC2. The percentage of *Soricidae* were respectively 16 and 23% in BOC1 and BOC2, but only 6% in POL, probably in relation to cultural anthropization.

The variation partitioning analysis gave hedges width and tree species richness of the hedgerows as the predominant explanatory variables, explaining the demographic structure of the small mammal community, and especially the predominance of *Clethrionomys glareolus*. Several studies have shown, on the contrary, higher densities of small mammals in small compared to larger patches (Diffendorfer et al. 1995; Nupp and Swihart 1996). Habitat quality is strongly influenced by the availability of resources (theoretically enhanced by patch size) and the risk of predation (Lin and Batzli 2001). Small mammals in many communities show preference for habitats with high vegetation cover (Kotler and Brown 1988), a fact that is closely related with the perceived

predation risk (Bowers 1988; Diaz 1992; Lagos et al. 1995). Living in a habitat with dense and thick vegetation is considered to be an antipredatory strategy against both aerial (Longland and Price 1991) and terrestrial (Jedrzejewska and Jedrzejewski 1990) predators. Moreover, we could make the hypothesis that a wide patch could limit the predation pressure by diminishing the edge effect.

The landscape unit POL and the proportion of vegetables in crop fields surrounding the hedgerows are also shown in the variation partitioning results to have a role in structuring the community. They totally overlap because vegetables are quite rare in the two other sites. Additionally to habitat characteristics, landscape is known to have impact on small mammal communities (Hansson 1977; Barrett and Peles 1999): due to its history and particular features, the POL landscape unit contributes to a particular structure of the small mammal community. The selection of the proportion of vegetables as a significant explanatory variable is only a consequence of the particular land-cover in POL which does not seem to have any ecological significance for *Clethrionomys glareolus*. It could have the role of a resource for species foraging in the agricultural mosaic such as *Apodemus sylvaticus*, but this is not the case of *C. glareolus*.

Conclusion

Landscape and local habitat characteristics played a major role in structuring the small mammal community in our three study sites, with a predominance of local habitat variables. Microhabitat features and, to a lesser extent, landscape characteristics determined the composition and dynamics of the small mammal assemblages.

For preserving small mammal diversity in agricultural landscape, preservation of dense hedgerow networks is crucial, particularly for species restricted to these semi-natural linear elements. Moreover, additionally to quantity of habitat, hedgerow quality play a major role by allowing hedges to host a greater abundance of small mammals.

Future investigations will be carried out on hedgerow management by the farmers which could influence seed and berry production as well as insect availability in arable hedges inducing fluctuations in rodent and shrew populations.

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