Communities of small mammals in six biotopes of northern Italy

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Spatial relationships and microhabitat selection were studied in syntopic populations of small mammals. Four hundred three individuals of 7 species (*Sorex araneus, Sorex minutus, Crocidura suaveolens, Crocidura leucodon, Clethrionomys glareolus, Apodemus sylvaticus, Mus musculus*) were trapped in six north Italian biotopes, between June 1988 and September 1989. The wood mouse was present in all biotopes and was, numerically, the dominant species; the bank vole was the second most abundant species. Habitat preferences were similar to those reported for northern Europe but the bank vole was also present in habitats other than ancient woodlands. Community diversity and richness were positively correlated with habitat structural diversity. The species selected micro- habitats that were significantly different from those available; ground cover at arboreal and grass level and litter structure were generally the most important variables. There were significant differences in microhabitat use among dominant species; the intensity of segregation was higher in mature woodland and alder grove than in the other biotopes, which may reflect their different management.

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Introduction

Habitat selection, at both coarse and fine grained levels, is the principal factor that segregates syntopic species of small mammals and allows their coexistence (MacArthur and Pianka 1966, Grant 1972, Dueser and Shugart 1978, 1979, Rosenszweig 1981, Yhaner 1982, and others). Research on habitat use by small mammals are usually based on the premise that spatial partitioning reflects the influence of present or past competition between syntopic rodents. Considerable disagreement exists, however, on the role of competition in structuring communities (Danielson and Gaines 1987). Schoener (1983) inferred that herbivores should not actively compete, because they are in the main primary consumers in ecosystems. Galindo and Krebs (1985) state that "early generalization that competition for space among different species of rodents is a widespread phenmomenon ought be placed among a number of working hypothesis". Danielson and Gaines (1987), Kincaid and Cameron (1982), Galindo and Krebs (1985), and others have found that factors other than competition influence resource partitioning by rodents.

The influence of interspecific competition in shaping the small mammal communities can only be tested experimentally, since spatial overlap does not imply absence of competition, which might be intense for the use of other resources (Grant 1972, Schoener 1983). Descriptive studies of habitat partitioning are however important because they can suggest possible competitive interactions between coexisting species.

The distribution and ecology of small mammals are well known in northern and central Europe, but very few studies have been conducted on these communities in southern Europe. Our research aimed to describe local distribution, abundance and microhabitat selection by syntopic species of small mammals in a number of typical north Italian planar biotopes.

Study areas

Small mammal communities were studied within 5 km of Pavia (NW Italy), in the following 6 biotopes:

(1) Grassland, an abandoned 10 ha field, dominated by *Capsella* sp., *Taraxacum* sp. and *Chaenopodium* sp. with occasional bushes and trees.

(2) Shrubland, 9 ha dominated by bushy *Salix caprea*, with lower level *Rubus* sp., and occasional trees (*Populus* sp., *Robinia pseudoacacia*).

(3) Poplar grove, a 10 ha grove of *Populus* sp.; grasses and bushes were scarce because they were regularly removed by ploughing.

(4) Willow grove, a 11 ha woodland dominated by even-aged woody *Salix* sp. and *Robinia pseudoacacia*, with lower level *Salix caprea* and *Rubus* sp.

(5) Alder grove, a 8 ha woodland dominated by even-aged woody, arboreal level *Alnus glutinosa* and by lower level bushy *Salix caprea* and *Rubus* sp.

(6) Mature woodland, a 35 ha mesic woodland dominated by mixed-age *Populus alba* and *Quercus* sp.; several species of lower level shrub occur, including *Crataegus monogyna* and *Rubus* sp.

These biotopes represent the different grades of structural complexity that may be found in the semi-natural lowland environments of northern Italy.

Sampling methods

Small mammals were trapped by 100 snap traps, regularly placed at 10 m intervals in a 100×100 m grid, and by 20 pitfall-traps placed in a inner grid (20 m intervals). The latter were used to capture shrews (following Grodziński *et al.* 1966). Snap traps were used because our sampling scheme required analysis of stomach contents (paper in preparation). In order to preserve the original microhabitat features we did not place pitfalls near the snap-traps (see also Dueser and Shugart 1978), and so pitfall captures should be considered as supplements to snap trap captures, in which we trapped more than 50% of the Insectivores. Traps were baited with cheese and were checked four times every 24 h (at dawn, three hours after dawn, three hours before dusk, at dusk). Each trapping session lasted 120 hours.

The grid was set up every 4 months from 29 June 1988 to 10 September 1989 in each of the 6 biotopes, for a total of 17 trapping sessions (i.e. 3 in each biotope, except for the poplar grove, where there were only 2 sessions), and for a total of 85 days of trapping, and 8500 trap-nights.

Microhabitat characteristics were measured at each site where a mammal was trapped; measurements at 82 trapping sites were incomplete, and therefore the measurements at the 321 other sites only were analyzed. The same measurements were replicated during each capture session at 16 spots regularly dispersed within the grid in order to sample the available microhabitat.

The following microhabitat characteristics were measured, using a modified version of the method described by Dueser and Shugart (1978): Canopy Cover – overstorey (in percentage); Herbaceous Cover – grass (in percentage); Litter Depth – penetration of a graduated scale into the vegetal debris covering the soil (in cm); Understorey – number of contacts of understorey stems, at shoulder height (160 cm), along 2 perpendicular 10 m transects centered on the spot (in no./m); Shrub – number of contacts of shrub stems, at shoulder height (160 cm), along 2 perpendicular 10 m transects centered on the spot (in no./m); Stump Density – within a 5 m radius around the site; Stump Size – average circumference of the stumps in a 5 m radius around the site (in cm); Overstorey Dispersion – average distance to the nearest overstorey tree, in each of the four quarters

around the trap site (in m); Overstorey Size – average circumference of the 4 nearest overstorey trees in the 4 quarters around the trap site (in cm); Understorey Dispersion – average distance to the nearest understorey tree, in each of the four quarters around the trap site (in m); Understorey Size – average circumference of the 4 nearest understorey trees in the 4 quarters around the trap site (in cm).

The four vegetational strata were defined as: Grass = herbaceous, annual vegetation; Shrub = woody vegetation, height < 2 m; Understorey = trees with circumference < 24 cm at breast height (160 cm); Overstorey = trees with circumference > 24 cm at breast height (160 cm).

Data analysis

The linear regression method for population estimates (Grodziński *et al.* 1966) could not be applied since the trapping grids were not prebaited (Gurnell 1980) and so we calculated population densities using the probabilistic model proposed by Janion *et al.* (1968).

To ensure normality habitat variables were transformed when necessary using arcsin transformation for percentage data, and logarithmic transformations for overdispersed data.

Microhabitat variables were analyzed using Discriminant Analysis (Stepwise routine) in order to study species' habitat selection in relation to availability; we tested the differences between the sites where a species was captured from the habitat available within the biotopes occupied by the same species. Discriminant analysis was also used to study habitat segregation between species; we tested the differences of the dominant rodent species' capture sites in each biotope. Only those variables which were not affected by multicollinearity were entered in the discriminant analysis; the variables were entered sequentially, and an ANOVA test was run to determine which variable had to be added to the discriminant function at each step (Green 1974, Noon 1981).

Microhabitat selection was also analyzed using a categorical, qualitative approach: indices of overlap between species and breadth in habitat use were calculated from microhabitat "categories" obtained by Principal Components Analysis on the values of the 11 variables (Green 1979). A similar categorical analysis of continuous variables was adopted by Llewellyn and Jenkins (1987). At first we only used the variables measured at the sites sampling habitat availability; after a Varimax rotation, the first four axes accounted for 78.2% of the total variance, and we retained only these axes in subsequent analyses (see Table 1). "Availability" sites with positive factor

Table 1. Principal Components Analysis. Factor loadings of the variables on the first four axes. Total variance explained = 78.2%.

Variables	Axis I	Axis II	Axis III	Axis IV
Canopy cover	0.89	0.06	0.18	0.07
Litter depth	0.76	0.19	0.14	0.25
Understorey	0.62	0.51	− 0.02	− 0.08
Shrub	0.58	0.28	0.18	− 0.27
Overstorey dispersion	− 0.84	0.08	0.09	− 0.06
Understorey dispersion	− 0.72	− 0.47	0.19	0.1
Stump density	− 0.01	0.87	0.14	− 0.09
Stump size	0.32	0.78	0.25	0.11
Herbaceous cover	− 0.22	− 0.05	− 0.77	0.26
Overstorey size	− 0.09	0.21	0.74	− 0.06
Understorey size	0.09	− 0.03	− 0.06	0.92
Eigenvalue	4.22	1.68	1.1	1.03
% variance explained	63.2	7.6	6.1	1.3

scores on each axis were assigned to category 1, positive factor scores on the first three axes and negative factor scores on the fourth to category 2, *etc.* producing 16 micro-habitat categories. The values of the original variables in the 16 categories are reported in Appendix. As a second step we computed the factor scores for each capture site, and assigned each capture site to one of the 16 categories.

Indices of breadth and overlap in micro-habitat were then calculated for each specis of mammal from the frequency of capture sites in the 16 categories. Indices of structural diversity were calculated for each of the 6 biotopes from the proportion of categories adopted from those derived by PCA.

Breadth and overlap were calculated by:

$$\text{Breadth} = 1/R \times \Sigma p_i{}^2 \text{ (Levins 1968)}$$

where p is the proportion of the resource i used by species, and R is the number of resource types.

$$\text{Overlap} = 1 - 0.5 \Sigma |p_{xi} - p_{yi}| \text{ (Schoener 1974)}$$

where the p is the proportion of the resource i used by the species x and y.

Breadth and Overlap indices range from $1/R$ (use of only 1 resource) to 1, and from 0 (use of completely different resources) to 1.

The structural diversity of the biotope and the diversity of the small mammal community were calculated by:

$$H = -\Sigma p_i \log_2 p_i$$

where the p are, respectively, the proportions of sites of category i in the biotope, and the proportion of individuals of species i in the community.

Dendrograms were obtained by the UPGMA clustering method, calculated on a similarity matrix obtained from overlap index.

Results

Communities and biotope selection

Four hundred three individuals of 7 species were captured: the insectivores, pygmy shrew *Sorex minutus*, common shrew *Sorex araneus*, white-toothed shrew *Crocidura leucodon* and lesser white-toothed shrew *Crocidura suaveolens* and the rodents, bank vole *Clethrionomys glareolus*, wood mouse *Apodemus sylvaticus* and house mouse *Mus musculus*.

The wood mouse was the only species that was present in all biotopes; it had the greatest biotope use breadth, and dominated the other species numerically (Table 2). The bank vole

Table 2. Population density in the 6 biotopes (individuals/ha) and species' biotope use breadth.

Species	Grassland	Shrubland	Poplar grove	Willow grove	Alder grove	Mature woodland	Breadth in biotope use
Sorex minutus				1.44			0.17
Sorex araneus		1		1.67	1.34	3.03	0.29
Crocidura suaveolens		0.67		0.67		1.67	0.41
Crocidura leucodon		1.01		0.74	0.67		0.48
Clethrionomys glareolus		1.34		3.32	10.15	5.27	0.45
Apodemus sylvaticus	8.9	9.52	1.67	9.14	27.44	31.6	0.67
Mus musculus	2						0.17
Species richness	2	5	1	6	4	4	

and the insectivores were only found in naturally wooded biotopes. The pygmy shrew and the house mouse were the most stenotopic (Table 2).

Species richness was higher in naturally wooded biotopes than in other areas. Both the richness and the diversity of the community (calculated from the results of each trapping session) were positively correlated to the micro-habitat diversity within the biotopes (Fig. 1). Habitat diversity was calculated from the categories identified by the Principal Components Analysis (Appendix A). Qualitative-categorical analysis attributed the highest structural diversity to the alder grove and willow grove, an intermediate diversity to mature wood and shrubland, and the lowest diversity to the grassland and the poplar grove (Fig. 1).

Microhabitat selection

All species were captured at sites with differing characteristics. Sites associated with the same species varied sometimes however in different biotopes (Table 3). In the wooded biotopes the bank vole and the wood mouse selected sites with a lower arboreal cover than availability. The common shrew selected sites with similar or slightly higher arboreal cover than availability. This species also showed a preference for sites with a higher grass cover than that available at average sites. Multivariate analysis confirmed these differences: in 12 of the 15 cases tested (Table 4) discriminant analysis significantly discriminated the characteristics of the species' capture sites from the average availability within the biotopes. The variables which contributed most frequently to habitat discrimination were canopy cover, herbaceous cover and litter depth, overstorey dispersion and understorey size (Table 4). The characteristics of the ground and vegetation cover, both at the canopy and the grass levels, and in particular the size of tall trees and the proximity of bigger trees to trapping sites, were thus the habitat features that most influenced microhabitat selection by small mammals.

In the categorical analysis of habitat selection, each capture site was assigned to one of the 16 habitat categories identified along the axis created by the PCA (Appendix A). The first of
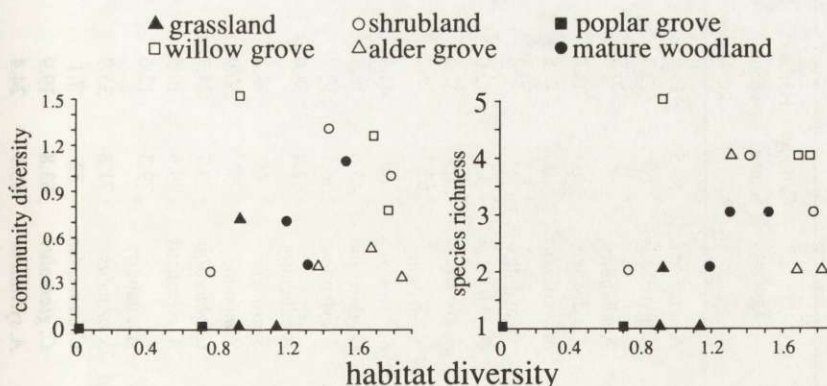

Fig. 1. Relations between the diversity of the microhabitats within the 6 biotopes, and the diversity and richness of the mammal species (Spearman rank test; $r = 0.523$, $p = 0.036$, and $r = 0.488$, $p = 0.051$).

Table 3. Average characteristics of the capture site of each species and average characteristics of availability in the six biotopes. Species with less than 3 captures are omitted.

Biotope	Species	Canopy cover	Herba-ceous cover	Litter depth	Under-storey	Shrub	Stump density	Stump size	Oversto-rey dis-persion	Oversto-rey size	Understo-rey dis-persion	Under-storey size	N
Poplar grove	Availability	57.5	13.7	0.9	0	0	0	0	4.9	96.6	28.2	9.2	24
	A. sylvaticus	60	12.3	0.8	0	0	0	0	5.1	97.6	40	14.1	5
Grassland	Availability	0	26.9	0	0	0	0	0	35.3	68.3	42.2	12.4	44
	A. sylvaticus	0	38.8	0.02	0	0	0	0	34.3	67.3	38.4	13.9	26
	M. musculus	0	47.8	0	0	0	0	0	67.2	75.3	34.6	16.3	6
Shrubland	Availability	5.7	50.5	0.004	0.7	3	0.2	10.1	16.2	61.1	9.6	11.3	46
	C. glareolus	5.3	82.9	0	1.3	2.3	0	0	12.3	45.3	7.9	14.9	4
	A. sylvaticus	7.9	51.3	0	1.2	5.1	0	0	18.1	50.9	8	10.8	10
Alder grove	Availability	63.7	15.2	3	5	8.1	4	47.3	5.5	71.6	4.9	12.4	44
	S. araneus	60	44.3	3.7	1.3	0	1.7	43.3	3.7	60.6	6.3	14.8	3
	C. glareolus	43.6	18.3	2.6	2.8	4.3	5.9	49.6	11	93.8	6.2	8.9	59
	A. sylvaticus	56.1	12.7	3.3	5.7	9.8	3.3	40.9	5	67.2	4.9	14.5	71
Willow grove	Availability	62.4	58.6	2.3	5.5	5.7	0.4	17	4.5	48.6	4.6	14.5	41
	S. araneus	75	78.4	1.5	3.6	3.6	0.2	8	3.3	45.5	4.7	13.6	5
	S. minutus	50	60.9	1.8	3.9	6.2	0.1	4.6	3.6	48.3	4.4	13.6	7
	C. glareolus	39.7	24.7	1.8	5.1	8.1	0.5	15.3	5.4	64.8	6.3	13	18
	A. sylvaticus	49.6	19.5	1.6	5.3	4.4	0.5	20.1	5.2	61.4	5.7	12.8	26
Mature woodland	Availability	79.3	12.6	2.3	8.2	13.7	2.5	53.8	6.1	100.3	3.9	12.9	43
	S. araneus	71.8	35.9	2.1	11.4	10.1	2.1	37.9	4.4	76.8	2.7	9.6	14
	C. suaveolens	82	7.1	3.5	7.6	20.2	2.2	83	4.4	117	3.1	15.1	5
	C. glareolus	63.8	19.9	1.8	4.6	9.1	1.8	46.3	5.6	81.2	4.2	12.3	18
	A. sylvaticus	65.9	24.4	2.3	8.2	13.2	2.3	55.1	6.8	108.1	4.1	12.6	33

Table 4. Microhabitat selection expressed by Stepwise Discriminant Analysis between capture sites of a species and the available habitat: standardized discriminant function coefficient. Only species with more than 3 captures in a biotope were analyzed; – indicates variables not entered in analysis. Key: Cg = Clethrionomys glareolus, As = Apodemus sylvaticus, Cs = Crocidura suaveolens, Sa = Sorex araneus, Sm = Sorex minutus, Mm = Mus musculus.

| Variables	Mature woodland				Alder grove		Willow grove				Shrubland		Grassland		Poplar grove
	Cg	As	Cs	Sa	Cg	As	Cg	As	Sa	Sm	Cg	As	As	Mm	As
Canopy cover	0.74	1	–	–	–	0.87	0.55	–	–	–	–	–	–	–	–
Herbaceous cover	–	–	–	0.75	–	0.66	0.84	1.0	–	–	0.70	–	1.0	0.40	–
Litter depth	–	–	0.82	–	–	–	0.46	0.71	1.0	–	–	–	–	–	–
Understorey	0.55	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Shrub	–	–	–	–	–	–	–	0.49	–	–	–	–	–	–	–
Stump density	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Stump size	–	–	–	–	–	0.59	–	–	–	–	–	–	–	0.84	–
Overstorey dispersion	0.48	–	–0.72	–	0.59	–	–	–	–	–	–	–	–	–	–
Overstorey size	0.47	–	–	–	0.81	–	–	–	–	–	–	–	–	–	–
Understorey dispersion	–	–	–	–	–0.60	–0.80	–	–	–	–	–	–	–	–0.69	–
Understorey size	–	–	–	–	–	–	–	–	–	–	0.65	–	–	0.48	–
N	18	33	5	14	59	71	18	26	5	7	4	10	26	6	5
Wilk's Lambda	0.69	0.89	0.85	0.68	0.59	0.87	0.59	0.42	0.90		0.8	0.9	0.9	0.7	
Chi-square	21.04	8.37	7.287	21.13	52.70	15.36	27.86	53.28	4.308	N.S.	9.092	N.S.	6.815	18.09	N.S.
p	0.0003	0.038	0.026	0.000	0.0000	0.004	0.000	0.000	0.037	N.S.	0.011	N.S.	0.012	0.001	N.S.

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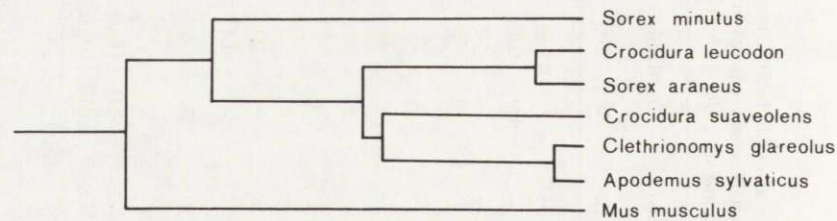
Fig. 2. Dendrogram of microhabitat category use by small mammals.

Table 5. Results of Stepwise Discriminant Analysis betweens pairs of dominant species in 5 biotopes: standardized discriminant function coefficient; – indicates variables not entered in the analysis. Key: *As = Apodemus sylvaticus*, *Cg = Clethrionomys glareolus*, *Mm = Mus musculus*.

Variables	Mature woodland $As - Cg$	Alder grove $As - Cg$	Willow grove $As - Cg$	Shrubland $As - Cg$	Grassland $As - Mm$
Canopy cover	–	–	– 0.84	–	–
Herbaceous cover	0.81	–	–	–	–
Litter depth	0.53	0.37	–	–	–
Understorey	1.1	– 0.35	–	–	–
Shrub	–	– 0.35	1.02	–	–
Stump density	–	– 0.49	–	–	–
Stump size	–	0.29	–	–	–
Overstorey dispersion	–	0.48	–	–	–
Overstorey size	0.75	0.48	–	–	–
Understorey dispersion	0.62	0.17	–	–	–
Understorey size	–	– 0.56	–	0.98	1
N	33 – 18	71 – 59	26 – 18	10 – 4	26 – 6
Wilk's lambda	0.59	0.44	0.80	0.70	0.83
Chi-square	24.8	103.9	8.7	7.9	8.3
p	0.0002	0.0000	0.013	0.005	0.019

these axes was determined by canopy cover, litter depth, understorey, shrub, overstorey dispersion and understorey dispersion (Table 1), and may be interpreted as a woodland gradient. The second axis was determined by stump density and stump size and may be interpreted as a gradient of the biotope floor's maturity. The third axis was determined by herbaceous cover and overstorey size, and describes the presence of open areas. The fourt axis did not fit any easy ecological explanation.

The 16 spatial resources defined by PCA are differentiated (Appendix A) and represent a fine grained description of each study area. Spatial overlap, derived from frequencies of capture sites for each pair of species classified into the 16 categories (Fig. 2), shows that the more abundant wood mouse and bank vole largely overlapped in all biotopes. The insectivorous guild (particularly pygmy shrew, common shrew and white toothed shrew) are well separated from e most from rodents. The most separated species is the house mouse, which reflect it's stenotopy.

Microhabitat segregation

The degree of microhabitat segregation among species was interpreted by discriminant analysis. This analysis was only possible between pairs of dominant species in each biotope because of the scarcity of data available for the other species: the wood mouse and the bark vole in mature woodland, alder grove, willow grove and shrubland; the wood mouse and the house mouse in grassland. From an ecological standpoint this procedure seems most appropriate considering the dominant role played by the wood mouse and bank vole in small mammal communities of central and southern Europe (Herrera and Hiraldo 1976).

The results of this discriminant analysis show that the dominant species selected different microhabitats in each biotope; the microhabitats of each species pair differed significantly (Table 5). Segregation was more intense in the mature woodland and in the alder grove than in the other biotopes; the intensity of segregation may be empirically tested by the values of Wilk's lambda in Table 5. The low values of this index in the mature woodland and the alder grove (0.59 and 0.44 respectively) suggest that in these biotopes the species were more segregated than in the other biotopes. On the other hand, low microhabitat discrimination in the willow-grove, the shrubland and in grassland were confirmed by high values of Wilk's lambda. The microhabitat features that contributed to spatial segregation varied between biotopes. In the mature woodland, canopy cover, understorey dispersion and overstorey size influenced segregation. In the alder grove the segregation was due to many variables, and stump density, overstorey dispersion, overstorey size and understorey size played major roles. In the other biotopes only one or two variables contributed to the segregation, which reflected the simpler structure of these biotopes; these were canopy cover and shrub in the willow grove, and understorey size in the other habitats.

Discussion

Communities and biotope selection

Our results show that rodent communities in northern Italy differ from those of northern and central Europe where communities are dominated by *Microtinae* (Banach 1987, Mazurkiewicz and Rajska-Jurgiel 1987, Aulak 1970). In our study areas the wood mouse was the most abundant and eurytopic species. Bank vole was the only microtine species and was present only in natural woodlands, thus showing the same habitat preference exhibited in northern and central Europe (Aulak 1970, Malzhan and Fedyk 1982, and others). In northern Europe bank vole is typical of afforested biotopes while in our study areas it was present in differing seral stages of woodlands and in the shrubland (Table 2).

Data on the distribution of small mammals in Italy has mostly been derived from owl pellets and only a few studies have used standard capture methods. Our results agree with a preliminary study (Canova 1988) which showed similar habitat preferences in wood mouse and bank vole, but contrast with the results from Mediterranean areas of Italy (Boitani *et al.* 1985), where the wood mouse is distributed only in wooded and in covered sites. In our study areas wood mouse was present both in covered and in open areas and this difference may reflect different adaptive behaviour in Mediterranean and in continental biotopes.

In contrast to other European rodent communities, our communities did not include either yellow necked mouse *Apodemus flavicollis*, typical of mature woodland, or field voles (*Microtus* sp.), typical of grassland. Our data agree with the scarce literature data available for Italy and seems to confirm a scarcity of these species from the lowlands of northern Italy. Insectivores were also found only in wooded habitats or in shrubland (Table 2). Pigmy shrew and common shrew are habitat generalists (Gurnell 1985) and elsewhere they are also common in grassland and pastures (Churchfield 1986). We think that the absence of these species from our poplar grove and grassland is due to intensive agricultural practices (ploughing and pesticides) that have reduced ground cover and food supply. In our data insectivore density is lower than rodent density (Table 2) and this may be due to differing trapping success rates for snap traps and pitfalls. However ecological theory would suggest that since shrews are secondary consumers, they will occur with a lower density than herbivores and seed eaters of similar body size in an ecosystem.

Species richness and community diversity were positively related to the structural diversity of biotopes (Fig. 1), as occurs in birds communities. The relation between habitat complexity and diversity of bird communities is probably associated with the strong devel- opment of a vertical habitat component in the more advanced successional stages, which permits the exploitation of a wider range of foraging niches (MacArthur and MacArthur 1961, Fuller 1982). The wood mouse is the only species in our study areas that may show arboreal behaviour (Toschi 1965, Delany 1974), though we never observed this behaviour, whereas the other species live mainly on the forest floor, or are fossorial. The increasing richness and diversity associated with increasing structural complexity of the habitat should therefore depend on greater trophic availability (Schoener 1983) or may be due to greater complexity of the roots of the trees, which may also be important considering the fossorial behaviour of these mammals.

Interseasonal variation in habitat diversity is higher for the young seral stages (shrubland and willow grove) and for the poplar grove (Fig. 1). This probably reflects the presence of environmental factors (flooding, removal of fallen logs, ploughing and grass cutting in the poplar grove) that strongly influence the habitat structure on a seasonal basis. The high interseasonal variability in the diversity index may condition the validity of previous ex- planation of correlation between habitat and community diversity. We should not exclude the possibility that factors other than structural diversity (i.e. food availability, parasites, food supply etc.) are primary determinants of small mammal community structure.

Mature woodland was not the most diversified biotope (Fig. 1). This may reflect the reduction in structural complexity in the older successional stages (Odum 1973, Begon *et al.* 1986).

The mammal species richness was lowest in the poplar grove, thus confirming Malzhan and Fedyk's (1982) suggestion that ploughing limits small mammal populations. Small mammal communities were indeed richer and more abundant in unploughed poplar groves (Canova 1988) than was observed in this study.

Microhabitat selection

Microhabitat selection may reflect the anti-predatory behaviour or the foraging behaviour of the species (Schoener 1983) and the habitat structure probably determines the quality and the abundance of food (Dueser and Shugart 1979). On the other hand, microhabitat selection may be due to inter-specific competition. In this case the microhabitats selected by competitors should have complementary characteristics (Rosenzweig and Winakur 1969, Rosenzweig 1973, Dueser and Shugart 1979). Our results show that ground cover and litter structure, as well as tree size and proximity to capture site, were the microhabitat features that were most selected by small mammal species compared to the available habitat (Table 4). This seems to confirm the strong influence of ground cover and structural features at arboreal level in shaping microhabitat selection by small mammals (Dueser and Shugart 1978, Yahner 1982, and others).

The shrews were the most generalist species, and only ground cover or litter structure strongly influenced their microhabitat preference. These preferences may reflect the foraging habits of these forest floor explorers, but they do not agree with previous findings for similar species of North America (Dueser and Shugart 1978, Yahner 1982), where a general preference for dense trees around the trap site was shown. Our results confirm Gurnell's suggestion (1985) that shrews are habitat generalists in all stages of habitat succession. Rodents generally showed a higher specialization in microhabitat selection. No complementarity was observed between the selected habitat features. Wood mouse and the bank vole selected microhabitats char- acterized by a high canopy and herbaceous cover; tree size and proximity to capture sites were also important, thus confirming the habitat preference showed by similar species in North America (Dueser and Hallet 1980, Yhaner 1982).

Microhabitat segregation

Several authors have warned that competitive interaction and overlap in resource use may not be positively related (Colwell and Futuyma 1971, Abrams 1980, Glasser and Price 1988). Extensive overlap in spatial use should demonstrate any coexistence of populations which may be due to a wider segregation in other principal niche axes *sensu* Hutchinson (1959) (food, activity-rhythm, etc.) or to a fine-grained selection of habitat.

One of the aims of our research was to investigate patterns of spatial segregation between dominant small mammal populations. All the pairs showed, to different degrees, a significant separation using a fine grained scale (Table 5). The microhabitat features contributing to separation between populations varied between biotopes, and this showed that in each community coexistence is guaranteed by means of species-specific adaptation to the biotope. Discriminant analysis also showed that segregation was higher in the mature woodland and the alder grove than in other biotopes. These results are difficult to interpret. Perhaps the intense management of the willow grove and the shrubland in the recent past is significant. For the willow grove, shrubland and grassland the lower degree of segregation is possibly due

to the absence of a stable equilibrium between populations. These biotopes are located near the river Ticino and irregular flooding may play a role in reducing population density under the equilibrium level.

In the mammal communities in the grassland, the population dynamics may be influenced by agricultural practices in the surrounding cultivated fields. Predation, in this simplified biotope, may play a major role in depressing population density compared to other biotopes.

Some evidence of microhabitat partitioning between the two dominant species of rodents was detected in each community. It cannot however be excluded that coexistence is achieved (to a greater degree) by means of different use of food resources, and/or different activity rhythms, or vertical segregation in habitat use. Moreover the numbers of bank vole and wood mouse in shrubland and of house mouse in grassland are small (Table 5) and this might have produced the spatial segregation we describe. Conclusive explanations of coexistence patterns between dominant species will be provided by a selective removal experiment.

References

Abrams P. 1980. Some comments on measuring niche overlap. Ecology 1961: 44 – 49.

Aulak W. 1970. Small mammal communities of the Bialowieza National Park. Acta theriol. 15: 465 – 515.

Banach A. 1987. Small mammals communities in a complex of forest biotops. Acta theriol. 32: 229 – 244.

Begon M., Harper J. L. and Townsend C. R. 1986. Ecology. Individuals, Populations and Community. Blackwell Scientific Publication, London: 1 – 854.

Boitani L., Loy A. and Molinari P. 1985. Temporal and spatial displacement of two sympatric rodents (*Apodemus sylvaticus* and *Mus musculus*) in a Mediterranean coastal habitat. Oikos 45: 246 – 252.

Canova L. 1988. Segregazione spaziale in una comunita di micromammiferi della pianura padana occidentale. Boll. Zool. 55 (suppl.): 48.

Churchfield S. 1986. Shrews. Mammal Society Series. London: 1 – 20.

Colwell R. K. and Futuyma D. J. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567 – 577.

Danielson B. J. and Gaines M. S. 1987. Spatial patterns in two syntopic species of microtines: *Microtus ochrogaster* and *Synaptomys cooperi*. J. Mammal. 68: 313 – 322.

Dueser D. D and Hallet J. G. 1980. Competition and habitat selection in a forest-floor small mammal fauna. Oikos 35: 293-297.

Dueser R. D. and Shugart H. H. 1978. Microhabitat in a forest-floor small mammal fauna. Ecology: 59: 89 – 98.

Dueser R. D. and Shugart H. H. 1979. Niche pattern in a forest floor small-mammal fauna. Ecology 60: 108 – 118.

Fuller R. J. 1982. Bird habitats in Britain. T and AD Poyser. Calton: 1 – 320.

Galindo C. and Krebs C. J. 1985. Habitat use and abundance of deer mice; interactions with meadow voles and red-backed voles. Canad. J. Zool. 63: 1870 – 1879.

Glasser J. W. and Price H. J. 1988. Evaluating expectations deduced from explicit hypotheses about mechanisms of competition. Ecology 51: 57 – 70.

Grant P. R. 1972. Interspecific competition among rodents. Annal Rev. of Ecol. Syst. 3: 79 – 106.

Green R. H. 1974. Multivariate niche analysis with temporally varying environmental factors. Ecology 55: 73 – 83.

Green R. H. 1979. Sampling design and statistical method for environmental biologists. Wiley, New York: 1 – 180.

Grodziński W., Pucek Z. and Ryszkowski L. 1966. Estimation of rodent numbers by means of prebaiting and intensive removal. Acta theriol. 11: 297 – 314.

Gurnell J. 1980. The effects of prebaiting live traps on catching woodland rodents. Acta theriol. 25: 255 – 264.

Gurnell J. 1985. Woodland rodents communities. [In: Ecology of woodland rodents. J. H. Flowerdew, J. Gurnell and J. H. Gipps, eds]. Symp. Zool. Soc. London: 377 – 402.

Herrera C. M. and Hiraldo F. 1976. Food-niche and trophic relationships among Europaean owls. Ornis Scand. 7: 29 – 41.

Hutchinson G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93: 145 – 159.

Janion M., Ryszkowski L. and Wierzbowska T. 1968. Estimated numbers of rodents with variable probability of capture. Acta theriol. 13: 285 – 294.

Kincaid W. B. and Cameron G. N. 1982. Effects of species removal on resource utilization in a Texax rodent community. J. Mammal. 63: 229 – 235.

Levins R. 1968. Evolution in changing environments. Princeton University Press.: 1 – 284.

Llewellyn B. J. and Jenkins S. H. 1987. Patterns of niche shift in mice: seasonal changes in microhabitat breadth and overlap. Am. Nat. 129: 365 – 381.

MacArthur R. H. and MacArthur J. W. 1961. On bird species diversity. Ecology 42: 594 – 598.

MacArthur R. H. and Pianka E. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603 – 609.

Mazurkiewicz M. and Rajska-Jurgiel E. 1987. Numbers, species composition and residency of a rodent community in forest and field-forest ecotones. Acta theriol. 32: 413 – 432.

Malzhan E. and Fedyk S. 1982. Micromammalia of the cultivated Wizna Fen. Acta theriol. 27: 25 – 43.

Noon B. R. 1981. The distribution of an avian guild along a temperate elevational gradient: the importance and expression of competition. Ecol. Monogr. 51: 105 – 124.

Odum E. P. 1971. Fundamentals of ecology. Saunders, London: 1 – 584.

Rosenzweig M. L. and Winakur J. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50: 558 – 571.

Rosenzweig M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid rodent species. Ecology 54: 111 – 117.

Rosenzweig M. L. 1981. A theory of habitat selection. Ecology 62: 327 – 335.

Schoener T. W. 1974. Some methods for calculating competition coefficients from resource utilization spectra. Am. Nat. 108: 332 – 340.

Schoener T. W. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240 – 284.

Toschi A. 1965. Fauna d'Italia. Vol. 7 Mammalia. Edizioni Calderini, Bologna: 1 – 515.

Yhaner R. H. 1982. Microhabitat use by small mammals in farmstead shelterbelts. J. Mammal. 63: 440 – 445.

Appendix. Average values for the 16 microhabitat categories identified by Principal Components Analysis.

Cate-gories	Canopy cover	Litter depth	Under-storey	Shrub	Overstorey dispersion	Understorey dispersion	Stump density	Stump size	Herbaceous cover	Overstorey size	Understo-rey size
1	4.5	0	0.4	2.7	21.7	18.3	0	0	37.7	46	10.2
2	4.6	0.3	0.2	1.1	14.2	20.6	0	0	54.4	61.8	14.6
3	30.4	0.3	0	0.3	20.3	35.4	0	0	18.9	85.9	9.2
4	0	0	0	0	41.3	50	0	0	25.7	101.9	14.8
5	4.3	0.2	4.5	1.5	21.2	4.8	7.5	47.3	50	77	6.5
6	9.2	0.3	1.4	1.8	14.7	8.2	0.6	26.1	70.3	69.5	17.3
7	15	0.8	0.5	7	15.6	9.1	7.5	78.3	20	90.5	7.1
8	35.5	2.2	3	0.8	8.6	10.5	4.8	68.4	17	128.6	13.7
9	70	2.3	9	11.3	3.4	2.7	0	0	29.9	43.6	10.3
10	73.3	2.5	2.9	2.2	3.8	5.2	0	0	68.1	43.8	15.2
11	74.1	1.9	2.5	8.1	4.5	14.5	0.2	16.6	4	88.9	9.9
12	74	2.8	2.8	8.6	4.7	5.8	0.6	24	10.8	86.5	16.6
13	71.7	2.2	9.4	10.9	3.7	2.6	1.9	42.7	34.4	56.6	8.9
14	68.6	2.7	6.4	4.5	3.41	4.1	2.3	55.9	38.7	52.5	14.9
15	67.8	2	8.2	18.6	5.3	3.5	2.9	45.8	6.3	88.6	10.7
16	74.8	3.4	6.4	8.4	5	4.5	2.7	62	9.8	85.3	14.8