Effect of land-use on small mammal abundance and diversity in a forest–farmland mosaic landscape in south-eastern Norway

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ABSTRACT

During the last century the boreal forests of south-eastern Norway have been converted into patchworks of agricultural areas, clear-cuts and even-aged conifer monocultures. Even though Scandinavian forest ecosystems are strongly influenced by small mammals' dynamics, the effects of anthropogenic changes on these communities are still debated. We conducted an extensive capture–mark–recapture study to examine the relative abundance and distribution of 11 species of small mammals during the reproductive season with respect to all available landscape-scale habitat types and fine-scale vegetation characteristics.

At the landscape scale, the highest abundance and diversity of small mammals was recorded in abandoned meadows. The community was dominated by *Myodes glareolus* in old abandoned meadows sparsely colonized by trees and bushes, and by *Microtus agrestis* in younger grass-dominated meadows, likely reflecting inter-specific competition and niche separation. Notwithstanding the remarkably low availability of both types of meadows, these habitats sustained by far the highest abundance of small mammals.

Intensively managed forest monocultures at logging age and cultivated fields sustained the lowest abundance of small mammals. However, while the former also supported the lowest species diversity, the latter unexpectedly sustained the highest number of species. Only *Apodemus sylvaticus* attained highest densities in cultivated fields, but its marked association with forest edges clearly indicates its need for landscape-scale complexity.

Contrary to previous theories, clear-cuts and forests overall did not support the highest abundance of *M. agrestis* and *M. glareolus*. Both young and mature forests failed to explain a significant amount of variation in community structure when taking into account other habitat types. However, a few old clear-cuts characterized by higher vegetational complexity, and a few stands preserving characteristics typical of late successional stages (moss, berries, woody debris) were able to support relatively high abundance of small mammals.

Our study shows that sampling in all available habitats at different spatial scales is essential for a comprehensive understanding of community dynamics in forest–farmland ecosystems, as even habitat types that are under-represented at the landscape scale might play a significant role for the community dynamics. Forest–farmland mosaic landscapes with a high degree of heterogeneity at both large spatial scale (*e.g.* meadows, shelterbelts) and at fine-scales (*e.g.* varied and multi-layered ground cover) allow for the conservation of small mammal diversity and abundance in human-dominated areas. Nonetheless, the low number of *Myodes rufocanus* trapped in this highly fragmented mosaic landscape supports the hypothesis that habitat fragmentation negatively affects the dynamic of this forest specialist.

1. Introduction

During the Holocene mature, multi-layered pristine forests, with dead trees and rich substrate became the most common habitat of the boreal and hemi-boreal zones of the northern hemisphere (Stokland et al., 2003). Forest structure and composition were strongly influenced by wild fires, which produced open-structured

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stands characterized by a deciduous forest phase and structurally complex understory vegetation (Hansson, 1992). During the last millennia most pristine forests worldwide have undergone two major anthropogenic transformations, by being converted into either productive agro-ecosystems or into timber production stands. Even though human exploitation of virgin forests traces back to the Stone Age, the most radical changes occurred at the end of the 19th and early 20th centuries, following the mechanization of both agricultural (Van Zanden, 1991) and timber extraction practices (Stokland et al., 2003). Hence, continuous multi-aged boreal forests have been turned into the modern landscape, *i.e.* a patchwork of farmlands, clear-cuts, and dense, fast growing, even-aged conifer monocultures characterized by an overall younger age and by a considerably lower ecological complexity compared to virgin forests (Esseen et al., 1992; Hanski, 2005; Angelstam et al., 1985).

In recent years, the growing demand for sustainable land-management practices has produced a massive amount of literature investigating the impact of agriculture (Burel et al., 2004; Silva et al., 2005) or forestry practices (Hansson, 1992; Fitzgibbon, 1997; Bayne and Hobson, 1998; Kozaikiewicz et al., 1999; Carey and Harrington, 2001; Constantine et al., 2004; Sullivan and Sullivan, 2006) on a range of species, including small mammal communities, worldwide. The general picture that emerged indicates that clear-cutting and agricultural practices alter species abundance and community structure by favoring open-habitat species such as *Microtus* spp. (Hansson, 1978) or forest–field mosaic species such as *Apodemus* spp. (Kozaikiewicz et al., 1999) and *Peromyscus* spp. (Pearce and Venier, 2005) at the expense of the forest-dwelling *Myodes* spp. (Hansson, 1999; Rosenberg et al., 1994; Sullivan and Sullivan, 2001; Pearce and Venier, 2005). However, literature provides so many exceptions to this general trend that the overall picture becomes blurred (see Wolk and Wolk, 1982; Hansson, 1978, 1999; Kirkland, 1990; Gliwicz and Glowacka, 2000; Moses and Boutin, 2001; Sullivan and Sullivan, 2001; Ecke et al., 2002). A similarly unclear picture appears when considering the relationship between forestry practices and species diversity (Kirkland, 1990): while some studies show that old natural forests support higher species diversity than plantations (Saitoh and Nakatsu, 1997), others report an opposite trend (Sullivan and Sullivan, 2001; Constantine et al., 2004).

The widespread disagreement on the impact of land-use practices on small mammal communities suggests that these are affected by factors other than just "farming" or "clear-cutting" *per se*. Instead, the abundance and diversity of small mammals is likely to be mostly affected by the degree of ecological simplification associated with each specific landscape management practice both at the landscape scale and at finer spatial scales. Indeed, it is well established that complex and heterogeneous ecosystems support a higher diversity of ecological niches and, thus, a higher carrying capacity for all members of small mammal communities (Fitzgibbon, 1997; Carey et al., 1999; Carey and Harrington, 2001; Bowman et al., 2001; Martin and McComb, 2002; Pearce and Venier, 2005). However, to date literature focused mostly on fine-scale aspects of habitat heterogeneity (*e.g.* litter depth, number of dead trees, crop species) or on some landscape features in the area surrounding the trapping site (*e.g.* edge density, patch size; Bayne and Hobson, 1998; Bowman et al., 2001; Silva et al., 2005). To our knowledge, the relationship between the abundance and distribution of species composing a small mammal community and all available types of habitat at the landscape scale has been overlooked. This may lead to an interpretation of community dynamics biased by an unknown abundance and diversity of species in proximate, but non-sampled habitat types, which may play a significant, or even a key-role in the ecological settings of a given study area.

Nowadays the hemi-boreal region in Scandinavia can be described as a fine-scaled mosaic of cultivated fields, meadows, clear-cuts, dense even-aged reforestation blocks and forest stands at the logging maturity age (Hansson, 1992). Landscape-scale heterogeneity is particularly high in south-eastern Norway, where the widespread low-density human presence and the small average size of land properties are responsible for a considerable amount of edge habitats and for much smaller land-management units compared to well studied areas of Sweden or America (Esseen et al., 1992). In addition, following the decline in livestock numbers, areas formerly used as rough grazing or hay meadows have been abandoned and are slowly reverting to forest, thus providing a potentially important habitat in terms of biodiversity (Moen, 1998).

Small rodents are regarded as the heart of many northern terrestrial food webs as they are important prey species for a large number of mammalian and avian predators and are primary consumers of plants, lichens, fungi and invertebrates (Hörnfeldt et al., 1990). Their characteristic inter-annual cyclic fluctuations in densities have long been recorded in Scandinavia (Ims and Fuglei, 2005) for bank voles (*Myodes glareolus*), grey-sided voles (*Myodes rufocanus*), field voles (*Microtus agrestis*) and lemmings (*Lemmus lemmus*; Henttonen and Hanski, 2000). No conclusive agreement has been reached on the causes driving these fluctuations, but the increased irregularity with local disappearances of the cycles (*e.g.* Hansson, 1999) and the declining trend detected in the three most abundant vole species in the boreal ecosystems (bank voles, grey-sided voles and field voles; Ecke et al., 2002) has arisen concern.

Given the importance of small rodents dynamics for Scandinavian forest ecosystems and the long-term speculation about the impact of land-use changes on these dynamics (Strann et al., 2002), we conducted this study to understand how small rodent communities are affected by this complex, fine-scale anthropogenic mosaic landscape. We investigate the relative distribution, abundance, and diversity of small rodents with respect to both all types of habitat available at the landscape scale, and to vegetation characteristics at fine spatial scales. We expect that the high diversity of food resources and cover associated with the different habitat types at the landscape scale supports a high overall abundance and diversity of small rodents, which reaches a maximum in those habitat types characterized by the lowest intensity of human use and by the highest structural heterogeneity.

2. Methods

2.1. Study area

We aimed at studying small mammal communities in the forest–farmland mosaic landscape characterizing south-eastern Norway during the reproductive season. Hence, we conducted the study in a central area of south-eastern Norway (*i.e.* Østfold and Akershus counties, 59°38′N, 11°08′E), in May–August 2003–2004. The project falls under the umbrella of a broader project (Panzacchi, 2007) on the ecology of red foxes (*Vulpes vulpes*) with respect to their main prey (*i.e.* small mammals) and alternative prey during spring (mostly roe deer *Capreolus capreolus* fawns; see Panzacchi, 2007, Panzacchi et al., 2008). The study area (ca. 133 km²) was made up of a fine mosaic of agricultural land (30%; for the most part cultivated fields – not only growing cereals or grass for silage production, but also grazing meadows and old abandoned meadows), lakes and rivers (12%) and intensively managed even-aged forest plots (58%), for the most part coniferous (*Picea abies* and *Pinus sylvestris*) with scattered patches of deciduous trees (in particular *Betula* spp.). Pristine forests are virtually absent from the study area, and the oldest forests are regrowth forests at logging maturity (*i.e.* ready to be harvested; Stokland et al., 2003). The landscape composition of the study

area is representative of that characterizing south-eastern Norway, and encompasses an environmental gradient with a slightly higher proportion of forested habitat in the northern side of an east-west highway crossing the whole region at the expenses of agricultural land. The study area lies in the hemi-boreal biogeographical zone; during the study period the average precipitation was 4.7 mm/day, and the average temperature was 16.3 °C (Norwegian Meteorological Institute, www.met.no). In accordance to previous studies demonstrating that small mammals show multiannual cycles only above 60°N (Hanski et al., 1991), in our study area population dynamics are relatively stable (Geir Sonerud, personal communication).

2.2. Trapping method

Small mammals were trapped using Ugglan Special multicapture live-traps (Hansson, 1994). Each trap was provided with a metal roof and with a polystyrene insulating mat. Traps were baited with a diverse menu (*i.e.* apples, yarns soaked in peanut butter, wheat grains) to attract different species, and were checked every morning. The traps ($n = 216$) were organized in Small Quadrates (SQs, Myllmäki et al., 1971), which are 15 m × 15 m trapping units composed of 12 traps evenly positioned along the perimeter. Each year we performed 5 trapping sessions lasting 10 consecutive days each, for a total of 100 trapping days over 2 years. During each 10-day trapping session we positioned randomly 3 SQs in each of the 6 habitat types representative of south-eastern Norway (Table 1), for a total of 18 SQs. The Small Quadrate Method has been widely used in Scandinavian Countries (Myllmäki et al., 2008), and was adopted in our study site to obtain habitat-specific estimates of abundance. Other methods such as large trapping grids were discarded due to the patchiness and fragmentation of the study area, as one large grid would span over several habitat types and prevent us from obtaining habitat-specific estimates. Considering the relatively low number of traps composing a SQ compared to larger trapping grids, and the expected heterogeneity in small rodent abundance among habitat types, we maximized capture probabilities by increasing the number of trapping days, as recommended by White et al. (1982). As we wanted to obtain an estimate of the relative abundance of small mammals in each habitat types unbiased by the environmental gradient observed in south-eastern Norway, we sampled all habitat types alternatively in the southern and in the northern part of the above-mentioned highway. Hence, the first trapping session was conducted in the southern area; then, all traps were moved in the northern area – rearranged in all six habitat types – and so on. The landscape composition within a buffer of 1 km radius centered in each SQ reflected the latitudinal environmental gradient of the study area: 29% farmland and 71% forest in the southern part of the study area, and 19% farmland, 81% forest in the northern part. SQs were positioned in a central position within each habitat patch, and were never placed in the same position during different trapping session in a given year. The minimum distance between two SQ situated, respectively, in the northern and southern sub-areas was 13 km, the maximum distance 24 km. Within each sub-area, SQs were on average 2.80 ± 2.28 km apart. In 2003 we had to start sampling the habitat type "abandoned meadows" later compared to other habitats; hence, during each of the trapping sessions 1–4th we placed four SQs in each of the first five habitat types listed in Table 1, and in the 5th session we placed 2 SQs in each of these habitat types and 10 SQs in abandoned meadows. Within the perimeter of each SQ we recorded 16 vegetation parameters (Table 1). Other variables used in the analyses are described in Table 1.

For the purpose of our study we needed to recognize the individuals captured within each SQ during a 10-day trapping session. Hence, small rodents were individually marked by

Table 1
Description of the variables used for the analyses. Land-use descriptors and vegetation descriptors were recorded within the perimeter of each small quadrate – SQ (15 m × 15 m). The types of habitat were defined according to the standard Norwegian forest classification system (Børset, 1985) and to the macroscopic characteristics of the ground cover – for non-forested habitat. For most of the vegetation parameters we recorded the percentage cover and the average height within the SQ.

Parameter	Description
Habitat type	
Clear-cut	
Young forest	Young plantations (0–5 years) and pole sized stands (5–40 years)
Mature forest	Medium aged stands (40–90 years) and mature stands (>90 years)
Crop	Cultivated fields
Meadow	Grassy, uncultivated areas, often previously used for grazing
Abandoned meadow	Old unmanaged meadows with sparse trees and bushes
Vegetation descriptors	
N trees	*N* of trees within a SQ. 1–10, 10–20, 20–30, 30–40, >40
Tree height	
Moss, % cover/height	
Herb, % cover/height	Herbaceous plants
Crop	Cultivated cereals and rapeseed; present/absent
Crop height	
S berry, % cover/height	Small berries (*e.g.* blueberry and cowberry)
T berry, % cover/height	Tall berries (*e.g.* raspberry)
Bush, % cover/height	Woody plants < 1.5 m, berries excluded
Woody debris, % cover/height	Dead tree trunks, branches and woody fragments
Proximity to edges	
EDGE	Closest neighboring habitat type
DIST	Distance to the closest neighboring habitat type
Other	
DATE	Week number
RAIN	Average daily precipitation (mm) per trapping period
AREA	Sub-area

clipping fur (either in a stripe or in a spot) in a particular part of the back (*i.e.* starting from the right side, from the left, from behind, or from above the neck). In addition, distinguishing features like species, sex, size, reproductive status, and presence of scars or particular characteristics were recorded to facilitate individual identification (see also Graham and Lambin, 2002). The insectivorous shrews were not marked as they were a non-targeted species and often died in the traps due to their high metabolism.

2.3. Estimation of population size

We performed a capture–mark–recapture analysis, CMR, to estimate the size of the population of each of the three most common rodent species in different habitat types. We assumed that within each 10-day trapping session the population was closed, and we selected the closed capture Huggins estimator (Huggins, 1989) in the software MARK 4.3 (White and Burnham, 1999). The relatively high proportion of individuals recaptured, in addition to the fact that mortality never occurred for *Apodemus* spp., and varied between 0% and 1% for *Microtus agrestis* and *Myodes* spp., provided support for the assumptions. First, for each individual marked we developed the capture history, *i.e.* a vector indicating the number of trapping occasions (1 if the individual was captured, 0 if the animal was not captured). The habitat type characterizing the SQ where the individual was trapped was added as a grouping factor to the matrix, and time was added as a

continuous covariate. The resulting three matrices – one for each species – were analyzed by using eight different models that differ in their assumed sources of variation in probability of capture (p_i) and probability of recapture (c_i). Model M_0, assumes equal capture probability for all animals on all trapping occasions; M_b assumes different capture and recapture probabilities; M_t assumes that capture probability varies with time; M_h assumes different capture probabilities for different individuals. These basic models (M_0, M_t, M_t, M_h) were repeated assuming different capture probabilities in each of the six habitat types ($M_{0\ hab}$, $M_{t\ hab}$, $M_{t\ hab}$, $M_{h\ hab}$). The most parsimonious model was selected by comparing their Akaike Information Criterion corrected for small sample sizes (AIC$_c$, Burnham and Anderson, 2002). For each species, the abundances estimated by the most parsimonious models in different habitat types were compared with chi-square tests.

2.4. Analysis of the relationship between species and environment

First, we investigated possible effects of year, sub-areas and period (fixed factors) on the overall number of individuals captured in each SQ (dependent variable) by using generalized linear models, *glms*, with a negative binomial distribution, which is commonly used to describe the distribution of count data in which the variance is greater than the mean (Crawley, 2002). After, we investigated the relationship between environmental variables and the number of individuals trapped. A principal component analysis (PCA, Jongman et al., 1995) was used to reduce correlated parameters describing the percentage vegetation cover to a few principal components (PCs). Only components that explained more than 10% of the variance among variables were considered. Before we performed the PCA, all variables were scaled according to Becker et al. (1988). Proportion data were arcsine-square root transformed following Zar (1984). Each PC was interpreted based on the highest variable loadings. The relationship between the abundance of each of the three most common species (dependent variable) and environmental variables (*i.e.* the PCs – Table 4 – and AREA, DATE, RAIN, EDGE and DIST – Table 1) was investigated by using *glms* assuming a negative binomial distribution.

For the analysis of the relationship between environmental variables and small mammal community we chose ordination methods. At first we inspected the general structure of the data by using a detrended correspondence analysis, DCA (Hill, 1974; Hill and Gauch, 1980) to determine the length of the gradient and choose the type of response to be used in the following analyses, *i.e.* linear or Gaussian. Since the length of the first DCA axis was below 3 standard deviation units, we adopted a linear response model, as recommended by ter Braak and Prentice (1988) and ter Braak (1995). Rare species were down-weighted. The DCA-plot of species revealed that the yellow-necked mouse was distant from the other small rodent species. Since this would affect the gradient length and since this species occurred in low numbers, we decided to exclude it from the DCA. As the DCA gradient length was 2.8, we chose a linear response model (ter Braak and Prentice, 1988; ter Braak, 1995).

Then, in order to determine which fine-scale (*i.e.* vegetation characteristics) and large-scale environmental variables (*i.e.* habitat types) were most relevant for the species' assemblage, we performed a stepwise redundancy analysis, RDA (Rao, 1964). This constrained ordination method selects the linear combination of environmental variables giving the smallest total residual sum of squares, and uses it to explain the variation in species composition (ter Braak, 1995).

We explained the variation in small mammals' assemblage in two separate RDA analyses: one by using vegetation parameters (vegetation-RDA) and the other by using habitat types (habitat-RDA) as constraining variables. By dividing the constrained inertia

(the sum of all canonical eigen values) for the total inertia (a measure of the total amount of variance in a dataset) it is possible to find how much of the variance in species' assemblage is accounted for by the selected combination of environmental variables. We tested for both *marginal* and *conditional effects* (Legendre and Legendre, 1998) of each environmental variable on the species assemblage: the effect of each variable was first tested alone and, after, constrained by other variables that explained a greater proportion of variance. This stepwise procedure was performed using Monte Carlo permutation tests (ter Braak, 1992; 1000 permutations) with the *permutest.cca* routine in the Vegan package (R software). Only variables whose conditional effect was significant (α = 0.1) were used in the RDA.

Shrews were excluded from these analyses as they were a non-target species and, consequently, the trapping method adopted did not allow assessing their relationship with environmental variables. The analyses were performed using the R 2.4.0 for Windows (www.r-project.org); the RDA was performed using the package *Vegan* (Oksanen et al., 2005).

2.5. Diversity indices

Species diversity was estimated by the combination of the index of species richness and PIE Hurlbert's (1971) index of species evenness, calculated using the *Ecosim 7.69* software (Gotelli and Entsminger, 2006). Since the estimated richness is strongly dependent on the sample size (*i.e.* the number of specimens in the community), in order to compare samples of different sizes it is necessary to calculate their expected richness at standardized size. This can be done through rarefaction analyses (Olszewski, 2004). Hence, for each habitat type we performed 1000 iterative simulations by randomly sub-sampling a growing number of individuals and, in order to rank the diversity indices in different habitat types, we standardized the sample sizes according to the habitat type with the lowest number of individuals.

3. Results

During the course of the study, 1121 individual small mammals, belonging to 11 different species, were trapped (Table 2). The low number of water voles captured may be due to the relatively small size of the traps, not designed for capturing this species. The overall abundance of the three most common species, *i.e. M. glareolus, M. agrestis* and *A. sylvaticus*, increased during the course of summer (t = 3.086, df = 189, P = 0.002) but did not vary among years (t = −1.064, P = 0.289) or sub-areas (t = 0.028, P = 0.978).

3.1. Population estimates

The population size of the three most common species was best estimated using models based on different assumptions (Table 3). For bank voles and wood mice the most parsimonious model (M_b) assumed different capture and recapture probabilities. In particular, for both species capture probability (0.100 ± 0.019 and 0.101 ± 0.034, respectively) was much lower than recapture probability (0.343 ± 0.012; 0.223 ± 0.019). For field voles the best model (M_t) assumed that capture and recapture probabilities increased with time during the 10-day trapping period.

The estimated population size of each of the three species differed among the six habitat types (Fig. 1): bank voles were more abundant in abandoned meadows and less abundant in crops (χ_5^2 = 190.568, P < 0.001); field voles thrived in meadows and avoided mature forests (χ_5^2 = 274.675, P < 0.001); wood mice preferred crops and avoided clear-cuts (χ_5^2 = 126.661, P < 0.001). The cumulative population estimate for the three species calculated within the perimeter of the SQs differed among habitat

Table 2
Number of small mammals captured in 2280 night/traps during May–August 2003 and 2004 in south-eastern Norway, divided per species and habitat type; the last two columns summarize the total number of captures and recaptures.

Latin name	Common name	Mature forest	Young forest	Clear-cut	Crop	Meadow	Abandoned meadow[a]	TOT Capture	TOT Recapture
Myodes glareolus	Bank vole	51	69	46	4	36	112	318	692
Myodes rufocanus	Grey-sided vole	8	7	6	0	0	4	25	59
Microtus agrestis	Field vole	0	8	33	16	118	48	223	352
Apodemus sylvaticus	Wood mouse	7	9	3	50	12	15	96	143
Apodemus flavicollis	Yellow-necked mouse	0	0	1	6	0	1	8	18
Mus musculus	House mouse	0	0	0	2	0	0	2	1
Sorex araneus	Common shrew	22	92	95	5	73	150	437	[b]
Sorex minutus	Pygmy shrew	0	2	0	2	0	1	5	[b]
Neomys fodiens	Water shrew	0	1	1	0	0	0	2	[b]
Myopus shisticolor	Wood lemming	0	0	0	1	0	0	1	[b]
Arvicola terrestris	European water vole	0	0	1	0	3	0	4	0
TOT		88	188	186	86	242	251	1121	1266

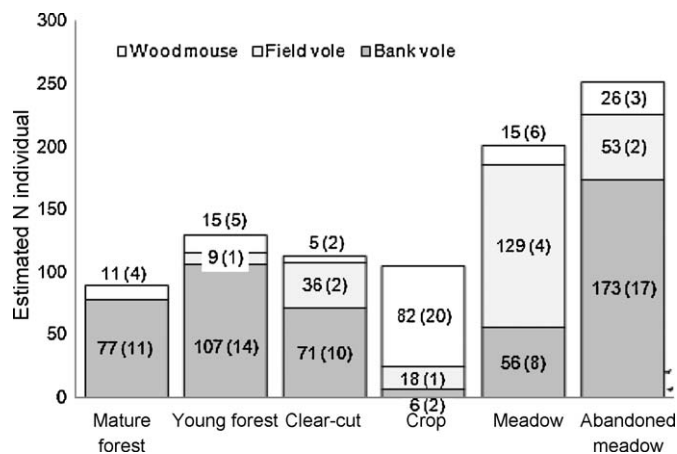[a] Corrected according to the lower number of small quadrates (n=25) compared to all other habitat types (n=33).
[b] Not marked at capture.

Table 3
Selection of the most parsimonious models describing the population size of the three most common small rodent species based on capture and recapture probabilities.

Species	Model selection Model	AICc	ΔAIC_c	ω_i	k
Myodes glareolus	M_b	3308.0	0.000	1.000	2
	M_t	3385.2	77.20	0.000	10
	$M_{t\ hab}$	3428.8	120.8	0.000	60
Microtus agrestis	M_t	2142.1	0.000	0.971	10
	M_b	2149.1	7.020	0.029	2
	$M_{b\ hab}$	2210.0	67.93	0.000	9
Apodemus sylvaticus	M_b	942.7628	0.000	0.997	2
	M_0	954.4380	11.675	0.003	1
	M_t	957.9305	15.168	0.001	10

The basic models were built on different assumptions: M_0, similar capture and recapture probabilities; M_t, same as M_0, but probabilities vary with time; M_b, capture and recapture probabilities differ; these models were repeated assuming different capture probabilities in each habitat type ($M_{0\ hab}$, $M_{t\ hab}$, $M_{b\ hab}$, $M_{h\ hab}$). Models are ranked by the AIC$_c$, and the most parsimonious model for each species is reported in the first raw; k = number of parameters, ω_i = Akaike's weights, i.e. normalized likelihood of the models.

types ($\chi^2_5 = 137.793$, $P < 0.001$), being highest in abandoned meadows and meadows, and lowest in mature forests.

3.2. Factors affecting species abundance

Nine variables describing vegetation cover were reduced to three PCs, which explained 64% of the variance in the dataset (Table 4). PC1 was strongly negatively correlated with the number and height of trees and with the proportion of moss and small berries. Therefore, PC1 can be interpreted as a proxy (with negative sign) for late successional stages; PC2 was positively correlated with the proportion of non-cultivated herbaceous vegetation and bushes, and can be interpreted as a proxy of ground cover complexity; PC3 was positively correlated with the proportion of woody debris and tall berries and, thus, was related to old, productive clearings colonized by raspberries.

According to the most parsimonious models (Table 5) the abundance of bank voles increased with the amount of old mossy forests rich in blueberries (−PC1, $P < 0.001$), by ground cover complexity (+PC2, $P < 0.001$), and by raspberry-rich clearings (+PC3, $P = 0.058$). The type of habitat at the edge was also included in the best model, and bank vole abundance was negatively

Table 4
Results of the principal component analysis, PCA, of the vegetation descriptors. An interpretation of the principal components (PCs) is provided, based on the highest variable loadings for each variable. Continuous variables have been scaled, and those describing the proportion of cover have been arcsine-square root transformed.

Interpretation of PCs	PC1 Late successional traits	PC2 Ground cover complexity	PC3 Berry-rich clearings
Loadings			
Tree height	−0.535		
N trees	−0.430	0.119	
Moss, % cover	−0.441	0.170	
Herb, % cover	0.143	0.609	−0.400
Crop	0.284	−0.597	−0.148
Bush, % cover		0.412	0.232
Small berry, % cover	−0.472	−0.112	
Tall berry, % cover		0.198	0.514
Woody debris, % cover			0.695
Importance of components			
Standard deviation	1.686	1.294	1.100
Proportion of variance	0.316	0.186	0.135
Cumulative proportion	0.316	0.502	0.636

Fig. 1. Population estimates (S.E. on the brackets) for the most frequently trapped small rodents (*Myodes glareolus*, *Microtus agrestis*, *Apodemus sylvaticus*) calculated by the capture–mark–recapture analysis, inside the small quadrates (SQ) located in each habitat type. The population estimates in the abandoned meadow were corrected according to the lower number of small quadrates in this habitat type (n = 25) compared to all other habitat types (n = 33).

Table 5
Set of generalized linear models explaining the index of abundance of the most common small mammals captured with vegetation descriptors, represented by the PCs (Table 4), and with other variables (AREA, DATE, RAIN, EDGE and DIST, see Table 1). Models were ranked according to the AIC$_c$, with the most parsimonious model on top of each list.

Species	Model	AIC$_c$	ΔAIC$_c$	ω_i	k
Myodes glareolus	PC1 + PC2 + PC3 + EDGE + DATE	598.32	0.00	0.45	10
	PC1 + PC2 + PC3 + EDGE + DATE + AREA	599.78	1.46	0.22	11
	PC1 + PC2 + PC3 + EDGE + DATE + RAIN	600.28	1.96	0.17	11
	PC1 + PC2 + EDGE + DATE	600.48	2.16	0.15	9
Microtus agrestis	PC1 + PC2 + PC 3 + EDGE + DATE + AREA	431.67	0.00	0.43	11
	PC1 + PC2 + PC3 + EDGE + DATE + AREA + RAIN	432.93	1.26	0.23	12
	PC1 + PC2 + PC3 + EDGE + DATE	433.22	1.55	0.19	10
	PC1 + PC2 + PC3 + EDGE + DATE + DIST + AREA	433.88	2.21	0.14	12
Apodemus sylvaticus	PC1 + PC2 + EDGE + DATE + AREA − RAIN	300.40	0.00	0.32	11
	PC1 + PC2 + EDGE + DIST + DATE + AREA + RAIN	300.51	0.11	0.30	12
	PC1 + EDGE + DIST + DATE + AREA + RAIN	300.80	0.40	0.26	11
	PC1 + PC2 + PC3 + EDGE + DIST + DATE + AREA + RAIN	302.40	2.00	0.12	12

affected by the proximity of mature forests ($P = 0.026$). In addition the abundance of bank voles increased as summer progressed ($P = 0.020$). The abundance of field voles also increased with time ($P = 0.003$), and was affected positively by the complexity of the ground cover (+PC2, $P < 0.001$), and negatively by late successional stages (+PC1, $P < 0.001$) and woody debris (−PC3, $P = 0.037$). In addition, the abundance increased in the northern sub-area ($P < 0.001$) and was higher when the neighboring habitats were meadows ($P = 0.026$), abandoned meadows ($P = 0.002$), crops ($P = 0.004$) or old forests ($P = 0.003$), but not clear-cuts ($P < 0.001$). The wood mouse, on the contrary, was more abundant in the southern sub-area ($P = 0.054$) and decreased as the season progressed ($P = 0.011$), as the species typically exhibit annual population cycles with lowest densities in summer (Tattersall et al., 2004). As expected, wood mice were also positively affected by the proximity of meadows ($P = 0.060$) and cultivated fields ($P = 0.078$), and were correlated positively to crops (−PC2,

$P = 0.032$) and negatively to older successional stages (+PC1, $P = 0.007$). During rainy weeks, the number of captures of wood mice was lower ($P = 0.029$).

3.3. Factors affecting community structure

The vegetation-RDA (Table 6a) showed that the selected vegetation variables accounted for 31.4% of the variation in the assemblage (Table 6a). The permutation test indicated that the vegetation parameters explained a significant amount of the variance in species' assemblage (*Pseudo-F* = 9.081, $P < 0.001$). Field voles showed affinity with the height and proportion of herbs, while wood mice showed affinity with the proportion and height of cultivated species. Bank voles strongly positively correlated with the amount of berries, while yellow-necked mice and grey-sided voles did not show specific affinity with any of the environmental variables (Fig. 2a).

Table 6
Summary of the stepwise redundancy analyses considering the five most common small rodent species (number of captures/small quadrate – SQ) trapped within 147 SQs.

(a) Vegetation-RDA	Total variance	Constrained variance			Percentage of explained variation	
	13.775	4.323			31.38%	
	Eigen values	RDA1	RDA2	RDA3		
		2.348	1.576	0.389		
		Biplot scores			Permutation test	
	Constraining variables	RDA1	RDA2	RDA3	Pseudo-F	P
	Herb height	−0.820	0.351	−0.176	21.609	<0.001
	Herb, % cover	−0.799	0.345	−0.061	2.428	<0.010
	Crop, % cover	0.114	−0.841	−0.052	16.047	<0.001
	N trees	0.540	0.362	−0.149	2.323	0.065
	Crop height	0.089	−0.687	0.230	5.084	0.006
	Tall berry, % cover	0.200	0.528	−0.431	6.517	0.003
	Bush height	0.259	0.259	0.006	2.451	0.061
(b) Habitat-RDA	Total variance	Constrained variance			Percentage of explained variation	
	13.775	3.936			28.57%	
	Eigen values	RDA1	RDA2	RDA3		
		2.414	1.362	0.159		
		Biplot scores			Permutation test	
	Constraining variables	RDA1	RDA2	RDA3	Pseudo-F	P
	Abandoned meadow	0.186	0.596	0.756	5.418	<0.001
	Meadow	−0.959	0.105	−0.063	28.070	<0.001
	Crop	0.072	−0.901	0.422	16.247	<0.001
	Clear-cut	0.026	−0.037	−0.511	2.209	0.086

The analyses were conducted separately by using 16 vegetation parameters (a) and 6 habitat types (b) as constraining variables. Only variables which were significant ($\alpha = 0.1$) after the conditional permutation test was considered. The variables used are described in Table 1. For each analysis we present the total variance, the constrained variance, the percentage of explained variation and the eigen values for the RDA axes.
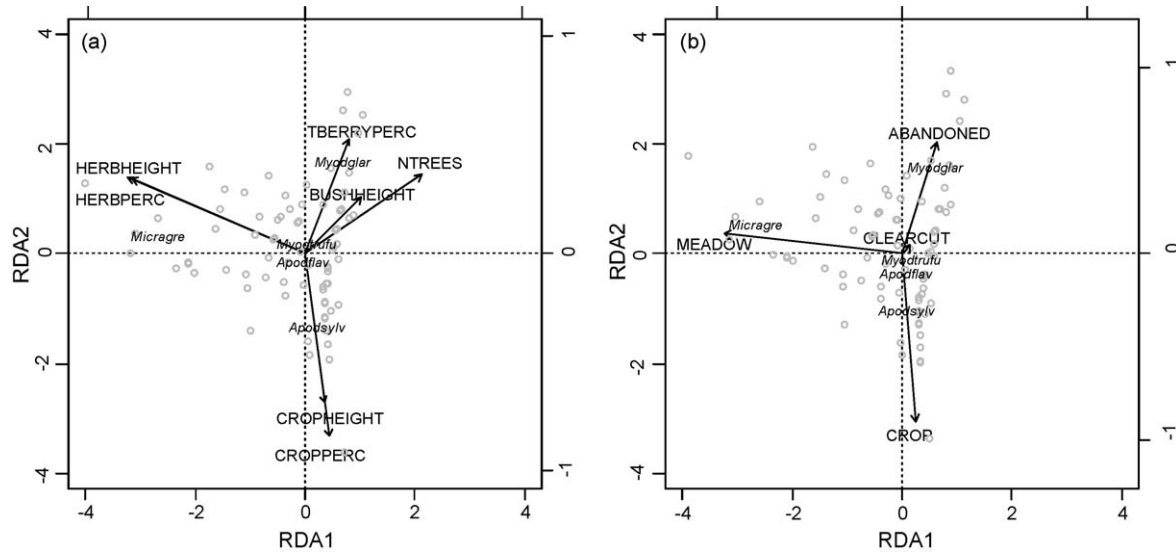
Fig. 2. Biplots of (a) vegetation-RDA and (b) habitat-RDA. Relationship between vegetation parameters (a) and habitat types (b), and the five most frequently trapped small rodents' species, as determined by stepwise redundancy analysis. The length and direction of each vector is proportional to the strength of the association between the environmental variables within each plot and the RDA axes. For abbreviations see Tables 1 and 2.

Permutation tests showed that forested habitats did not significantly contribute to explain the variance in species assemblage when taking into account more important habitat variables (mature forest: $P = 0.387$; young forest, $P = 0.677$). Thus, forest habitats had to be excluded from the habitat-RDA. The habitat-RDA (Table 6b) explained 28.6% of the variation in species' assemblage, and the selected variables explained a significant amount of the species' variation ($Pseudo$-$F = 14.201$, $P < 0.001$; Table 6b). Field voles showed affinity with meadows, while wood mice were strongly associated to crops. Bank voles correlated positively with abandoned meadows, while yellow-necked mice and grey-sided voles did not show affinity with any of the habitat types (Fig. 2b).

3.4. Species richness

A clear asymptote in species richness was reached only for mature forests and meadows (Fig. 3), indicating that further sampling in these habitat types would not have revealed higher
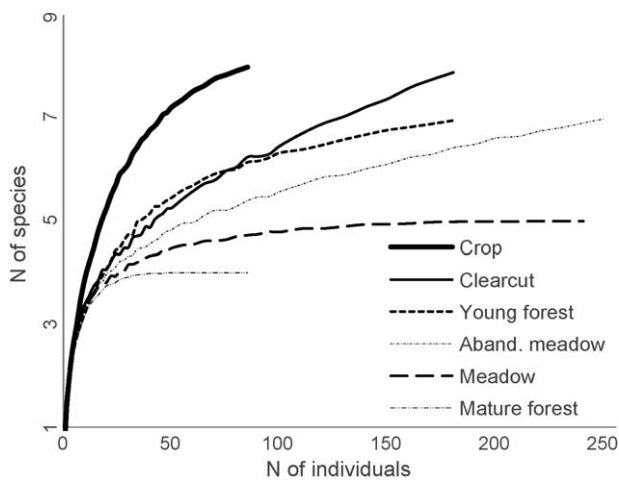
Fig. 3. Rarefaction curves illustrating how species richness increases with capture size within each habitat type. Each curve has been constructed by performing 1000-iteration simulation by randomly sub-sampling a growing number of individuals within each habitat type.

Table 7
Comparison between the index of species richness and the PIE Hurlbert's indices of evenness (Hurlbert, 1971) in different habitat types. The indices were calculated with the software EcoSim (Gotelli and Entsminger, 2006) by standardizing the sample size in each habitat type with respect to the habitat type containing the lowest number of individuals (*i.e.* crop, $n = 86$).

Habitat type	Richness			Evenness		
	Estimate	95% C.I.		Estimate	95% C.I.	
		Lower	Upper		Lower	Upper
Clear-cut	6.21	4.00	8.00	0.65	0.59	0.70
Young forest	6.13	5.00	7.00	0.62	0.57	0.67
Mature forest	4.00	4.00	4.00	0.59	0.58	0.61
Crop	7.99	7.00	8.00	0.62	0.61	0.63
Meadow	4.75	4.00	5.00	0.65	0.59	0.70
Abandoned meadow	5.41	4.00	7.00	0.66	0.61	0.70

species diversity than we observed. On the contrary, species richness may have increased with a higher sampling effort in the other habitat types. The figure shows that the highest species richness was recorded in crops and the lowest in mature forests. However, species richness did not significantly differ between crops and clear-cuts, while it was significantly lower in mature forests compared to young forests (Table 7). Species evenness reached the highest values in abandoned meadows, but the difference was significant only when compared to mature forests, which supported the lowest relative distribution of individuals among species.

4. Discussion

The landscape-scale sampling design adopted in our study allowed us to obtain a clear picture of the relative distribution of species composing the small mammal community with respect to all available non-urban habitat types in a wide area representative of the mosaic landscape of south-eastern Norway. Furthermore, the study of the relationship between small rodent distribution and fine-scale vegetation descriptors allowed us to control for the high environmental heterogeneity within each landscape-scale habitat category, and to improve our understanding of the overriding factors affecting species abundance and distribution.

As expected old abandoned meadows, which are characterized by the lowest intensity of human use and by the highest structural heterogeneity (*i.e.* presence of ground-, bush- and canopy-cover), supported the highest densities of species compared to all available habitat types. The result was consistent both when considering the minimum number of individuals alive belonging to all trapped species (Table 2) and the more accurate population estimates based on CMR for the three most common species (Fig. 1). The overall availability of this habitat was minimal, as meadows and abandoned meadows covered together less than 5% of the study area (Panzacchi et al., 2009). Nevertheless, all types of meadows supported by far the highest abundance of small mammals during the reproductive period and, thus, likely play a key-role for the overall small mammal community. Notwithstanding the close similarity between these two habitat types, small mammal communities were clearly dominated by bank voles in abandoned meadows and by field voles in meadows, potentially reflecting both inter-specific competition (Huitu et al., 2004), and the partial trophic niche separation between the two species – bank voles being a mixed granivorous–folivorous species (Hansson, 1999) while field voles prefer grass stems (Hansson, 1971). Wood mice which, typically, show marked preferences for agricultural lands (Tattersall et al., 2002), still attained high densities in meadows and abandoned meadows or benefited from their proximity. Indeed, the use of habitat edges allows for a simultaneous access to different resources and, thus, positively affected the more opportunistic species – *i.e.* the wood mice (see Hansson, 1994) – while negatively affecting the supposed forest specialist bank voles (see Zwolak, 2008).

Not only did abandoned meadows support the highest species evenness, but also the fact that the rarefaction curve (Fig. 3) attained high values without reaching an asymptote indicated a good potential in terms of species richness. Interestingly, abandoned meadows supported both a higher overall abundance and diversity of small mammals compared to their more intensively exploited twin habitat, *i.e.* meadows. A similar negative relationship between the abundance of small mammals and the degree of exploitation of grasslands has been recorded in studies focusing on the effect of grazing intensity (Evans et al., 2006; Schmidt et al., 2009). Semi-natural grasslands are well known for being one of the richest habitats in terms of plant species in northern Europe (Rosef and Bele, 2005). This vegetational complexity reaches its maximum in abandoned meadows, and allows for a pre-interactive niche diversification (*sensu* Carey and Harrington, 2001; *i.e.* availability of different ecological niches which creates the potential for the coexistence of different species) which accounts for the high observed diversity and abundance of small mammals.

None of the species studied reached highest densities in either clear-cuts or young forests, although the overall abundance of small mammals supported by these habitats was not negligible. In particular, in contrast with previous studies indicating that that clear-cutting has altered small mammal communities by favoring field voles (Ims, 1991), we did not detect high abundance of this species on clear-cuts. On the contrary, the so-called "mature forest specialist" bank vole reached higher densities on clear-cuts compared to field voles. Note, however, that the specific vegetation characteristics associated with each clear-cut were the key-factors determining the occurrence of different species. Generalized linear models showed that while field voles used grassy areas and avoided raspberry-rich clearings, bank voles were positively affected by the latter (Table 5). However, this analysis alone did not allow us to distinguish between a positive effect of woody debris and/or raspberry on bank voles. The redundancy analysis clarified this issue by showing that bank voles were strongly associated with raspberries, but neither woody debris (Fig. 2a) nor

clear-cuts (Fig. 2b) were among the most relevant variables affecting the species' distribution. We deduced that only old clear-cuts with a relatively high degree of structural complexity and productivity (*i.e.* colonized by raspberry bushes) were able to support abundant bank vole populations (see also Moses and Boutin, 2001; Pearce and Venier, 2005). Similar and even stronger conclusions can be drawn regarding young forests and mature forests. While, on the one side, these two habitats were not even selected among the most relevant variables explaining species assemblage in the RDA, on the other, the overall number of small mammals – in particular of bank voles – in these habitats was not negligible. The strong association between bank voles and parameters related to late successional traits such as high trees, moss and blueberries (*i.e.* negative association with PC1; see also Selås, 2006) and ground cover complexity (PC2) suggests that the relatively high abundance reached in few of the forests plots is more related to fine-scale ecological features rather than to forest age class *per se* (Tables 1 and 5, Fig. 2). Hence, while a few forest stands characterized by a complex ground cover dominated by berries, moss and woody debris had relatively high abundance of bank voles (Fig. 1), most forests were poor habitats unable to support high densities of small mammals.

Indeed, mature forests and cultivated fields sustained the lowest abundance of small mammals compared to all available habitats. However, while intensively managed forests at logging maturity also supported the lowest species diversity, further lowering the importance of this habitat for small mammal communities, cultivated fields sustained the highest species richness. It is widely accepted that the intensification and expansion of modern agriculture is among the greatest current threats to biodiversity worldwide (Pimentel et al., 1992; Hanski, 2005; Michel et al., 2006). However, agro-ecosystems that maintain a high degree of structural complexity – *e.g.* shelterbelts, interspersed woodlots and an overall high spatial heterogeneity – may provide an opportunity to conserve small mammal diversity in human-dominated areas (Paoletti et al., 1992; Bignal and McCracken, 1996). This seems to be the case for agro-ecosystems in south-eastern Norway, which are embedded in a matrix of forested areas and semi-natural grasslands and still have the potential to attract generalist species. However, these artificial ecosystems are unable to sustain entire small mammal communities year round (Todd et al., 2000; Tattersall et al., 2004). Only one species – the wood mouse – reached high summer densities in this habitat type (see also Hansson, 2002; Tattersall et al., 2002, 2004), but its marked association with field margins reflected a clear need for ecological complexity at the landscape scale (see also Hansson, 1994; Bayne and Hobson, 1998). It is difficult to establish whether the sporadic presence of species other than wood mice in cultivated fields could be interpreted as a spill-over effect from meadows and abandoned meadows, which sometimes – but not necessarily – were close to agricultural areas.

Our study shows that sampling in all available habitat types is essential for a comprehensive understanding of small rodent community dynamics in forest–farmland ecosystems. Even habitat types that are under-represented at the landscape scale might play a significant role for the community dynamics of a given study area. Further investigations are required to understand the consequences of these high-density spots for population dynamics, and in particular possible implications for source-sink dynamics (Pulliam, 1988). Our results highlight the importance of little exploited agricultural areas (*i.e.* meadows and abandoned meadows) rather than clear-cutting, for small rodent communities, and do not support the hypothesis that forestry is changing community structure by leading to an increase in the abundance of field voles. On the contrary, the community of small rodents was largely dominated by bank voles, which were trapped in all types of

habitat – even though they showed a clear preference for structurally complex vegetation cover. According to the widespread idea that habitat fragmentation is a major cause of the long-term decline of *C. rufocanus* (Christensen et al., 2008), few individuals were trapped in this highly fragmented mosaic landscape. It would be interesting to compare these results with similar studies conducted in northern areas characterized by multi-annual cycles in vole abundance and by a lower availability of agricultural areas and grasslands. Lastly, our results highlight the importance of fine-scale vegetational characteristics in determining the impact of land-use practices on small rodent communities (see also Carey et al., 1999; Carey and Harrington, 2001; Bowman et al., 2001; Ecke et al., 2002; Pearce and Venier, 2005). Optimal species' requirements in terms of cover, food and inter-specific relationships are not necessarily associated to coarse-scale habitat types defined according to an anthropocentric point of view, but largely depend on the ecological complexity produced by each specific land-management practice.

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