

Introduced Lagomorphs as a Threat to “Native” Lagomorphs: The Case of the Eastern Cottontail (*Sylvilagus floridanus*) in Northern Italy

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Introduction

Eastern cottontails were introduced in Pinerolo (southwest of Torino), Italy, near the Pellice River, in 1966 (Spagnesi 2002). By the 1980s, the population expanded into the region of Piemonte with localized groups in the province of Alessandria (Prigioni et al. 1992), reaching 25–27 cottontails/km² in the late 1990s, and the percentage of cottontails in the total of all mammals killed on roads rose from 2.2% in 1995 to 6.0% in 1997 (Silvano et al. 2000). At the end of the 1990s, the species was present in the western part of Lombardia and in some localities in the south side of the Po River (Fig. 1). Presently, Eastern cottontails are also present in the regions of Veneto, Emilia Romagna, Marche, and Toscana in response to population growth and additional releases to increase the potential for small game harvesting. Meriggi (2001) observed that in release sites, cottontails preferred the successional and weedy vegetation with dense brushy cover along rivers where they can find cover from predators. He also speculated that cottontails might compete with native Lagomorphs (European hare, *Lepus europaeus*, and European rabbit, *Oryctolagus cuniculus*), especially in poor habitats, limiting their population size to a low level. A prerequisite of competition would be that Eastern cottontails have similar habitat requirements as other native Lagomorphs. In this chapter, we analysed the potential competition between Eastern cottontails, European hares and European rabbits by investigating the habitat requirements of Eastern cottontails in two areas of northern Italy.

Materials and Methods

Study Areas

We studied cottontails in two areas (A: 45°05 N, 8°42 E and B: 45°15 N, 8°56 E) located between the Ticino and Po Rivers. The climate was similar in both areas; annual rainfall averaged 800 mm and was concentrated in spring and

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P.C. Alves, N. Ferrand, and K. Hackländer (Eds.)
Lagomorph Biology: Evolution, Ecology, and Conservation: 153–165
© Springer-Verlag Berlin Heidelberg 2008

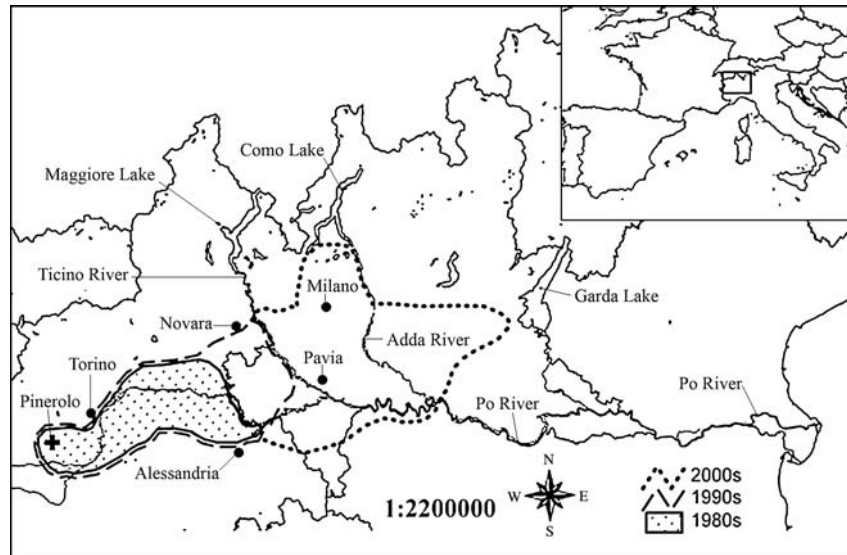


Fig. 1 Eastern cottontail expansion in northern Italy

autumn. The yearly temperature averaged 12°C (January 1.0° and July 22.5°C). The two study areas were characterized by similar plant communities and different cottontail densities as estimated by line-transect censuses (study area A: 65.6 cottontails/ km^2 , $\text{SD} = 5.64$, mean transect length of 15.9 km, $n = 30$; study area B: 35.6 cottontails/ km^2 , $\text{SD} = 5.84$, mean transect length of 21.2 km, $n = 20$) carried out during the first 2 h after sunrise and before sunset, in late spring–early summer, when we observed the greatest probability of detecting cottontails (for details on the method see Buckland et al. 2001). In both study areas, European rabbits were absent and hares were occasionally observed (study area A: 0.1 hares per km of transect; study area B: 0.03 hares per km). Study area A (325 ha) included croplands (71.4%), especially rice (50.4%), maize (9.1%), winter cereals (6.4%) and legumes (5.5%). Natural vegetation was present in small mesophyll broad-leaved woods (8.7%), along hedgerows, field edges, ditches, and dirt roads (row habitats, 14.7%), and in fallow fields (0.7%). Farmsteads were 4.5% of the area. In study area B (416 ha), croplands dominated with rice (21.7%), maize (17.9%), and winter cereals (5.8%) the most common. A small area was used for poplar plantations (3.5%) and hay fields (1.0%). Woodlots were 25.6% of the area, row habitats 17.1% , and fallow fields 5.7% . Farmsteads only covered 1.8% of the area.

In woods of both areas, common overstory species included oaks (*Quercus robur pedunculata*), white poplars (*Populus alba*), black poplars (*Populus nigra*), alders (*Alnus glutinosa*), willows (*Salix* spp.), hornbeams (*Carpinus betulus*), elms (*Ulmus campestris*), cherries (*Prunus avium*), and locusts (*Robinia pseudoacacia*). The understory plants included hazels (*Corylus avellana*), hawthorns (*Crataegus* spp.), brambles (*Rubus* spp.), elders (*Sambucus* spp.), and cornels (*Cornus mas*).

Methods

We mapped vegetative cover types in both study areas by direct surveys and then digitalized these with ArcView 3.2. We examined habitat use by cottontails from May 2002 to November 2003 using three different methods.

First, use was assessed by defining the distribution of cottontails in each study area. We selected 100 plots with a radius of 1 m that were randomly distributed. Within the plots, we determined the presence/absence of cottontails based on fecal pellets. Cottontail pellets were distinguished from European hare ones by their smaller size and from leveret ones by their different shape. Anyway, the hare density was so low in our study areas that the probability to find hare pellets in a given plot could be considered negligible. Plots were surveyed once a season. The range of cottontails was delineated by kernel analysis at 99 and 50% of occupied plots using program Ranges 6 V.1 (Kenward et al. 2003). We then compared the abundance of individual cover types in the range to their availability in the study area using Jacobs index of preference (Jacobs 1974):

$$PI_i = [(X_1/Y_1) - (X_2/Y_2)] / [(X_1/Y_1) + (X_2/Y_2)]$$

where X_1 is the surface of the i^{th} habitat type included in the range, Y_1 is the whole surface of the range, X_2 is the surface of the i^{th} habitat type included in the study area, and Y_2 is the whole surface of the study area. The index ranges from -1 to $+1$, taking positive values if the usage of the i^{th} cover type is greater than its availability and negative values if the usage is less than availability. To test the reliability of the Jacobs indices, we re-sampled the random points 1,000 times in each study area by the bootstrap method (Dixon 1993) and redefined the ranges by the kernel analysis at 99 and 50%. We then calculated the Jacobs index of preference for each bootstrap sample and for each habitat. Finally, we checked for the normality of indices distribution and tested for significant deviations of the index values from 0 (neutral selection) by the one-sample Student's t -test (Hesterberg et al. 2005).

Our second method included direct observations of cottontails within 100-m buffers along trails that we traveled weekly by car and designed to span both study areas. The observed frequencies and proportions of cottontails in each habitat type (observed usage proportions) were then calculated and compared with those expected (expected usage proportions) by means of χ^2 goodness-of-fit test and Bonferroni simultaneous confidence intervals analysis (Manly et al. 1993). We tested the null hypothesis that cottontails used cover types in accordance to their availability.

For our third approach, we compared the micro- and macro-habitat characteristics of the random plots with and without cottontail pellets using discriminant function analysis. We measured 11 micro-habitat variables within the 1-m radius plots and ten macro-habitat variables (percentage of habitat types) within a 100-m radius buffer from the plot centre (Appendix 1). Discriminant function analyses (DFA) were performed to differentiate plots with and without fecal pellets. Only those variables that differed between occupied and unoccupied sites

(based on one-way ANOVA, $P < 0.10$) were entered in the DFA, as suggested by Green (1974) and Noon (1981). All cover-type analyses were conducted with ArcView 3.2. Statistical analyses were performed by SPSS/PC + Version 11.0.

Results

Fifty random plots out of 100 in study area A and 27 in study area B were occupied by cottontails. Considering the range delimited by the kernel analysis at 99%, woods and fallow fields were selected in both study areas, whereas legumes, farmsteads and row habitats were selected only in study area A, and maize fields and poplar plantations only in study area B (Fig. 2a, b). Considering

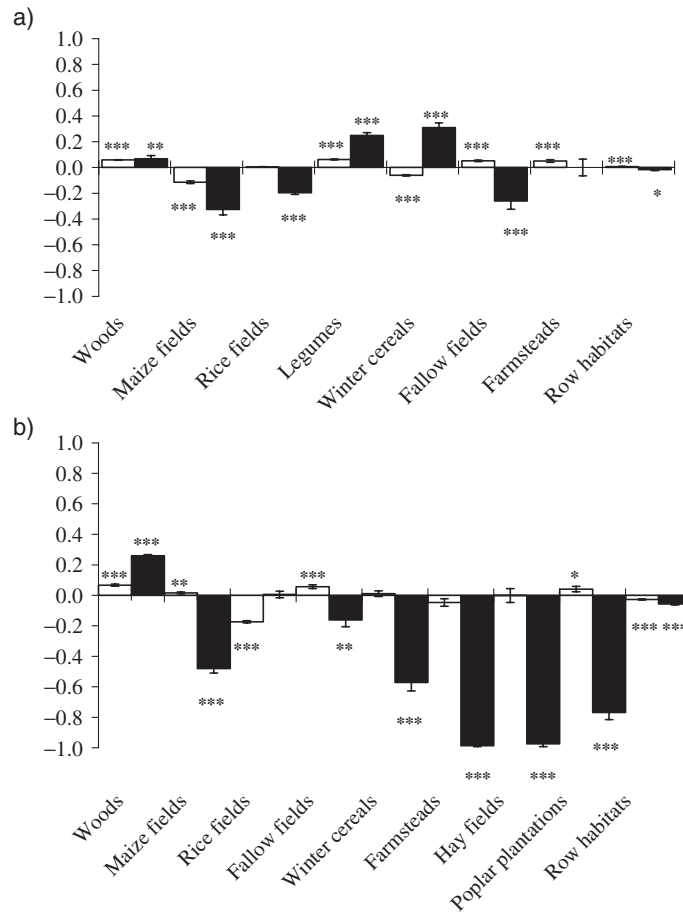


Fig. 2 Average values (SE) of Jacobs Index of preference for the use of habitat types in cottontail range defined by Kernel Analysis at 99% (*white columns*) and 50% (*black columns*) in study area A (a) and B (b) (***) $P < 0.0001$, ** $P < 0.01$, * $P < 0.05$; pooled seasons)

the “core area” (distribution delineated by the kernel analysis at 50%) in study area A, woods, legumes and winter cereals were selected, whereas maize, rice, and fallow fields were avoided, and farmsteads were used as their availability (Fig. 2a). Only woods were selected in study area B, whereas the other habitat types were avoided, with the exception of rice fields that were used as their availability (Fig. 2b).

From χ^2 and Bonferroni confidence interval analyses, significant differences between the observed and expected use of habitat types were found. Fallow fields, farmsteads, and row habitats were selected in area A but only row habitats were selected in area B. Crops were generally avoided in both study areas (Table 1).

Significant differences between average values of habitat variables in plots with and without cottontails occurred in both study areas. In study area A, the percentages of woods and row habitats and the litter thickness were greater in plots with cottontails than in those without, whereas the distance from the nearest wood edge and the percentage of rice fields were greater in plots without cottontails (Table 2). In study area B, a similar pattern of the percentages of woods, row habitats, litter thickness, and of the distance from the nearest wood edge resulted; moreover the cover percentage of dead leaves was greater in plots with cottontails (Table 2).

The function derived by DFA significantly discriminated plots with pellets from those without in both study areas. In study area A, the percentage of row

Table 1 Results of Bonferroni simultaneous confidence interval analyses for the use of habitat types by cottontails (*EUP* expected usage proportion; *OUP* observed usage proportion; pooled seasons)

Habitat types	Study area A		Study area B	
	EUP	OUP	EUP	OUP
Woods	0.09	0.10	0.26	0.05**
Maize fields	0.09	0.01**	0.18	0.02**
Rice fields	0.50	0.04**	0.22	0.02**
Fallow fields	0.01	0.04**	0.05	0.05
Winter cereals	0.06	0.03**	0.06	0.02**
Legumes	0.06	0.01**	-	-
Hay fields	-	-	0.02	0.00**
Poplar plantations	-	-	0.03	0.00**
Farmsteads	0.04	0.09**	0.02	0.00
Row habitats	0.15	0.68**	0.17	0.84**
Chi-square	1467.11		564.95	
P	<0.0001		<0.0001	

** Significant differences at $P < 0.01$ (selected habitats in bold)

Table 2 Average values (SE) of habitat variables with significant differences ($P < 0.1$) between random plots with cottontail pellets (presence) and without (absence) for both study areas (one-way ANOVA; pooled season)

Habitat variables	Presence	Absence	F	P
<i>Study area A</i>	<i>N = 92</i>	<i>N = 308</i>		
Woods	9.6 (1.95)	5.8 (0.73)	4.85	0.028
Rice fields	11.7 (2.37)	29.4 (2.26)	16.73	<0.0001
Legumes	6.4 (1.88)	2.9 (0.65)	5.01	0.026
Winter cereals	9.7 (2.55)	5.4 (1.17)	2.87	0.091
Farmsteads	10.0 (2.70)	4.9 (0.99)	4.91	0.027
Maize stubbles	9.0 (2.22)	19.1 (1.89)	7.50	0.006
Rice stubbles	9.4 (2.47)	3.3 (0.78)	9.43	0.002
Row habitats	13.2 (0.66)	9.9 (0.36)	19.25	<0.0001
Herbaceous cover	11.4 (1.57)	7.5 (0.86)	4.89	0.028
Bushy cover	0.7 (0.24)	0.3 (0.07)	3.43	0.065
Litter thickness	0.42 (0.03)	0.28 (0.02)	14.75	<0.0001
Brightness	0.92 (0.02)	0.93 (0.00)	3.50	0.062
Distance from nearest wood edge	9.88 (1.88)	21.79 (1.61)	14.59	<0.0001
<i>Study area B</i>	<i>N = 46</i>	<i>N = 354</i>		
Woods	47.5 (4.69)	26.8 (1.72)	16.75	<0.0001
Rice fields	5.4 (1.73)	13.0 (1.39)	3.71	0.055
Row habitats	17.9 (1.59)	14.1 (0.60)	4.61	0.032
Herbaceous cover	20.7 (3.28)	14.9 (1.09)	3.19	0.075
Dead leave cover	4.6 (0.90)	2.4 (0.30)	6.00	0.015
Litter thickness	0.40 (0.04)	0.28 (0.02)	5.59	0.019
Distance from nearest wood edge	2.13 (0.78)	10.6 (0.96)	8.73	0.003

habitats and rice fields, the litter thickness, and the distance from the nearest wood edge were the most important variables in the discrimination, as the standardized coefficients and correlation coefficients showed (Table 3). DFA correctly classified 71.3% of original cases: 77.2% of cases with pellets and 69.5% of cases without. In study area B, the percentage of woods and row habitats, the litter thickness, and the distance from the nearest wood edge were the variables with the greatest contribution in the discrimination (Table 3). DFA correctly classified 66.0% of original cases: 71.7% of cases with pellets and 65.3% of those without.

Table 3 Results of the discriminant function analyses between random plots with and without pellets of cottontails (pooled seasons)

Habitat variables	Standardized discriminant function coefficients		Correlation coefficients	
	Area A	Area B	Area A	Area B
Woods	0.099	0.675	0.219	0.647
Rice fields	-0.221	-0.092	-0.407	-0.304
Legumes	0.412	-	0.223	-
Winter cereals	0.149	-	0.169	-
Farmsteads	0.234	-	0.221	-
Maize stubbles	0.210	-	0.306	-
Rice stubbles	-0.405	-0.173	-0.273	-0.318
Row habitats	0.353	0.485	0.437	0.339
Herbaceous cover	0.119	0.120	0.220	0.282
Bushy cover	0.065	-	0.184	-
Dead leave cover	-	0.077	-	0.387
Litter thickness	0.565	0.393	0.462	0.554
Brightness	-0.211	-	-0.179	-
Distance from nearest wood edge	-0.143	-0.075	-0.380	-0.467
Eigenvalue	0.253		0.101	
Canonical correlation	0.450		0.302	
Chi-square	88.43		37.78	
df	13		8	
P	<0.0001		<0.0001	

Discussion

Eastern cottontails were successfully introduced in both North America and Europe as a consequence of the population decline of autochthonous Lagomorphs in order to enhance game populations (Chapuis et al. 1985; Probert and Litvaitis 1996; Spagnesi 2002). The introduction success is generally linked to the dispersal ability of the species and to its attitude to colonize small patches of natural vegetation sparse in agricultural-dominated landscape (Probert and Litvaitis 1996). In Italy, the expansion of the main cottontail range occurred chiefly along the river network of the Po Plain by following the west-east direction with north-south ramifications, thus demonstrating the close relationship between cottontail presence and natural vegetation belts (Meriggi 2001).

Our analyses showed that cottontails selected woods and row habitats, including field margins and hedgerows with herbaceous, bushy and canopy cover along fields and streams in both study areas. Bruna (1952) observed that removal of bushy cover along fencerows eliminated travel lanes for cottontails and Vance (1976) indicated that reductions of fencerows caused declines among cottontail populations. Hedgerows and channel banks at the two study areas connected wooded sites and uncultivated areas. Additionally, in agricultural landscapes, row habitats could be used by cottontails for feeding in winter when the herbaceous habitats decreased (Silvano et al. 2000).

Thick layers of dead leaves and other plant litter and nearness to wood edges characterized habitats occupied by cottontails. This suggests that cottontails select habitats with dense permanent cover where there are fewer impacts from agriculture and where they can quickly find protection from predators (Linder and Hendrickson 1956). The tree canopy protects the cottontails from raptors and the dense understory makes it more difficult for many terrestrial predators to find and reach them. Friley (1955) noted that cottontails used forms located at bases of trees and shrubs. During winter, this behavior may decrease their exposure to prevailing winds, thereby facilitating homeothermy and minimizing energy expenditures (Gordon et al. 1968). Woodlots were related to the presence of cottontails in both study areas and the plots with cottontail pellets were significantly nearer to the woodlots than those without, underlining the importance of small woods for the species habitat suitability.

Habitat selection may depend partially on population density. At low density, all individuals should select the most suitable habitats, whereas at higher densities some individuals should use less suitable or suboptimal areas, culminating in use of marginally suitable areas at very high densities because of intraspecific competition (Fretwell and Lucas 1972). This pattern of habitat selection is found if the species uses one or a few habitat types or if the most suitable habitat is not available (Meriggi et al. 1992). Indeed, in study area A, where the population density was greater and natural woods were fewer than in study area B, cottontails included in the range also legumes and winter cereals in proportions greater than availability (Jacobs index) and selected (Bonferroni analysis) inhabited areas and fallow fields that may be suitable for feeding during the spring and summer because of the height of the herbaceous vegetation. Inhabited areas were made up of one big farmstead with lawns, scattered brushy cover, and ruins covered by brambles so that they may provide cover, and food and resting sites in the daytime. Among croplands, cottontails selected maize, legumes, and winter cereals, and avoided rice cultivations. Gottfried (1979) noted that wooded habitat types were conceivably isolated only in winter because cottontails probably could disperse through croplands during the growing season. We noted that crops were also used for feeding, except for rice cultivations where there was less herbaceous cover, and this is probably due to the usage of herbicides.

Eastern cottontails in Italy show the same habitat-use patterns as the species does in agriculture-dominated landscapes within its native range

(Swihart and Yahner 1984). Indeed, increasingly intensive agriculture is linked to declining cottontail populations (Edwards et al. 1981). Small patches of mixed cultivations and fragments of natural vegetation, as woods with understory and uncultivated areas connected by hedgerows with herbaceous and bushy vegetation characterize suitable habitats.

Our data also suggest that competition with native lagomorphs should be considered. European hare populations in Europe reach the highest densities in arable farmland. However, where agriculture is very intensive, hare numbers are reduced (Smith et al. 2005). Habitat diversity is positively associated with hare abundance and natural vegetation (fallow land, hedgerows, and small woods) can enhance landscape diversity, providing hares with food and cover throughout the year (Smith et al. 2005). Populations of European rabbit in Europe seem to be negatively affected by the changes in agricultural practices, in particular loss of scrubland. European rabbit density is positively associated to the ecotone that provides both food and refuge (Lombardi et al. 2003; Calvete et al. 2004; Carvalho and Gomes 2004). Competition among Lagomorph species can occur by direct interaction (interference competition), by simultaneous exploitation of limited resources (exploitation competition), as food and shelter (Pianka 1981; Probert and Litvaitis 1996), or by the ability to disperse and occupy suitable habitats. In the case of Eastern cottontails and autochthonous Lagomorphs species (*L. europaeus* and *O. cuniculus*), body size should be an important factor in winning direct aggressive interactions (Glazier and Eckert 2002). Thus there should be a dominance rank from hares, to European rabbits, to Eastern cottontails that can regulate the access to feeding patches. In fact the average weights recorded in northern Italy are 3893 g ($n = 66$, SE = 50.57; range 2,900–4,800) for hares (Meriggi et al. 2001), 1,548 g ($n = 49$, SE = 23.99; range 1,260–2,000) for rabbits (Prigioni, unpubl. data), and 839 g ($n = 20$, SE = 46.02, range 530–1,010) for Eastern cottontails (Vidus Rosin, unpubl. data). In the cottontail range in northern Italy, resources such as food and shelter are limited only during winter and, in particular, in some areas mainly cultivated with rice where hares can be forced to feed and use the field edges and the weedy vegetation along the channel banks, that are intensively used also by the Eastern cottontails. On the other hand European rabbits seem to be linked to the relict scrublands and natural broad-leaved woods. In these habitats, competition can effectively occur even if in the irrigated plain the habitat losses and the reduction of landscape diversity seem the main factors affecting hare and rabbit populations (Meriggi and Alieri 1989; Meriggi and Verri 1990). Populations of European hares and European rabbits are dramatically limited in Italy by habitat, diseases, and most important, by overhunting (mainly in the case of hares). On the contrary, hunting does not seem to be a limiting factor for cottontails that show a great dispersal ability expanding their range very fast. This attitude of Eastern cottontails is supported by the higher reproductive performance in comparison with the autochthonous Lagomorphs, in particular with hares (litter size: cottontails 5, min. 1, max. 12

- Chapman et al. 1977; Meriggi 2001; hares 2.4, min. 1, max 5 - Hansen 1992; Meriggi et al. 2001; Smith et al. 2005). In this situation, scramble competition can favor cottontails.

We need further research results in order to increase the knowledge about the competition between cottontails and autochthonous Lagomorphs; in particular, resource selection and exploitation (habitat and food) should be compared between allopatric and sympatric areas. In this way, niche shifts observed in sympatry should reflect the response to interspecific competition (Pianka 1981).

Moreover, important interactions among the three species may be through disease transmission. The results of seroepidemiological investigations, conducted in North Italy, indicate that cottontails may have a relevant role in the transmission of two of the three main diseases, myxomatosis, EBHS, and RHD, to native Lagomorphs (Lavazza et al. 2001). The high antibody prevalence found for myxomatosis confirms that cottontail is not susceptible to this disease but probably acts as a wild reservoir and plays an active role in the epidemiology of myxomatosis in rabbits, but not in hare, which is not susceptible to myxomatosis (Lavazza et al. 2001). Moreover, the results about EBHS indicated that some of the sampled cottontails could have been naturally infected by the EBHS virus developing a strong immunity, thus playing an active role in the transmission of EBHS to hares. On the contrary, from experimental infections, it seemed that cottontails are not susceptible to RHDV (Lavazza et al. 2001).

Acknowledgements: We thank C. Prigioni for the weights of European rabbits recorded in northern Italy. Paulo C. Alves, K. Hackländer, D. Williams, and an anonymous referee provided useful comments to the earlier drafts of the manuscript and kindly revised the English.

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Appendix

Appendix 1 Habitat variables measured within the 1-m radius plots and within the 100-m radius buffers

Habitat variables measured within the 1-m radius plots

Herbaceous cover (%)
Height of herbaceous cover (cm)
Bushy cover (%)
Height of bushy cover (m)
Canopy cover (%)
Height of canopy cover (m)
Dead leaves cover (%)
Litter cover (%)
Litter thickness (mm)
Brightness (ratio of the Lux measured on the point over the Lux measured in open space)
Distance from nearest wood edge (m)

Habitat variables measured within the 100-m radius buffers (%)

Woods
Maize fields
Rice fields
Fallow fields
Winter cereals
Legumes
Hay fields
Poplar plantations
Farmsteads
Row habitats
