UNIVERSIDADE TÉCNICA DE LISBOA

INSTITUTO SUPERIOR DE AGRONOMIA

PHYTOSOCIOLOGY APPLIED TO WILDLIFE MANAGEMENT - A STUDY ON THE POTENTIALITY FOR THE REINTRODUCTION OF CERVIDS IN THE MONTEMURO-FREITA-ARADA MOUNTAIN RANGE

TESE APRESENTADA PARA OBTENÇÃO DO GRAU DE DOUTOR EM ENGENHARIA FLORESTAL E DOS RECURSOS NATURAIS

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ANNALISA BELLU

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Abstract

The aim of the present thesis was to assess the use of phytosociology in wildlife management. In Section II, as a case study, I investigated red deer (*Cervus elaphus hispanicus*) and roe deer (*Capreolus capreolus*) free ranging populations occurring in the Natural Park of Montesinho, northeast Portugal, using faecal-pellet counts to assess deer use of semi-natural meadows (lameiros) and forest communities. Phytosociological classification contributed to explain red deer spring selective use of meadows at finer scales and performed better than other clustering criteria for classifying vegetation patches. At the landscape level, composition of the neighbouring vegetation mosaic, topography, and meadow's characteristics, as management status and dominant phytosociology, produced the best models for deer seasonal use of meadows. The forest use analysis revealed red and roe deer preference for oak forests over pine plantations, and habitat use overlapping between red and roe deer all year round. In Section III, I extrapolated the information gathered in Section II on deer use to build, for the Montemuro-Freita-Arada massif, a predictive map for roe deer use of meadows, showing a generally low use, with exception of isolated meadows closer to oak forest patches.

Key words: *Cervus elaphus hispanicus*, *Capreolus capreolus*, Montesinho Natural Park, habitat selection, scale, phytosociology, meadows, forests, Montemuro-Freita-Arada mountain range, habitat use modelling

Resumo

Com a presente tese pretendi avaliar a utilidade da fitossociologia em gestão de fauna. Na Secção II investiguei as populações bravias de veado (*Cervus elaphus hispanicus*) e de corço (*Capreolus capreolus*) do Parque Natural de Montesinho (nordeste de Portugal), usando contagens de dejectos para avaliar os padrões de uso de lameiros e de florestas. A fitossociologia, com um desempenho superior relativamente a outros critérios de classificação das manchas de vegetação, contribuiu para explicar à escala fina o uso primaveril de lameiros pelo veado. À escala da paisagem, a composição do mosaico de vegetação envolvente, a morfologia do terreno e as características dos lameiros (*e.g.* tipo de uso humano, associação vegetal dominante) produziram os melhores modelos de uso sazonal dos lameiros. A análise do uso das comunidades florestais revelou a preferência das duas espécies por florestas autóctones de *Quercus* spp., em detrimento dos pinhais, e a sobreposição de uso entre veado e corço ao longo do ano. Na Secção III extrapolei a informação obtida na Secção II, relativamente ao uso dos lameiros pelo corço, para construir um mapa preditivo de uso para o maciço Montemuro-Freita-Arada, que apontou um uso geralmente baixo, à exceção de lameiros isolados e próximos de carvalhais.

Palavras-chave: *Cervus elaphus hispanicus*, *Capreolus capreolus*, Parque Natural de Montesinho, seleção de *habitat*, escala, fitossociologia, lameiros, florestas, Montemuro-Freita-Arada, modelação de uso do *habitat*

To my family

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I. General introduction

1. Habitat-wildlife relationships

Wildlife management is an integrated science that applies scientific and technological knowledge to preserve, improve and create wildlife habitat, but also to limit animal population in specific cases. It also includes the creation and implementation of wildlife and wildlife habitat related laws. Its official institution as a “science” dates back to the 1930s in the United States with the work of Aldo Leopold, a forest ecologist who considered that wildlife management was necessary to restore and maintain diversity in the environment, jeopardized by human activities. A wide range of interests is encompassed by wildlife management, including practices to improve and create wildlife habitat, not only for game, but also endangered animal species; management of protected areas, or mitigation of wildlife impacts on human activities, such as protecting forest plantations and regeneration from high density population ungulates (Cote et al. 2004).

Whatever the goal, the success of wildlife management depends on the understanding of the relationship between target animal species and their habitat.

The interest in wildlife-habitat relationships can be traced to the beginning of natural history, with Aristotle (Morrison, Marcot, & Mannan 2006). It was, however, in the 17th and 18th century that Nature investigation re-gained a strong importance: during these century naturalists were above all focused on taxonomy, the classification of living organisms (e.g. Linnaeus, 1707-1778). The 19th century saw an increasing interest on Nature functioning, namely with Charles Darwin (1809-1882) and the publication of his work on the evolution of species (Darwin 1859), which aroused great scientific debates and can be considered as the beginning of modern Ecology (Morrison et al. 2006). Research on animal-environment relationship multiplied from the end of the 19th and the beginning on the 20th century, with important works on the distribution of animals (e.g.: Grinnel 1917, 1922; Lack 1933; Simpson 1940). These works led to the development of ecological concepts on which scientific literature focused along the last century and on which the debate is still open.

Before starting to further develop the habitat-wildlife relationships issue, it is essential to begin with the definition of these ecological concepts, that are at the basis of any wildlife distribution research (Acevedo & Cassinello 2009): the concepts of habitat and niche, and the concepts of habitat use and habitat selection. The different interpretations given to the former two concepts, since they first appeared on the scene, have often generated misunderstanding and confusion, hence the definitions that will be used throughout the thesis will be given hereafter.

Habitat has been defined as the physical space made up of the range of environments where the species occurs (Odum 1983). As Hall et al. (1997) affirm, in many cases habitat is confused with vegetation association or community, and a simple explanation or justification exists, especially for animal related researches: first of all, vegetation provides many of the fundamental resources for the individual persistence (Morrison et al. 2006), like food and shelter for instance. A second but no less important justification is that, speaking of a vegetation community we can refer not only to the plant species assemblage but also to the environmental characteristics or variables supporting such assemblage. The abstract formulation of habitat is that of a hyper-volume, in which each dimension corresponds to species-specific range of an environmental variable with an extensive spatial component, like for example, slope, aspect, soil moisture or elevation, including the related gradients occurring within the species range (Whittaker, Levin, & Root 1973).

Niche relates to the intra-community role, or the functional position of a species. The concept was first coined by Grinnell (1917), who analysed the relationships of the Californian thrasher with features of the environment the species lived in. Elton’s concept of niche (1927) considered the role of the species within the community, specifically its trophic position. Hutchinson (1957) promoted a mathematical approach, introducing the hyper-volume niche concept, and distinguishing between fundamental (the complete range of abiotic and biotic resources necessary for the species survival and reproduction) and realized niche (the predictably smaller niche that a species actually occupies when intraspecific relationships are accounted for). Whittaker (1973) differentiated between habitat (see above) and niche, considering the niche as an n-dimensional hyper-volume, with each dimension representing a specific range of local (as opposed to spatially extensive) environmental variables (e.g.: shelter, substrate, vertical position, dimension of prey species etc.), and including variables related to other co-occurring species. Odum (1983) discriminated spatial niche (the habitat of a species, sensu Whittaker et al. 1973), trophic niche (the role of the species within the food web), and hyper-volume niche (which matches basically the Hutchinsonian concept of niche).

Here I define habitat as the place (or range of places), characterized by spatially extended environmental variables, where a species lives, and fulfils its niche (sensu Whittaker et al. 1973) fundamental requirements. In other words, the habitat is the place or places offering conditions and providing the resources necessary for the survival and reproduction of a species (Hall et al. 1997; Morrison et al. 2006). In the present thesis (and wildlife management in general), the concept of habitat is more useful, with its spatially explicit connotation. Two other habitat related concepts, habitat use and habitat selection, are frequently used in wildlife-habitat relationship studies.

Habitat use relates to the way an animal uses the resources on offer whether physical, such as shelter provided by a particular topography or vegetation cover, or biological such as forage, occurring within a specific habitat (Hall et al. 1997).

Habitat selection is a complex process of hierarchical decisions that lead an individual towards a disproportionate use (either positive or negative) of a specific habitat in relation to its availability. These animal decisions relate to different scales of the environment (Johnson 1980; Hall et al. 1997; Morrison et al. 2006).

Habitat selection is determined by the animal responses to its niche requirements (Whittaker et al. 1973), and the scale at which selection is made determines the type of requirements (or their relative priority) that the animal is fulfilling (Senft et al. 1987). Understanding the causes of habitat selection across scales and the consequences that selection determines on the different habitat is crucial for both wildlife and land management (Morris, Clark, & Boyce 2008).

1.1 The importance of scale in Ecology and the definition of patches

Over the last decades the importance of the role of scale in understanding and interpreting any ecological phenomena has gained importance (Wiens 1989; Kotliar & Wiens 1990; Schneider 2001; Hobbs 2003). The concept of scale in ecology has seen an exponentially increase of its use from the 80’s decade (Schneider 2001), even if its introduction is far more older. What is and why it is so important the concept of scale in wildlife management?

Scale is “the resolution at which patterns are measured, perceived, or represented”, according to Morrison & Hall (2002); Turner & Gardner (1991) define it as the spatial or temporal measure of an object or a process. The concept implies two parts, the grain and the extent. **Grain** is the resolution at which a phenomenon or process is observed (researcher point of view) or occurs (organism point of view) and **extent** is the maximum width (in space or time) considered (Hobbs 2003). Scale can be approached from the organism or the researcher perspective. Considering the researcher standpoint, the grain is the size of his/her sample unit, whereas the extent is the area or time interval under investigation (Wiens 1989).

The importance of scale in ecology is related to environmental heterogeneity. According to Kotliar and Wiens (1990) definition, heterogeneity is the “spatial variance in system attributes” and depends on Contrast - the degree of difference between patches, and Aggregation - the spatial distribution or dispersion of patches, where patches can be defined as discrete areas “distinguished by discontinuities in environmental character states from their surroundings” Wiens (1976). Patches have an intrinsic degree of homogeneity (Forman 1995) that depend on the scale of observation. A patch is therefore the smallest homogeneous grain into which we split the environment for the sake of our research needs. A patch hierarchy can be outlined, where each level corresponds to a spatial scale of observation: the biosphere, which is divided into continents (and oceans), split into regions. A region is made up of different landscapes and each landscape of local ecosystems that can be further split into smaller patches accounting for their inside variability (Forman 1995). The hierarchy described above and the relative spatial scales are evidently delineated from an anthropocentric point of view: the scale of observation chosen in a specific research often reflects the researcher perception of the environment (Wiens 1989; Levin 1992).

Appropriate scales of observation depend on the range of patterns and processes that we are interested in, and on the question we aim to answer (Wiens 1989). Since different species (or individuals) perceive the environment through a particular range of scales, they may respond to the environment variability (heterogeneity or patchiness) in a specific way (Levin 1992). If the scale of observation doesn’t match the scale of occurrence of the observed phenomenon, or the scale perceived by the species in focus, the researcher may fail to detect authentic patterns (Etzenhouser et al. 1998).

The patterns and processes detected by ecological research, as well as the underlying factors affecting them, may differ substantially with the scale of observation (Wiens 1989; Levin 1992; Schneider 2001). It is important to realize how these patterns can vary across scales, by analysing patchiness at different scales and accounting for different environmental parameters according to the organism in study (Wiens 1976). Research on animal foraging behaviour, or habitat selection by large mammalian herbivores, often adopts hierarchical approaches (Senft et al. 1987; Bailey et al. 1996; Boyce et al. 2003; Fortin et al. 2003; Boyce 2006).

In their seminal works, Johnson (1980), Senft et al. (1987), and later Bailey et al. (1996) tried do interpret the hierarchical structure of animal distribution patterns focusing particularly on foraging decision process and the associated mechanisms. The selection orders as described by Johnson (1980) (specifically from second to fourth order, since the first order of selection is more related to evolutionary aspects of organisms), and Senft et al. (1987) hierarchical levels have been further developed and examined by Bailey et al. (1996).

Table 1. Ecological hierarchy as described by Johnson (1980), Senft et al. (1987), and Bailey et al. (1996).

	Johnson (1980)		Senft et al. (1987)		Bailey et al. (1996)	
	Selection order	Character of selection	Scales and units of selection	Foraging behaviour	Foraging spatial scales	Underlying behaviour and characteristics
↑ broader scale	First order	Physical or geographical range				
	Second order	Home range	Regional scale: landscapes	Selection of home range migration nomadism transhumance	Home range	Migration dispersal
					Camp	Set of feeding sites with same watering and resting points
	Third order	Habitat types within home range	Landscape scale: communities or large patches	Selection of feeding area	Feeding site	Foraging bout
					Patch	Break in foraging sequence (animal relocate itself)
	Fourth order	Patch selection within feeding site	Plant communities: plants, feeding station or micropatches	Diet selection	Feeding station	Set of bites without moving front feet
finer scale ↓					Bite	

For example, Bailey et al. (1996) related three nested foraging scales (camp, feeding site and patch) to Senft et al. landscape level (as in Senft et al. 1987), and to Johnson (1980) third order of selection, considering that different mechanism and factors influence animal decision at the different levels (see Table 1). Moreover, the camp and patch scales are also related to other spatial scales (the camp to the regional and the patch to the plant community level), underlying the interdependency of the hierarchical levels and the interaction among processes and causing factors.

The smallest scale at which an organism responds to environmental heterogeneity (or patchiness) is defined as the grain-response (Kotliar & Wiens 1990). Grain response is resource or function-specific (Wiens 1976) so, depending on the type of resource or process, the patch scale may vary. If we are interested in diet selection of a large herbivore, for example, the related patches we need to identify in our study area should be the resource units upon which the animal response is expressed (Wiens 1976), which could be either Bailey et al. (1996) “bite”, “feeding station” “patch” (see Table 1), according to the perspective of our investigation.

Once specified the scale of observation or analysis of a research, the identification or definition of patches follow. The criteria chosen to define patches and map heterogeneity must be relevant for the organism as well as for the processes that are being studied (Wiens et al. 1993). When dealing with terrestrial ecosystems and large mammalian herbivores, as in this thesis, patches are often defined according to vegetation characteristics. Important components of herbivores' habitats, such as food, bedding sites, thermal cover, hiding cover, etc. are provided by or related to vegetation. It is therefore crucial to understand how vegetation heterogeneity and the scale of this heterogeneity relate to animal distribution (Morrison et al. 2006). Furthermore, basing patch definition (and related spatial scale) on some kind of vegetation classification model has a twofold objective: on one hand, as previously said, to better understand animal use of its range, and of the different occurring vegetation types; on the other hand, to comprehend the animal impact(s) on the different types of vegetation (types obviously dependent on the classification criteria). The latter result might be central in many cases: for example when we are concerned with a specific fragile vegetation type, that need to be preserved through some kind of management measures, or when economic interests are affected by the animal population in study (e.g.: over-browsing in forest stands).

2. Vegetation classification

Vegetation can be defined as the assemblage of spontaneous plant cover of a specific area (van der Maarel 2005a). The term can be used in relation to a spatially restricted extent (e.g. the vegetation of a specific grassland) or in a broader extent (e.g.: the vegetation of the Central Europe lowlands).

Vegetation has a central role in ecology as it sustains the primary production of ecosystems (if we exclude saprophyte and parasite plants) being the support of trophic webs (Mueller-Dombois & Ellenberg 1974; Kent & Coker 1992).

Understanding and identifying vegetation patterns and dynamics are of prime relevance for assessing wildlife-habitat relationships: vegetation is simultaneously cause and result of the site-specific environmental conditions affecting wildlife. This is particularly relevant when dealing with herbivore species which depend directly on vegetation, and which can be associated, with different degrees of specialization, to specific vegetation types, as a result of evolutionary and co-evolutionary driving forces (Stebbins 1981).

Classifying vegetation cover means dividing it into discrete portions or classes, in other words, classification is a simplification of the diversity of vegetation into a relatively low number of classes. Conceptually, in any classification, the variability within classes is expected be lower than the between classes variability.

It is possible to recognize patterns within the vegetation of an area, although this identification depends on the scale of observation and also on the scale of the specific landscape patchiness, which is related to the environmental heterogeneity (e.g.: topographic gradients, lithology, land use). As a rule, when we scale up, from fine towards broader scales, we lose details, trading off part of the variability for more statistical predictability (Wiens 1989; Levin 1992): all the existing small scale, within communities differences, related to small scale environmental gradients, are averaged out when we observe vegetation from a wider perspective, allowing the visualization of discrete vegetation units, determined by more appreciable (to the human eye) ecological gradients.

Vegetation classification methods can be divided into two main groups: floristic and physiognomic/structural.

2.1 Physiognomic/structural classifications

Physiognomic/structural approaches are useful for coarser scale classifications, and they take into account either physiognomy, which is the general appearance of vegetation, or structure, which is related to the spatial arrangement of the vegetation. These classifications identify relationship between vegetation characteristics (structural and physiognomic) and environmental factors. In Table 2 a schematic review of some of the main classifications is given.

Table 2 – Some of the main vegetation classification methods based on physiognomic/structural characters (information retrieved from: Mueller-Dombois & Ellenberg 1974; Kent & Coker 1992; van der Maarel 2005b).

Author	Year	Paper/Book title	Description of the method criteria
Raunkiær	(1904), 1934	The life forms of plants and statistical plant geography	Essentially based on the height above ground of the perennating buds, considered related to climate conditions during the most adverse season. Five principal categories exist (phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes) and are further subdivided according to other structural characters.
Dansereau	1951	Description and recording of vegetation upon a structural basis	The method employs six criteria to classify vegetation: plant growth form; plant size; plant cover; leaf function (evergreen, deciduous); leaf size and shape; leaf texture. Each criterion corresponds to a different symbol, thus the final result is a symbolic profile diagram of the dominant species of an area.
Küchler	1967	Vegetation mapping	The method is hierarchical, starting from two broad categories, woody and herbaceous species; woody vegetation is further divided according to leaf characteristics, whereas herbaceous vegetation is divided into graminoids, forbs and lichens+mosses. Further distinctions are related to leaf characteristics and to height and cover of vegetation. As each category is defined by a letter or a number, the description of a vegetation stand results in a formula, which should ease map construction.
Fosberg	(1961), 1967	A classification of vegetation for general purposes	The International Biological Program adopted the classification, with the aim to classify vegetation at the world scale. It is a hierarchical method, the first level corresponding to gross vegetation cover (closed, open and sparse vegetation). Each category is divided into formation classes, considering both height and continuity of vegetation. A third level takes plant function (evergreen, deciduous, etc.) into account, and a fourth level considers leaf texture and size, and dominant species growth form. The "output" of the latter is the formation group, which corresponds to a map unit.
Mueller-Dombois & Ellenberg	(1967), 1974	Tentative physiognomic-ecological classification of plant formation of the earth	The objective of this classification was world vegetation mapping at the scale of 1:1 million. Like Fosberg's, it is a hierarchical classification and the first level (formation classes) is related to structural features, height and spacing of dominant plants. A further separation is achieved with leaf function (evergreen, deciduous, etc.). Ecological features, like

			macroclimates, are used to characterize among formation groups (third level). Other environmental features are employed to distinguish among formation (e.g.: lowland, mountain) and leaf characteristics (e.g.: broadleaved, microphyllous, etc.) for the subformation. The latter two levels are the main map units.
Box	1981	Macroclimate and plant forms: an introduction to predictive modelling in phytogeography	The objective of the method is a classification based only on plant structure accounting for climatic constraints. Each plant form is classified by a set of structural criteria: structural type (e.g.: tree, shrub); leaf form and consistency; relative plant and leaf size; seasonal activity pattern (e.g.: evergreen). A climatic envelope is attributed to each growth form (vegetation type) through predictive modelling.

Physiognomic/structural classifications have some advantage when compared to floristic ones: i) they don’t require a profound acquaintance with local flora; ii) they are less labour intensive; iii) they reduce vegetation diversity into a relatively small number of units, permitting comparison of floristically different vegetation communities on the basis of their physiognomic and ecological correspondence (Mueller-Dombois & Ellenberg 1974). Consequently, one of the main applications of physiognomic/structural classifications has been the mapping of vegetation at global scale (Box & Fujiwara 2005). However, as main disadvantage, they are not useful in distinguishing vegetation communities at fine scales.

2.2 Floristic classifications

Classifications based on floristic data allow to account for the great diversity of the vegetation cover, hence are suited for more detailed analyses and descriptions. Floristic classifications began to be increasingly used in vegetation research from the beginning of the past century, and became thereafter progressively preponderant, particularly in Europe (Werger & Sprangers 1982).

2.2.1 The relevance of Clements’ and Gleason’s approaches

Since the beginning of vegetation ecology studies, the existence of vegetation types, i.e. of recurring plant assemblages, related to some environmental factor, was recognized: in 1805, the naturalists Humboldt used the term association, although considering physiognomic characters, and sustained that “plant species associate differently according to altitude and temperature gradient” (apud Géhu 2011). Nevertheless, the generalization of floristic classifications in the early 20th century coincided with the beginning of a debate on the essential nature of vegetation, which confronted the discrete vegetation community and the continuum approaches.

Such discussion was rooted on Clements's holistic view of vegetation, and on the individualistic view of his opponent, Gleason.

Clements (1916) describes the plant ecological succession as the dynamic change of vegetation cover observed over time after some kind of disturbance has cleared the previous cover. Within this dynamic process of shifting vegetation it is possible to observe stages in vegetation corresponding to different plant communities. That is, there is a set of species thriving in a specific set of environmental condition, which in turn characterizes that stage of the ecological succession. Shifting from one plant community to another is hence related to changes environmental conditions (Eliot 2007). Behind this dynamic process lies a range of causes that varies in both composition and relative importance along the time. Among them, climate has a leading role: climate is a relatively fixed factor of an area, thus it sets the general path, or better said, the final direction of a succession (Clements 1916). Indeed, according to Clements, regional climate conditions determine the type of potential vegetation of an area, i.e. the vegetation that would cover that area in absence of disturbances, in other words, the climax. But climate does not control the whole process: a number of factors participate, and Clements (1916) distinguished among initial, ecesis, reaction and stabilizing causes.

Initial causes correspond to both the disturbance that cleared an area from its former vegetation cover, and the resulting environmental conditions that colonizing plants will find.

Ecesis causes regard plant species characteristics related to their successful establishment in the specific habitat (for example: dispersal capacity of the surrounding vegetation).

Reaction causes are related to the ability of the settled plants of modifying the environment, promoting or also preventing the colonization by other organisms. These modifications regard for example soil properties, water balance, and shade levels.

Stabilizing causes are those related to the ability of certain plants to alter environmental conditions to the point of preventing further changes, in other words the ability of maintaining themselves, as long as no important disturbance episode occurs: these stabilizing factors are characteristics of the climax community.

Clements recognizes that departures from climax and from "typical" successional path are frequent. Frequency and/or intensity of a disturbance (defined as an event that eliminate plant biomass and release resource to other plant species) may prevent the development of a climax community and fix the succession in a pre-climax or even in an earlier stage. The colonization by well-adapted alien species may also determine successional paths different from the original one.

Although Gleason started from a view of the vegetation close to that of Clements, in 1917 and then in 1926 (Gleason 1917, 1926) he published two papers in which he opposes the author's holistic vision of the vegetation and the very concept of plant community. Gleason emphasised the individualistic character of plants: plants migrate, germinate, grow and disseminate independently and according to individual ranges of environmental requirements. Gleason (1926) accepted that plant communities (considered as plant assemblages, or stands) could be recognised in the landscape, more easily in ones than in others, but defends that such communities cannot be classified into particular plant association types. Underlining the individualistic character of plants, he affirms that the vegetation cover of any area is the result of:

> *" […] the fortuitous immigration of plants and an equally fluctuating and variable environment"*

In his paper, Gleason (1926) sustains that vegetation is the result of contributing causes, among which migration and environmental selection are the prominent. Therefore, recurrence of similar communities is only due to similarity of the contributing causes in the area. Where conditions vary abruptly, the result is a clear change in the vegetation; but where the environmental conditions change gradually, vegetation also changes progressively and recognizing distinct association becomes impossible. Gleason challenges the whole holistic Clements' idea of considering plant associations as individual representations of a general group (in the same way an individual plant "belongs" to a species), and as stages of typical or fixed successional sequences.

Although Clements' theory had prevailed in the first half of the last century, from the 50ies it was Gleason's and his followers' individualistic approach that gain relevance. Gleason ideas merged in the theory of the vegetation continuum, which is essentially founded on the principles of species individuality and of community continuity.

Curtis & McIntosh (1951), for example, described the intergrading sequence (or gradient) of plant community in their Wisconsin study area as a "Vegetational continuum", and, although recognizing the existence of a certain vegetation pattern, with more or less similar recurrent groups of species, rejected the possibility of categorizing them into abstract entities. These recurrent groups were related to the dominance potentiality of a small group of tree species, each of them adapted to a combination of the regional climate and local soil conditions (Curtis & McIntosh 1951).

Within the continuum theory framework, vegetation analysis can be carried out with two different approaches: direct ordination or direct gradient analysis, that consists in the analysis of the variation of floristic composition along an established environmental gradient, and indirect gradient analysis, that begins with the evaluation/identification of a floristic pattern (used by Curtis & McIntosh 1951), followed by its environmental interpretation is the approach from floristic patterns. Unlike indirect gradient analysis, the starting point of direct ordination is the recognition of a specific environmental gradient, without considering any existing visible pattern in the vegetation cover, and the investigation of floristic variability is then carried out along the gradient. The drawback of direct ordination, as pointed out by Mueller-Dombois & Ellenberg (1974), is the difficulty of identifying fine scale cause-effect relations of plants and communities distribution, because of the existence of multiple influencing factors. The use of different methodologies to analyse vegetation, and of different way of manipulating the data gathered, may affect the type of conclusions (Daubenmire 1966).

The gap between the two approaches towards vegetation nature was certainly deepened by misunderstandings. In an overview on the past, present and future of vegetation classification, Mucina (1997) stressed some of them:

- a conceptual confusion, between concrete and abstract concepts: while the continuum concept refers to an abstract environmental space, the community concept refers to a spatially explicit reality (Austin & Smith 1989)
- differences in the scale of observation of the phenomena;
- the assumption that the continuous nature of vegetation prevents the possibility of classifying it;
- naturalness vs. arbitrariness of plant communities; that is, can communities be considered natural units? And which type of communities, all of them or just the “stable” or climax one?

However, the community *vs.* continuum debate has become purely speculative, and the usefulness of vegetation categorization has been widely recognized (Rivas-Martinez 2005a), even by those supporting the individualistic distribution idea (see, for example, Grossman et al. 1998). Austin (2005) for example, suggested that the concept of community as a property of the landscape, linked to the pattern of environmental variables of the specific landscape, as defined by Austin & Smith (1989), can be useful and should be employed for management purposes. Moreover, the species individuality principle, advocated by the continuum theory, does not exclude the possibility that different species may have similar responses to environmental gradients even though not coincident and, therefore, similar distributions (Mueller-Dombois & Ellenberg 1974).

2.2.2 The concept of plant association and the phytosociological method

The concept of plant association is central in the vegetation community approach and, although the term had already been introduced and used (by Humboldt, for example; see above), the first formal definition was conveyed in 1910, in the Brussels International Botanical Congress, by Flahault and Schröter (apud Géhu 2011):

> *‘‘An association is a plant community of specific floristic composition with uniform physiognomy and consistent ecological growth conditions. The association is the elementary unit of synecology’’*

This initial definition was too restrictive if taken literally, causing criticisms: it seemed to imply that communities belonging to an association should have the same floristic composition and ecological conditions, which is virtually impossible, apart from fortuitous cases.

Braun-Blanquet (1932) alerted for the narrowness of the mentioned definition, pointing out that communities of a particular association need to have similar (and not equal) floristic composition. He distinguished between the association, the abstract concept, and the individuals or stands, which are the concrete realities that are analysed in nature.

The current concept of association, the phytosociological fundamental abstract unit, includes different types of information: floristic, deriving from the concrete phytocoenoses on which the association is defined; chorological, corresponding to the concrete (potential) distribution of the communities (coenotope); and ecological, corresponding to the set of environmental condition in which the specific community is found (synhabitat, see Monteiro-Henriques 2010).

The association is therefore defined by a specific set of species, characterized by different degrees of fidelity. Fidelity is a fundamental concept in the Braun-Blanquet methodology, and briefly, can be defined as a measure of concentration of occurrences (or abundances) of a species within the relevés of a specific plant community (Bruelheide 2000); a high fidelity value, that is, a high frequency of occurrence of a particular plant species within the plant inventories (relevés), means a high diagnostic value of that species, in other words, such species is useful to identify the association (or vegetation type) of a relevé. According to the degree of fidelity, species within a relevé are classified as “differentials”, “characteristics” and “companions”. “Differential” species are those used for sharp discrimination among associations (or sub-associations) with few characteristics. “Characteristic” species may occur in more than one plant community type, but are expressly recurrent in one particular association: each association (and higher rank syntaxa) is defined by a group of characteristics (i.e. the floristic information mentioned above). “Companions” are species with no diagnostic value, as they might occur in many vegetation types. Plant associations are grouped into higher ranks (“alliances”) when sharing diagnostic species, and so on (“alliances” into “orders”, and “orders” into “classes”).

2.2.2.1 The phytosociological method

In his Plant Sociology, Braun-Blanquet (1932), who was the first to describe Phytosociology as a scientific methodology, defined the five levels of investigation that the method includes: i) the organization of plant community; ii) synecology, or the ecology of communities; iii) syngenetics, which deals with communities dynamic, or succession; iv) synchorology, related to the geographical distribution of communities; and v) systematics, which concerns the classification of community and the construction of a hierarchical framework.

The phytosociological approach encompasses different stages: i) analytical, comprising entitation and sampling; ii) synthetic, corresponding to classification; and iii) evaluative, in which the consistency of the results of the former stages is analysed (Aguiar 2001; Capelo 2003; Monteiro-Henriques 2010).

Entitation is the process of identification/recognition (or segmentation) of discrete vegetation “types” within which samples are to be located (Mueller-Dombois & Ellenberg 1974). Entitation through objective methods, is impractical: discovering vegetation patterns objectively, i.e. using random sampling, takes an enormous sampling effort, since samples are scattered through vegetation and may frequently include segments of clearly different vegetation communities. Phytosociology uses a top down approach, implying the development of a working hypothesis (the vegetation pattern visually recognized) before any quantitative analysis.

Traditional phytosociological method, as described by Braun-Blanquet (1932), suggests “preferential” sampling, or ”typical stand” sampling, as opposed to random sampling, meaning that any relevé should be conducted in area of uniform floristic composition, soil characteristics and relief. Presently, phytosociologists keep on using preferential sampling, in that they tend to focus sampling effort within “stands” that fit a subjective *a priori* idea of a particular vegetation community, avoiding, for example, sampling species-poor or “transitional” communities, more difficult to classify within the existent syntaxonomic system (Chytrý & Rafajová 2003). As a consequence, the large vegetation databases that have been gathered in various European countries are generally unbalanced, with underrepresentation of those aforementioned communities (transitional or species poor), which indeed may characterize great part of the vegetation cover. For these reasons, and because it does not possess the randomness that is needed for valid standard statistics results

(Botta-Dukát et al. 2007), preferential sampling is considered a weak point of this methodology, as, for instance, it is prone to generate biased estimates of vegetation characteristics. When stratified random sampling and subjective sampling (preferential) are compared, the latter shows a greater proportion of species-rich plots (Hédl 2007). However, when the objective is to evaluate species richness of a specific site (like a diversity hot-spot), subjective sampling is preferable, as it requires fewer plots to cover the overall diversity.

The classification phase consists in the discrimination of the relevés (on a floristic base) using manual tabular comparison and/or mathematical methodologies. The manual sorting of the relevés table comprises the quantitative determination of the fidelity of the species occurring within the relevés: was originally based on the intuitive comparison of the degree of presence and abundance within all the association tables belonging to a same regional territory (Chytrý et al. 2002). Currently various statistical approaches are being tested for the determination of diagnostic species, and the related literature is abundant (see for example: Dufrêne & Legendre 1997; Bruelheide 2000; Chytrý et al. 2002; Tichý & Chytrý 2006; Cáceres, Font, & Oliva 2008; Cáceres & Legendre 2009). Mathematical approaches have seen a progressive implementation and development since the sixties, thanks to the parallel development of statistical analysis and computer science. The advent of computer based ordination and classification has provided more formality to the phytosociological method, enhancing objectivity and consistent data analyses (Mucina 1997; Grabherr, Reiter, & Willner 2003).

Modern computer technologies can be employed to overcome the problems of the traditional phytosociological method (specifically the subjectivity of preferential sampling): Grabherr et al. (2003), for example, tested the existing information on Austrian forests (based on Braun-Blanquet relevés) by analysing the vegetation through an objective stratified random sampling design, aided by GIS techniques, taking topographical and ecological variables into account (e.g.: altitude, climate, aspect), and systematically positioning the relevés at the four corner of a randomly chosen plot(s) of each of their smallest ecologically homogeneous strata. The resulting classification was largely in accordance with the phytosociological one, suggesting the existence of ecological species groups, as sustained by Phytosociology.

Currently, in South-western Europe, Phytosociology is divided into three complementary branches: Phytosociology sensu strict (s.str.), Dynamic or Successional Phytosociology and Catenal Phytosociology. The first one, that have been previously discussed, focuses on the study and classification of phytocoenoses, as defined by Westhoff & van der Maarel (Westhoff & van der Maarel 1978; apud van der Maarel 2005a):

> *"[…] a piece of vegetation in a uniform environment with a relatively uniform floristic composition and structure that is distinct from the surrounding vegetation"*

Dynamic Phytosociology focuses on vegetation series, that is, on the temporal succession of plant communities. Here the abstract unit is the sigmetum, which represent all the plant communities, or successional stages distributed in a specific chorological unit, called tessella, an ecologically uniform territory, i.e. characterized by a specific combination of environmental conditions, (sigmahabitat, see Monteiro-Henriques 2010), and by a unique type of potential natural vegetation. These communities are linked dynamically, that is, they replace each other in a particular order (Rivas-Martinez 2005a).

Catenal Phytosociology deals with the geoseries of vegetation, which corresponds to the edaphohygrophilous, mesophilous (climatophilous) and edaphoxerophilous series of a specific bioclimatic belt. The abstract unit is called geosigmetum, its chorological unit is the pluritessella characterized by a specific array of environmental variables (geohabitat Monteiro-Henriques 2010). The general model of a catena matches to the topographical frame of valley – piedmont – slope - crest, with corresponding soil moisture and thickness gradient and related vegetation types (Rivas-Martinez 2005a). Dynamic and Catenal Phytosociology have important application at the landscape and regional scale, above all in relation to land management and planning (e.g.: Theurillat 1992; Pedrotti 1993, 2004; Blasi, Capotorti, & Frondoni 2005; Blasi & Frondoni 2011).

2.2.3 Other classification methods

Among the existing floristic classification methods we briefly describe the British and American methods, which both share common points with Phytosociology.

The British National Vegetation Classification (BNVC) is described in a series of five volumes (British Plant Communities), edited by Rodwell (Rodwell 1998a; b; c; d, 2000). It is entirely based on floristic composition and includes natural, semi-natural and main artificial vegetation types, basically, all the terrestrial plus fresh and brackish water vegetation communities of Great Britain (North Ireland excluded). It is a new classification, meaning that it is based on new sampling and data gathering (i.e. started from 1975). The sampling design is standardized and the analytical stage also follows a protocol: (stands are chosen according to floristic composition and structural uniformity; sampling plots dimension are pre-fixed, according to the vegetation type; the DOMIN scale (see details in Kent & Coker 1992) is used for abundance estimation. All samples are used in the analysis and the among-samples similarity is based only on the quantitative floristic records). The environmental variables data, gathered during the sampling stage, are used for the successive ecological characterization of the defined communities. The BNVC fundamental unit is the community, which is defined/described by a specific combination of species (with correspondent frequency and abundance values), by a description encompassing its physiognomy, phenology, set of influencing environmental conditions (e.g.: rainfall, temperature, continentality, geology, topographic position, etc.). Two lower ranking group types exist: the sub-community and the variant (comparable to Phytosociology sub-association and variant). Similarly to Phytosociology, plant species can have a diagnostic value and according to this are defined as constant, preferential/differential and associated (corresponding respectively to characteristic, differential and companion species in the phytosociological method). In the fifth volume of the series is included the “Phytosociological Conspectus of British Plant Communities”, where the communities described by the BNVC are ordered within the European phytosociological hierarchy.

The United States National Vegetation Classification (USNVC) (Grossman et al. 1998; Jennings et al. 2009) is a massive and still in course work, considering the extension of the US territory. It was design to be appropriate for mapping at multiple scales and practical for conservation purposes. The starting and fundamental assumption is that vegetation fits the continuum concept (see above), and that its classification into discrete units, although considered as arbitrary, it is necessary for the organization and transmission of all the existing information about vegetation, as well as for management and conservation purposes. Hence, the occurrence of similar groups of species (though intergrading continuously into one another) in ecologically similar environments is recognized (Grossman et al. 1998). The USNVC is a mixed physiognomic and floristic classification, relative to actual (not potential) natural vegetation. It is a hierarchical classification and comprises seven levels of which five are based on physiognomy, adapted from the UNESCO system (UNESCO 1973), and two on floristic composition (Table 3). The definition of association adopted by the USNVC is that proposed by Flahault and Schröter in 1910 (see 2.2.2). Data gathering and analyses are standardized (Jennings et al. 2009): for example, sampling areas are stratified and transects delineated according to ecological and topographical gradients; each transect is divided into ecologically homogeneous units, which in turn are divided into sub-units characterized by uniform vegetation. Finally, sampling plots (of predefined shape and size) are randomly chosen within a set of representative sub-units.

Table 3 – USNVC hierarchical levels and correspondent main characters for the definition.

Hierarchical levels	Characters for definition
Formation class	cover percentage and dominant vegetation height
Formation subclass	leaf character, persistence, growth form
Formation group	structural vegetation layers, leaf morphology, macroclimate and topography
Formation subgroup	degree of naturalness
Formation	structurally and physiognomically defined vegetation types, with a clear ecological characterization and landscape position
Alliance	group of association with one or more common dominant species
Association	distinctive floristic composition, physiognomically and environmentally uniform

2.2.4 Phytosociological studies and applications in Portugal

The application of phytosociological method to the study of vegetation began in Portugal in the first half of the last century. Major developments of the method and related applications occurred from 1990, as reported by a review on the Portuguese phytosociological studies by Costa (2004), particularly through collaboration with Spanish phytosociologists. The number of publications progressively increased, as well as the understanding and systematization of the vegetation cover of the Portuguese territory. Considering the more recent works, four of them are worth mentioning for their national scale:

- “Biogeografia de Portugal Continental” by Costa et al. (1999), which provided a spatially explicit proposal (detailed map) of the Phytogeography of mainland Portugal;
- “Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level” (2001), and “Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001” (2002) by Rivas-Martínez et al., which are a catalogue of all the phytosociological units (from class to association) described and recognized in Spain and Portugal
- “A Methodological Approach to Potential Vegetation Modeling Using GIS Techniques and Phytosociological Expert-Knowledge: Application to Mainland Portugal” by Capelo et al. (2007), in which, as the title suggests, the authors presented a method to model Portuguese potential vegetation and provided, as main output of the study, a map of the potential natural vegetation (i.e. map of the vegetation series) of the entire mainland Portuguese territory.

The concrete application of the phytosociological method in Portugal began in the eighties, as related by the review of Espírito-Santo (2004). Phytosociology has ben applied to conservation and management of natural resources, mainly in environmental impact assessment plans, land-use planning at different scales as well as nature conservation and management plans. The characterization of the sites proposed by Portugal for integration within the Natura 2000 network was also based on Phytosociology (ALFA 2004).

2.3 Vegetation classification methods applied to wildlife or animal habitat use studies

Vegetation provides food and shelter to wildlife thus is particularly meaningful, mainly when considering herbivores. A number of different methods have been used, to classify vegetation in wildlife research, varying from physiognomic to floristic methods. The method chosen depends on the process being investigated, aims of study, scale of observation of the phenomena on focus, and characteristics of target species including its size and general ranging behaviour.

Physiognomic/structural classifications are generally employed in large-scale studies. Saïd & Servanty (2005), for example, in order to assess which landscape feature affected roe deer distribution in the Chizé Forest, categorised vegetation units using a simplified structural classification (e.g.: low scrubs; grassland; dense forest; etc.). The same kind of categories was used by Acevedo et al. (2005), in an analysis of roe deer colonization constraints in the Iberian mountains. In a study on red and fallow deer habitat use, conducted in the Doñana National Park (Spain), Braza & Álvarez labelled habitat units using physiognomic descriptors (e.g.: marsh, shrubs), although each unit may include different plant communities. Mixed physiognomic/floristic classifications are also frequent in wildlife research: Boyce et al. (2003), for instance, discriminated vegetation patches according to both structure and, for the forest types, to the dominant tree species. Similarly Hemami et al. (2004) distinguished forest patches according to structure and to percentage cover of a number of understory species.

When the habitat use pattern is analysed at a more detailed scale, the method used to classify vegetation may also need a greater detail to account for the variability of the vegetation cover. Considering the literature, it is possible to find both physiognomic/structural and floristic classification. The long-term research on the red deer population of Rhum, Scotland (Clutton-Brock, Guinness, & Albon 1982) used floristic classification for assessing habitat selection at the plant community scale (Clutton-Brock et al. 1982), or interactions between red deer and cattle (Gordon 1989a; b; c; Gordon & Illius 1989). In even more detailed scale studies, such as assessment of diet selection, often it is the plant species and not the community to be considered (Pettorelli et al. 2001; Dumont et al. 2005).

Few references have been found on the use of Phytosociology in wildlife research: searching in the ISI Web of Science^{SM} for example, using the terms phytosociology and phytosociological together with animal related ones (wildlife, grazing, habitat use, ungulate; among others) the number of documents in which the methodology is used either for animal habitat description (Mian 2003; Cabrera-García, Montes, & Weinmann 2006; Putfarken et al. 2008; Fakhar-I-Abbas, Tanveer, & Mian 2009) or for assessing animal impacts on vegetation (Chytrý & Danihelka 1993; Höft & Höft 1995) is very small.

Compared to the United States National Vegetation Classification (USNVC), European Phytosociology classification has a finer resolution, meaning that it tends to classify a higher number of levels of vegetation units (Loehle 2011). It can be criticized that many of the levels might not be perceived as differences in habitat value by wildlife species (Loehle 2011), but this is highly related to the species in focus and to its sensitivity to patchiness grain (Kotliar & Wiens 1990). Considering the lack of references on the subject, it is a challenge to evaluate the applicability and usefulness of Phytosociology to wildlife habitat use research, considering that currently, it is widely used in Europe for describing and mapping vegetation cover at the landscape scale. Specifically, taking the Portuguese reality into account, where great part of the vegetation cover of the territory has been classified according to this methodology, an assessment of its value beyond the vegetation science domain seems pertinent.

3. Deer species in focus

Red and roe deer are widespread in Europe occupying a large geographical area and a range of different habitats (Putman & Flueck 2011). Both species are characterized by high ecological plasticity and diet variability (Putman & Flueck 2011). Below I resume a description of the two species, with emphasis on habitat use in the Mediterranean region.

3.1 Red deer

Red deer (*Cervus elaphus* L., 1758) is a widespread ungulate, naturally distributed in the Northern hemisphere (Europe, Asia minor, Caucasian region and North Africa) and introduced in the Southern hemisphere (South America and Oceania). The related North American elk, or wapiti (*Cervus canadensis* Erxleben, 1777), long thought to be a subspecies of red deer, is now considered a different species, according to mitochondrial DNA analyses (Ludt et al. 2004). Red deer is usually classified into different subspecies throughout its range of distribution (but see Ludt et al. 2004 for a discussion).

In Portugal, red deer (*Cervus elaphus hispanicus*, Hilzheimer 1909) free ranging populations occur along the Portuguese-Spanish border namely: i) Natural Park of Montesinho; ii) Moura/Barrancos; and iii) Castelo Branco/Idanha-a-nova. The species is also expanding in the Peneda-Gerês National Park (Salazar 2009). Red deer was also re-introduced in the Serra da Lousã during the 90’s, and in different properties (where they are usually enclosed) from south to north Portugal, for hunting purposes.

Red deer is brown-reddish during summer and grey-brownish in winter. Rump patch colour tends to vary within the geographical range, from bright yellow in the Eastern subspecies to creamy/whitish in the Western ones. Dimension also varies along the European range, with Corsican deer (*Cervus elaphus corsicanus* Erxleben, 1977) being the smallest (stag: 95 to 100 cm to shoulder; 120 to 130 kg, Beccu 1989) and the Caspian (*Cervus elaphus maral* Gray, 1850) the largest (stag: 150 cm; 270 kg).

Red deer is characterized by sexual dimorphism, with males (stags) being bigger (175 to 250 cm long; 130 to 150 cm to shoulder and weighs 160 to 270 kg) than the females (hinds) (160 to 210 cm long; 100 to 130 cm to shoulder; and weigh 120 to 170 kg). Males also differ from females having stronger neck muscles and, although not in all subspecies, a neck mane wore during autumn. Besides body size, sexual dimorphism is evident in the antlers, carried only by males: antlers begin to grow in spring and are shed generally at the end of winter. Outside rut season (August/October) stags and hinds live normally in separate groups: female groups are normally composed by various adult hinds, with their offspring and a number of sub-adults; young males also tend to cluster together, although groups are smaller; adult stags can show a stronger territoriality, travelling alone or sometimes in the company of few male sub-adults. When calving season approaches (May), female groups split and mothers seek isolation and protection in more secluded areas of their range, where they give birth to one, rarely two offspring. Red deer is considered as an intermediate feeder (sensu Hofmann 1989), switching from graminoids, to forbs and browse according to local, as well as seasonal forage availability (Hofmann 1989; Gebert & Verheyden-Tixier 2001). Forage characteristics and availability, and hence diet selection, depend on the habitat types (sensu vegetation communities) occurring in the different ranges that red deer populations occupy, varying from closed coniferous and broadleaved forest stands, to open moorlands and to open woodlands like the Portuguese montado (Bugalho et al. 2009) or the Spanish dehesa. Differences in plant community selection can also be observed between the two sexes: due to the bigger size, males have greater gut capacity and manage to better exploit lower quality forage, than smaller females (van Soest 1996). Evidences of stags and hinds of a same population feeding on different communities exist (e.g.: Clutton-Brock et al. 1982; Staines, Crisp, & Parish 1982; Gordon 1989b; Bugalho, Milne, & Racey 2001).

3.2 Roe deer

Roe deer (*Capreolus capreolus* L., 1758) is the most abundant cervid in Western Eurasia and it is widely distributed, from northern Scandinavia to the Mediterranean Sea, and from Portugal to Turkey, Iran and the Caucasian region (Wilson & Reeder 2005).

In Portugal the species occurs naturally in the mountainous areas North of the Douro River (Montesinho, Peneda, Amarela, Gerês, Cabreira, Marão, Coroa, Nogueira, Bornes and Reboredo Mountains; Vingada et al. 2010), and it is expanding into other areas, thanks to both natural colonization coming from the Spanish border, and reintroduction projects (e.g. in Serra da Lousã and Gralheira Massif in the 90’s). Re-introductions have aimed hunting purposes and re-stock of prey for the endangered Iberian wolf (*Canis lupus signatus*) population occurring South of the Douro River (six confirmed wolf packs, according to Pimenta et al. 2003).

Roe deer are small cervids (95-135 cm long; 65-75 cm to shoulder; 15–30 kg) reddish during summer and brown to dark brown in winter, with a white rump patch. Sexual dimorphism is evident in the antlers, carried only by males and in the rump patch, which is heart-shaped on females (does) and kidney-shaped on males (bucks). Roe deer is a timid species, mainly crepuscular, tending to avoid human disturbances (Hewison et al. 2001) and showing high variation in space and habitat use patterns throughout its range (Danilkin & Hewison 1996). Males are highly territorial, from spring to autumn, and the area defended may include females' ranges. Adult females, although living in a same area, normally smaller than male's, along the years, are not as territorial and frequently their ranges can overlap. Does tend to form small familiar groups while adult males lives alone, except during winter, when territoriality is weaker and bigger groups are more frequent (Prior 1995; Danilkin & Hewison 1996).

Roe deer is usually associated to wooded habitats, (Putman 1986), but shows great plasticity and opportunistic behaviour, colonizing more open areas, including agricultural lands. Roe deer using open habitat tends to form larger groups than in wooded habitat (Gerard et al. 1995; Jepsen & Topping 2004), possibly as an antipredator strategy (Barja & Rosellini 2008). According to Tixier & Duncan (1996) review on European roe deer diet selection, the species feeds on a variety of food items, according to spatial and seasonal availability: roe deer is a concentrate feeder (sensu Hofmann 1989) switching from a browse (forbs and shoots) to a frugivorous and granivorous diet when food availability allows it.

3.3 Foraging behaviour and plant community selection

Foraging behaviour is expressed at multiple spatial and temporal scales. For ungulate herbivores, selection of a particular plant community for foraging depends on availability and also quality (Moser, Schütz, & Hindenlang 2006) of the food items. At the bite and feeding station levels, (sensu Bailey et al. 1996) selection can be accidental (exclusively related to species abundance or to a highly palatable neighbourhood, Gómez et al. 2001; Baraza, Zamora, & Hódar 2006), or it can be intentional (dependent on the herbivore's preferences). Diet selection is related to morphological and physiological characteristics and to body size: small bodied roe deer, for example, spends more time and energy selecting a higher quality diet, probably because it requires less time to satisfy its energetic needs (Bailey et al. 1996). Pettorelli et al. (2001) pointed out that roe deer is less sensible to a reduction of forage availability and more to a reduction of its nutritional value. Larger herbivores, like red deer, tend to rely on a lower quality but more abundant diet to meet their higher energetic requirements, especially when availability is limited (Bailey et al. 1996). These differences may translate into a differential use of the same vegetation mosaic. Differences between sexes in the use of plant communities can occur in sexually dimorphic species like the red deer. Red deer males have higher energetic needs than females, due to their bigger size, and require higher intake rates and require higher intake rates. Clutton-Brock et al. (1982) assume the existence of an indirect competition between stags and hinds, in time of forage shortage: due to their smaller bodies (Focardi et al. 2003) and to morphological differences (Pérez-Barbería & Gordon 1998, 1999), red deer females in temperate climate may prevail in the exploitation of higher quality plant community, while males are forced into lower quality ones with higher biomass (Staines et al. 1982). In Mediterranean areas during summer, however, because of better physical ability in reaching tree canopies for browsing, red deer males may have nutritional advantages over females (Bugalho et al. 2001). As biomass and nutritional value of plant communities vary with species composition (González-Hernández & Silva-Pando 1999) and phenology, deer shift between plant communities to meet nutritional requirements (Clutton-Brock et al. 1982; Gordon & Illius 1989; Bugalho & Milne 2003).

3.4 Red and roe deer in the Mediterranean region, habitat use and general constraints

Red and roe deer are spreading in the Mediterranean region, thanks to three main causes: the land abandonment tendency of the last decades (MacDonald et al. 2000; Acevedo et al. 2005, 2010), particularly in mountainous and marginal areas, which was followed by the expansion of shrubs and forests favouring the colonization of deer as well as other ungulate species, such as wild boar; conservation issues, with the related increase of protected areas; and re-stockings and re-introductions (or novel introductions) for game-hunting purposes (San Miguel-Ayanz, García-Calvo, & García-Olalla 2010).

Red deer is well adapted to a wide range of habitats, from the dehesa or montado systems (Vargas, Calvo, & Aparicio 1995; Olea & San Miguel-Ayanz 2006; Bugalho et al. 2009; Pinto-Correia, Ribeiro, & Sá-Sousa 2011), to shrubland communities such as those of *Cistus* spp. or *Halimium* spp. (in the Doñana National Park, South of Spain; Braza & Álvarez 1987), to cork (Bugalho et al. 2001; Bugalho & Milne 2003) and holm oak woodlands (San José et al. 1997), or deciduous oak forests (the thesis study area). Although occupying a variety of habitats, red deer exploits preferentially ecotone areas, between open lands with herbaceous vegetation and wooded or shrubland areas, which provide shelter during the diurnal hours (Carranza 2007). The typically hot and dry summers that characterize the Mediterranean basin may represent a seasonal constraint for the red deer: dry summers mean scarce production and quality of the grass layer and consequent switch towards browse (San José et al. 1997). This situation can be frequent in montado and dehesa systems, where, high deer densities (common in hunting enclosures) can endanger tree regeneration (Vargas et al. 1995), although, in a montado system in Portugal, with a relative high deer density, it was shown that oak seedling mortality in summer was similar between plots protected and not protected from deer browsing, possibly due to water scarcity during summer (Bugalho et al. 2006). In Mediterranean environments characterized by denser forests and maquis systems, high deer densities (up to 26/km^2) do not seem to endanger ecosystem processes like tree and shrub species regeneration (Lovari et al. 2007), probably because of the higher carrying capacity of these types of vegetation.

Red deer in Central Spain mountains exhibited a browsing behaviour, with woody species comprising more than 70% of its diet (Martínez 2009), but, more generally, diet selection comprises a greater percentage of graminoids and herbaceous forbs during spring (Carranza 2007).

Roe deer is considered a concentrate selector and its preferential diet includes highly nutritious vegetation species and plant parts (San José 2007). Due to the smaller gut capacity and retention time, roe deer is more sensitive to reduction in forage quality than the bigger red deer, which greater gut retention time allows a better exploitation of more fibrous forage, characterized by slower digestibility (van Soest 1996). In Spanish mountain ranges, roe deer selection of bramble (*Rubus* sp.), typical of the species diet across its Eurasian range (Tixier & Duncan 1996), is common, as well as selection of *Pterospartum tridentatum*, *Halimium* sp. and *Erica* sp. Similarly, Virgós & Tellería (1998) found a preference for patches with higher cover of *Erica* sp. and of leguminous shrubs, especially within holm oak forest patches.

With regard to habitat use (sensu vegetation type), roe deer is more adapted to mesic conditions and, if compared to red deer, preferentially uses more concealing than open habitats (Ramos et al. 2006; Barja & Rosellini 2008), although the species can be found in agriculture lands and in other sub-optimal habitats as a consequence of recent colonization related to expanding populations (Tellería & Virgós 1997; Acevedo et al. 2005; San José 2007). In Italy, for example, roe deer populations are found in both deciduous and sclerophyllous oak forests (Cimino & Lovari 2003; Ferretti et al. 2011), as well as in Mediterranean scrublands (Börger et al. 2006). Researches conducted in Spain showed the existence of a restriction in roe deer distribution and habitat selection towards more humid and productive areas: for example, the species seems to prefer mesic pine and oak forests (*Pinus sylvestris* and *Q. pyrenaica*), concentrated in mountainous areas over the more xeric holm oak forests, occurring in both mountain and foothills (San José et al. 1997; Tellería & Virgós 1997; Virgós & Tellería 1998), probably being constrained by forage scarcity and lower quality during the dry season in the holm oak forests. In the Mountain range of Central Spain Mateos-Quesada (2005) observed a greater use of chestnut over pine and oak (deciduous and evergreen) forests. In the Serra da Gardunha (Portugal), roe deer was shown to prefer higher elevations during summer, apparently to avoid higher temperature (Carvalho et al. 2008). In the more xeric range of the Mediterranean basin, the presence of free water sources during the dry summers is certainly an ecological constraint for this species (Tellería & Virgós 1997; Wallach et al. 2007). In rural landscapes, the lack of natural open water may drive roe deer into cultivated and irrigated fields, which may lead to conflicts with resident human population (Wallach et al. 2007). Roe deer shows great behavioural plasticity when living in rural landscapes, characterized by a mosaic of natural and semi-natural vegetation patches and cultivated crops, and includes agricultural crops in the diet when availability/quality of other forage sources is lower (Abbas et al. 2011). This intraspecific plasticity is also reflected by different social behaviour, such as differences in typical group size between forest dwelling and field roe deer (Jepsen & Topping 2004).

Few studies have focused on habitat use by sympatric red and roe deer within the Mediterranean range, but some evidences show that red deer can affect negatively roe deer distribution (Torres 2011). Analogous findings (of outcompeted roe deer) are reported by studies on co- occurrence with other ungulate species, like for example fallow deer (Focardi et al. 2006; Ferretti, Sforzi, & Lovari 2010). In the North of Portugal (Cortez 1997; Faria 1999), red and roe deer forage preferentially on shrubs, like *Pterospartum tridentatum*, *Halimium alyssoides*, *Rubus* sp. and *Erica* sp.; grass and herbaceous leguminous; leaves and acorns of both *Quercus rotundifolia* and *Q. pyrenaica*. Cortez (1997) considers that diet overlapping between red and roe deer is not significant, due to seasonal shifts in forage preferences of both deer species. But according to Vingada (Vingada 1991, apud Valente e Santos 2009), habitat use overlapping may occur, specifically in younger coniferous plantation (*P. pinaster*) and both deciduous and sclerophyllous oak forests (*Q. pyrenaica* and *Q. rotundifolia*), used mainly as shelter habitat.

4. Research objectives and Thesis outline

Land use changes are modifying European landscapes. Land abandonment in particular and human migration fluxes, from marginal towards more productive and industrialized areas are occurring (MacDonald et al. 2000). Land abandonment favour shrub encroachment into old agricultural fields and ultimately woodland expansion, affecting wildlife populations. Wildlife species, as, for example, bird species associated with agricultural landscapes, may be negatively affected (Suárez-Seoane, Osborne, & Baudry 2002; Sirami et al. 2008), whereas mammalian herbivores such as roe and red deer (Gill & Beardall 2001) may benefit from abandonment of rural areas by human populations.

To fully comprehend the complexity of animal-landscape relation multiple scale studies of habitat use are needed (chapter 1.1). When the objective is understanding and managing the effect of large herbivores on specific habitats or vegetation communities, a finer scale approach is crucial (Gordon, Hester & Festa-Bianchet 2004).

In fine scale researches, the heterogeneity of landscape is accounted for by defining different types of patches, generally according to some classification of the occurring vegetation communities. With this thesis I aimed to assess whether phytosociological classification can be useful in describing fine scale habitat use of large mammalian herbivores, like red and roe deer. Phytosociology is a powerful tool for interpreting and managing the landscape mosaic (Capelo 2003; Espírito-Santo 2004). Phytosociological models have been developed for a great part of the Portuguese territory (Costa 2004; Capelo et al. 2007). Vegetation has also been exhaustively described in Portugal, at a regional level, using phytosociology (e.g.: Aguiar 2001; Honrado 2003; Monteiro-Henriques 2010, related to Northern Portugal). It is therefore an appealing challenge to assess its value beyond vegetation science boundaries, as a tool for wildlife-habitat relationship research.

In Section II I investigated habitat-use patterns of red and roe deer populations occurring in an area of the Natural Park of Montesinho (NPM). Like other Mediterranean mountainous areas (MacDonald et al. 2000), NPM has suffered a decline of human presence and activities, and it is a challenging opportunity to explore wildlife-habitat relationships in a human shaped landscape. I focused on deer use of meadows and forests communities.

In the study area the traditional livestock farming system of pastures and hay meadows, known as “lameiros” system, is still present even though declining. The traditional management, typical of Portuguese Northern mountain ranges, has created a peculiar human shaped landscape of recognized conservation value (Pinto-Correia & Vos 2004). Lameiros, however, have been progressively abandoned due to socio-economic reasons including low agriculture incomes and old age of local people.

In chapter 8 and 9, deer use of semi-natural hay meadows is investigated at two scales: a finer scale, the patch scale (sensu Bailey et al. 1996), and a coarser one, the landscape level.

Specifically, in chapter 8, I investigated spring use of meadows patches by red deer. After clustering patches according to different criteria, I aimed to assess whether red deer is selective at the patch scale and which patch classification and clustering criteria helps explain deer use of meadows' types better.

In chapter 9, red and roe deer use of meadows was analysed using a multi-scalar approach. In this study I aimed to assess what kind of environmental factors affect deer use of meadows and which is the best performing vicinity size to analyse landscape scale features. In addition, I wanted to verify whether coarser and finer scale variables (in relation to the landscape scale used) influenced deer use pattern.

In the NPM study area forest vegetation cover is largely represented by pine plantations with interspersed patches of autochthonous oak forests (deciduous and evergreen ones). In chapter 10, I focused on the comparative use of this three different forest types by sympatric red and roe deer.

Chapter 8 to 10 are in paper format, as they were thought and developed in order to be submitted to scientific journals.

In Section III, using a modelling approach based on the information gathered in the Natural Park of Montesinho area, I built a predictive map for roe deer use of semi-natural meadows of an area of the Montemuro-Freita-Arada massif, corresponding to the potential distribution area of the *Holcus mollis-Querco pyrenaicae* Sigmetum.

Section IV comprises a general discussion of the results of the Thesis.

II. Red and roe deer habitat use in the Natural Park of Montesinho

5. Study area

5.1 Location

The study area is located in the Natural Park of Montesinho (NPM), Northeast Portugal (Figure 1a). NPM is a 75 000 ha area, and is included within the Pan-European network of protected areas Natura 2000 (PTCON0002). The study area corresponds to an 8 x 6 km rectangle in the eastern part of the NPM (Figure 1b).

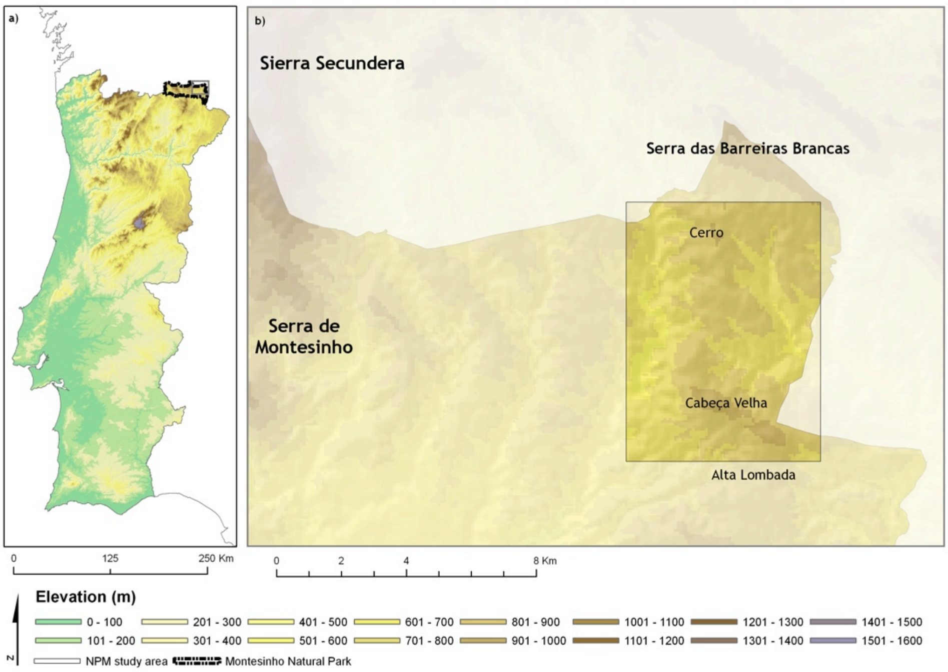

Figure 1 - Location of the study area, with reference to hypsometry: a) location of the Natural Park of Montesinho (dotted line); b) zoom of the study area location.

Numerous watercourses cross the area (Figure 2). It is visible in the map the slightly meandering course of the Rio de Onor, the principal river running in the area: erosive processes are more pronounced in schistic lithology, the dominant type in the study area, than in granitic ones, determining the typical rounded relief. Steep valleys occur where the water lines cross quartzitic crests (Aguiar 2001).

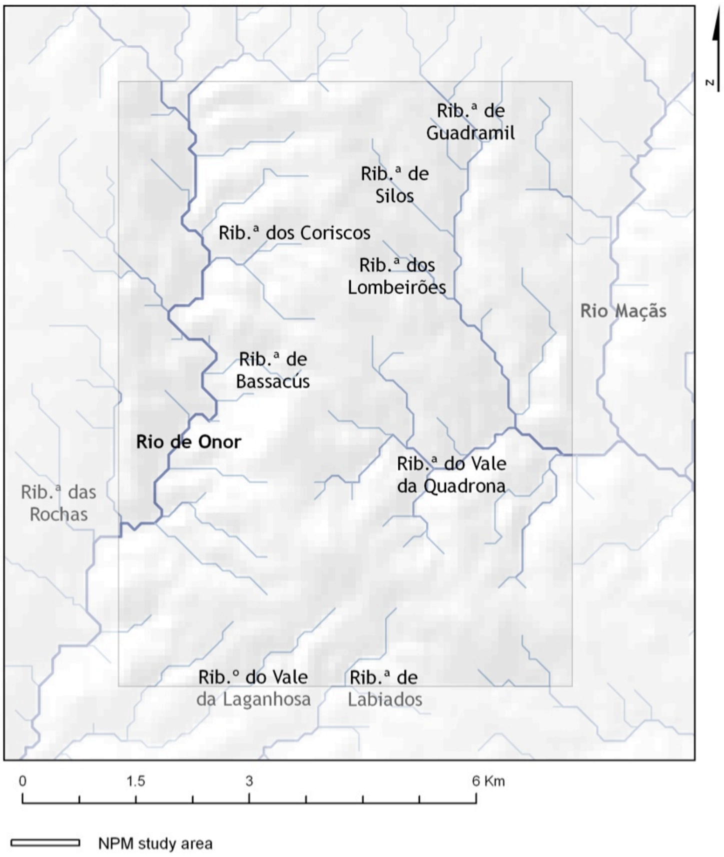

Figure 2 – Hydrological map of the NPM study area.

5.2 Bioclimatology

Monteiro-Henriques (2010) has recently published some bioclimatic maps, following the Rivas-Martínez World Bioclimatic Classification (RMWBC, see Rivas-Martínez 2007), using temperature (Silva 2005) and precipitation (Nicolau 2002) geostatistical estimations (1960-1990) for continental Portugal. Particularly the author compared two of the published versions of RMWBC (Rivas-Martínez 2005b and Rivas-Martínez 2007), concluding that, for the Montemuro-Freita-Arada massif the version of 2005 present a greater adjustment to the vegetation patches, namely to the natural forest remnants. Figure 3 shows thermotypes and ombrotypes map following Rivas-Martínez (2005b), adapted from Monteiro-Henriques (2010). The dominant thermotype in the Natural Park of Montesinho are supra-Mediterranean and supra-temperate, under humid to sub-humid ombrotypes. The selected study area is supra-Mediterranean, mainly under humid ombrotypes, with exception of its SW part, which presents a drier ombrotype (sub-humid). For information on definitions and indexes calculation formulas see Rivas-Martínez (2005b).

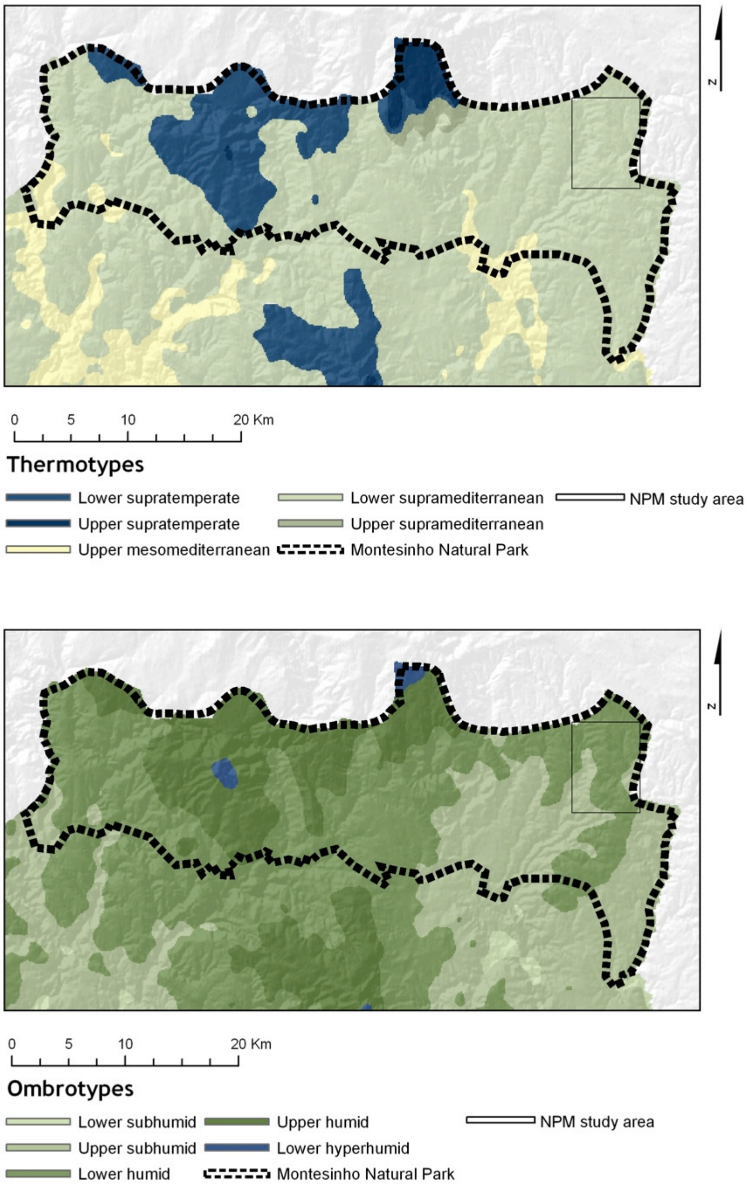

Figure 3 – Bioclimatic maps of the Natural Park of Montesinho adapted from Monteiro-Henriques (2010).

5.3 Geology, Lithology and Pedology

Five main lithological groups can be found in the NPM study area: i) Silurian metasediments (phyllite and schist); ii) Ordovician metasediments (slate and schist); iii) Devonian Gimonde formation (turbidite); iv) Silurian acid tuff; v) Ordovician metasediments (quartzite and schist). A geological/lithological synthesis of the study area is displayed in Figure 4, adapted from the Geologic Map of Portugal 1:500 000 (INETI 2007).

According to Aguiar (2001), and following the Food and Agriculture Organization of the United Nations (FAO) soil classification, leptosols dominate the most part of the study area. More developed soils (especially on foothills and valleys) correspond mainly to cambisols and to luvisols. Other soil types occurring in the area are: anthrosols (linked to agriculture) and fluvisols (related to alluvia).

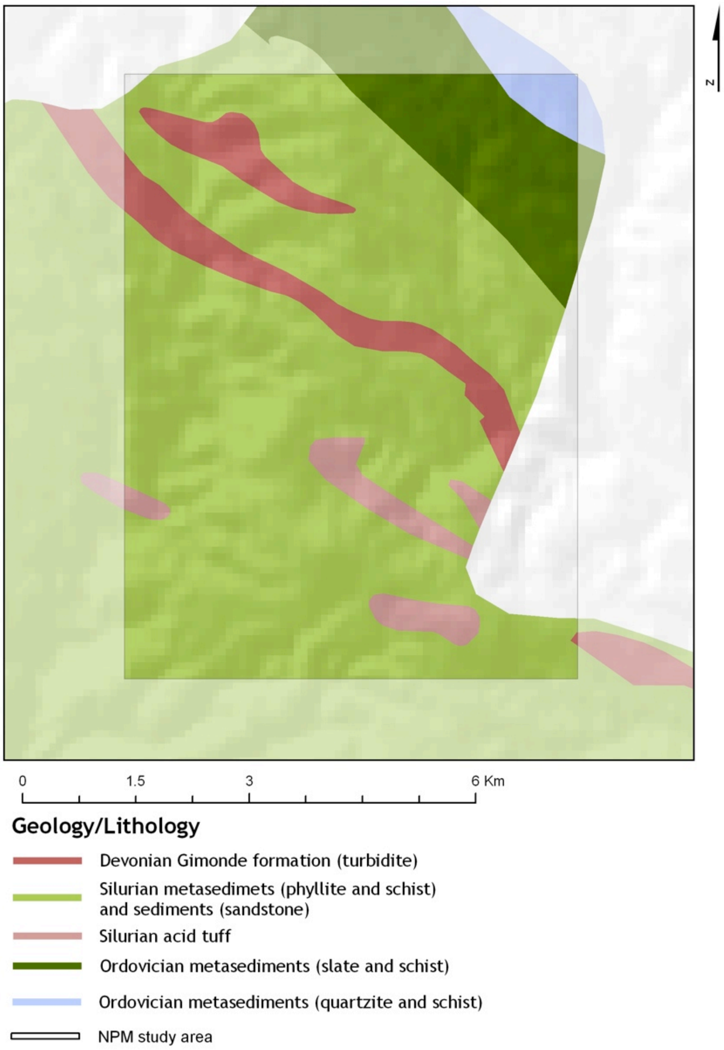

Figure 4 - Geological/lithological synthesis map of the study area, adapted from the Geologic Map of Portugal (INETI 2007)

5.4 Human presence and activities

The area of the Natural Park of Montesinho has been affected by the exodus of rural populations, which occurred in other mountainous marginal areas of the Northern Mediterranean basin, including Portugal. Between 1960 and 1996, the NPM area has lost more than half of its residents. Presently, population density is very low (around 9.5 inhabitants/km^2) and distributed among small rural villages. Considering only our study area, which includes part of the territory of three administrative centres (Rio de Onor, Deilão and Aveleda), population density is even lower (around 5/km^2, according to data retrieved from C.M. Bragança 2009).

The village of Rio de Onor is located on the border between Portugal and Spain, where a twin Spanish village -Rihonor de Castilla exists. The village peculiarity is the ancient communitarian management of rural activities that consisted, for example, in the communitarian flock (sheep and goats), fed on communitarian pastures guided by the residents. The recent extinction of this activity reflects the land abandonment trend characterizing the area and the ageing of the resident population. In Guadramil, the smallest of the villages, one of the resident still owned a small number of cows at the beginning of the fieldworks of the present thesis, but during the last field season (2009) they had been sold. Varge and Deilão, the other two villages, have a slightly different situation, with overall younger resident population and still active farming, although the rural activities decline is also evident.

Besides traditional rural activities (mainly subsistence agriculture and farming), local economy relies on ecotourism, with a few bed and breakfast accommodations and restaurants available.

5.5 Natural vegetation communities with landscape scale expression

The vegetation communities occurring in the study area have been studied and described recently in the exhaustive work of Aguiar (2001), on which the following subchapters are based.

5.5.1 Mesophilous vegetation

One mesophilous vegetation series (see chapter 2 for definitions) is described for the study area: the *Genisto falcate-Querco pyrenaicae* Sigmetum (previously *Holcus mollis-Querco pyrenaicae* Sigmetum, in Aguiar 2001; then reinterpreted as in Capelo et al. 2007). In the following subchapter a brief characterization of the climactic stage is given. Subserial communities are described in subchapter 5.5.3.

5.5.1.1 *Genisto falcate-Quercetum pyrenaicae*

The *Genisto falcatae-Quercetum pyrenaicae* corresponds to the climactic vegetation of the supra- and meso-Mediterranean sub-humid series *Genisto falcatae-Querco pyrenaicae* Sigmetum. These forests are dominated by *Quercus pyrenaica*. Considering the disturbance regime related to the long anthropic use, most of them should be considered as pre-climactic forests, and various species of the subserial associations are recurrently found.

Within its potential distribution area, this forest community is highly fragmented and scarcely represented, due to prolonged human disturbance regime (traditional rural activities; wildfires) and relatively more recent replacement with commercial forest stands (mainly coniferous). Fragmentation increases the “edge effect”, facilitating the colonization by species from the surrounding subserial communities (Aguiar 2001).

5.5.2 Edaphoxerophilous vegetation

Within the study area, the *Genisto hystricis-Querco rotundifoliae* Sigmetum is the series occurring in xerophilous positions. Hereafter, the climactic stage is described, and the characterization of the subserial communities is provided in 5.5.3.

5.5.2.1 *Genisto hystricis-Quercetum rotundifoliae*

The *Genisto hystricis-Quercetum rotundifoliae quercetosum rotundifoliae* is the climactic vegetation community of the holm oak series occurring in the study area, typically in the inferior supra-Mediterranean bioclimatic horizon, with sub-humid to humid ombroclimate (see definitions in Rivas-Martínez 2007), occupying edaphoxerophilous positions on steep slopes. Considering their edaphoxerophilous position and their fragmentation and degradation state, these forests have normally an open canopy, allowing the entrance and colonization of species typical of subserial communities.

Deciduous and sclerophyllous evergreen oak forests are expanding in the area, due to the colonization of old agricultural fields. In our study area, a mosaic of the two communities is relatively frequent in the ecotone zone, namely on the steep slopes. At a fine scale, the spatial heterogeneity of the soil (considering moisture, nutrients content and depth) reflects the distribution of the characteristic species of the phytosociological classes to which the two forest associations belong (*Querco-Fagetea* and *Quercetea ilicis*) (Aguiar 2001).

5.5.3 Mesophilous and edaphoxerophilous subserial vegetation

Vegetation communities of lower successional stages frequently occupy the potential distribution area of both oak forest types, if we exclude the area occupied by coniferous plantations. Hereafter a brief description, of the most representative shrub communities and perennial grasslands in the landscape of the study area is given, following Aguiar (2001), from later to initial ecological succession.

5.5.3.1 Tall shrub vegetation

Within this group, different shrub communities of the *Cytisetea scopario-striati* class occur, according to local climatic and soil characteristics, and to the direction (regressive or progressive) of the ecological succession. These communities can be subserial of both forest associations.

- The ***Genisto falcate-Ericetum arboreae*** is a pre-forest community, typical of regressive successions, dominated by *Erica arborea*, *Cytisus scoparius* and *Genista falcata.*
- The ***Cytiso scoparii-Genistetum polygaliphyllae cytisetosum multiflori***, and the ***Cytiso striati-Genistetum polygaliphyllae cytisetosum multiflori*** are linked to deep soils (pre-forest soils), and typically colonize old fields (progressive succession). *Cytisus scoparius, Cytisus striatus* and *Genista florida* subsp. *polygaliphylla* dominate the communities, with regular presence of *Cytisus multiflorus*. In the study area these communities are characterized by the presence of species of the *Cisto-Lavanduletea* (*Thymus mastichina* variant).
- The ***Lavandulo sampaioanae-Cytisetum multiflori*** is a heliophilous community that colonizes abandoned cultivated soils. It replaces the *Cytiso striati-Genistetum polygaliphyllae cytisetosum multiflori* in the thermophilous portions of the *Q. pyrenaica* series.
- The ***Genisto hystricis-Cytisetum multiflori*** is adapted to more shallow soils, and it is more associated to the sclerophyllous oak forests series. The characteristic species of the association are: *Genista hystrix*, *Cytisus multiflorus, C. striatus, C. scoparius* and *Pteridium aquilinum*.

5.5.3.2 Perennial grasslands

These communities' types can be part of different phytosociological classes, according to soil moisture content along the year, drainage characteristics and nutrients content. A characterization of part of these grasslands (*Stipo-Agrostietea*), together with synanthropic meadows of *Molinio-Arrhenatheretea* and *Nardetea* is provided in subchapter 6.1.1.

5.5.3.3 Heliophilous shrub communities

These communities belong to either *Calluno-Ulicetea* or *Cisto-Lavanduletea* classes.

As to the former, these are communities dominated by ericaceous and leguminous nano-phanerophytes and represent a resilient regression subserial stage of both forest types, very frequent in the study area.

- The ***Genistello tridentate-Ericetum aragonensis* var. of *Cistus ladanifer*** occurs typically on shallow acid soils, but also on deeper soils as the result of colonization of old agricultural fields. These communities can be dominated by *Erica australis* subsp. *aragonensis*, *Pterospartum tridentatum* subsp. *lasianthum*, *Halimium alyssoides* and *Erica umbellata*.

As to the *Cisto-Lavanduletea* communities, they occur on very shallow soils, either incipient or the result of erosion, and are dominated by species of the *Cistaceae* family and of the genus *Lavandula* and *Thymus*.

- ***Cistus ladaniferi-Genistetum hystricis*** communities are generally dominated by *Cistus ladanifer*, *Genista hystrix* and *Thymus mastichina*, and are subserial of *Q. rotundifolia* forests, but can also occur within the domain of the *Q. pyrenaica* series.

5.5.4 Edaphohygrophilous vegetation

The edaphohygrophilous vegetation occurs in a relatively narrow band (due to the schistic lithology and related geomorphology of the area) along the rivers and minor watercourses. The hygrophilous series with greater expression at the landscape scale is the *Galio broteriani-Alneto glutinosae* Sigmetum, in which alder forests represent the climactic stage. Bramble communities of the *Rubo ulmifolii-Rosetum corymbiferae*, willow communities (*Salix x* pseudosalviifolia), *Magnocaricetalia* and rush communities (*Juncion acutiflori*) are the natural subserial communities of that forest type.

The area of potential distribution of the alder series, and frequently also the adjacent area is occupied by semi-natural meadows: for centuries, resident people (of this and similar mountainous areas) area have enlarged the area of relatively permanent soil moisture through traditional irrigation techniques in order to enhance pastures and hay production along the year (see sub chapter 6.1 for more details). These anthropogenic meadows are grouped within the *Molinio-Arrhenatheretea* class.

6. Vegetation communities in focus

Within the present thesis I analysed deer use of two vegetation community types: semi-natural meadows and forest communities. Hereafter, a characterization of these communities is given, together with a brief delineation of the related studies.

6.1 Semi-natural meadow communities

The continuous browsing and grazing of the Pleistocene herbivorous mega-fauna had certainly influenced plant species evolution and vegetation dynamic in Europe (Vera 2000). Alongside with fire, the impact of that mega-fauna was extensive and strong enough to become visible on the pollen registries (Svenning 2002), therefore in the vegetation landscape itself. Up to 6000-3000 BC, before human impact began to be evident, western Europe was covered by forests with a varying degree of openness according to the local pressure of herbivores (van Wieren 1995). After the last glaciation, and particularly in the last 5000 years, the European man impacted species and ecosystems far more greatly. The localized openings in the forest matrix, where large herbivorous once grazed, gave place to agriculture areas and a large grassland-scrubland matrix, where domestic cattle fed. Natural and semi-natural grasslands expanded when human activities and domesticated livestock substituted the natural role of large herbivores. European landscapes and their different vegetation communities have been profoundly modified by human activities in the past. Nowadays, the traditional extensive agriculture and livestock production has been replaced in the lowlands and more fertile areas by intensive crop production and farming. In marginal areas, where traditional and extensive agriculture and farming had persisted, a progressive land abandonment has been occurring since the post war period, due to human migration fluxes towards more productive areas and to the ageing of the population (MacDonald et al. 2000). Mediterranean mountainous areas are a very good example of this phenomenon (Gonzalez-Bernaldez 1991; MacDonald et al. 2000; Chauchard, Carcaillet, & Guibal 2007).

The typical rural landscape in these areas is the result of many centuries of traditional extensive agriculture and farming and is characterized by a heterogeneous and fragmented vegetation and land use mosaic (Pôças, Cunha, & Pereira 2011), where meadows play an important role. Hay-meadows and pastures are semi-natural plant communities, meaning that their rich plant species assemblage reflects the hygrophilous regional species pool (Moreira, Aguiar, & Pires 2001), but they persistence and also their species diversity is linked to traditional management techniques. Semi-natural meadows of the Portuguese central and Northern mountain systems, “lameiros”, belong mainly to the *Molinio-Arrhenatheretea* phytosociological class, but may also include communities of the *Nardetea* (“Cervunais”) and of the *Stipo-Agrostietea* classes.

Meadows system normally develops alongside or in the proximity of rivers, and is maintained by traditional irrigation techniques, which consist in a network of ditches that channel water allowing it to spread over the entire meadow surface. This continuous irrigation permits an extended vegetative season since it satisfies plants water requirements during the dry season, and prevents frost during cold winters through the thermo-regulator effect of the water sheet (“rega de lima”). Conditional to water availability and thus to the extent of irrigation throughout the year, meadows can be classified as irrigated meadows, deficit irrigated meadows and non-irrigated meadows. Plant species composition reflect soil moisture gradients, and thus water availability (irrigation type) as well as microtopography (Aguiar 2001): from wettest to drier soils, within the *Molinio-Arrhenatheretea* class, *Juncion*, *Cynosurion* and *Arrhenatherion* communities are to be expected. Plant communities of the *Stipo-Agrostietea* class can be included within the meadows system, among the non-irrigated ones, or marginally, meaning that they are confined further away from the watercourses or irrigation ditches, frequently on the steeper sides of a meadow, i.e. on drier areas. Mountain meadows are normally grazed from the end of summer to the beginning of spring, when they are set aside until hay harvesting in summer.

The meadow system, beside the importance for the local economy, enhances landscape diversity by contributing to the mosaic of land uses, functions as a buffer zone against wildfires, prevents soil erosion, thanks to the continuous cover and to the enhanced infiltration. Lameiros represent a highly biodiverse ecotope: meadows are very rich in plant species and support a vast variety of organisms. Meadows importance is underlined by their classification within the Habitats Directive of the Natura 2000 network (Council of the European Communities 1992a; European Commission 2007): *Juncion* communities correspond to the habitat 6410 and *Arrhenatherion* communities to the 6510. *Nardus stricta* meadows are also classified within the Habitats Directive (priority habitat 6230*).

The system is disappearing in most areas, due to declining of the traditional extensive pastoralism, related to socio-economic reasons, including low agriculture incomes and old age of residents. Exceptions to this trend occur, for example, in Montalegre region (Northern Portugal), where Pôças et al. (2011) found an increase of 60% of the total cover of meadows along the past 30 years, which has been favoured by the implementation of European agro-environmental and livestock supports, the last one specifically with the aim of conserving the local Barrosã cattle breed. However, the general tendency encountered in marginal mountainous areas, and specifically in the area of the Montesinho Natural Park that this work considered, is of progressive abandonment.

Considering that this group of plant associations is strictly related to human specific activities (fertilizing, traditional watering, hay-harvesting and livestock grazing), the progressive land abandonment is bond to display effects on meadows floristic composition and on nutritional quality. For example, when management ceases, meadows closer to the water line are frequently colonized by species more typical of the surrounding fringe, as for example *Brachypodium rupestre* (Aguiar 2001). This situation is frequent in the study area: 14% of the floristic relevés realized in the sampled meadows belong to the Community of *B. rupestre*, described by Aguiar (2001). Conversely, when meadows are located further away from the water line, or on steeper slopes, and irrigation ceases, meadows develop towards communities of the *Stipo-Agrostietea* class: 30% of the relevés were classified as Community of *Avenula sulcata*, due to the dominance of this grass species. Progressive colonization of woody species (both shrubs and trees species) varies above all according to the local potential natural vegetation series, reflecting soil characteristics and moisture. For example, in a recent phytosociological study of the Paiva River's hydrographical basin (Monteiro-Henriques 2010), the author was able to describe a novel ash community, *Omphalodo nitidae-Fraxinetum angustifoliae*, that has taken advantage of the land abandonment process, re-colonizing abandoned meadows and fields that were occupying its potential area of distribution.

Preservation of traditional land-use system, such as semi-natural meadows has been a Nature conservation goal in Europe (WallisDeVries 1995; Plieninger, Höchtl, & Spek 2006) where conservation has been conducted through active management, namely by financial support to traditional agriculture and farming (van Wieren 1995) through agro-environmental schemes (regulation EU 2078/ 92; Council of the European Communities 1992b). Land-abandonment, however, is progressing in most of these marginal areas and becomes crucial to assess how wildlife and particular wild herbivores may use these areas. The use of abandoned farming systems by wildlife has been investigated elsewhere (e.g. boma in Africa; Muchiru, Western, & Reid 2008), but there is a lack of knowledge on the topic in Europe and particularly in Mediterranean areas.

Some research has been conducted on how wildlife herbivores may affect the persistence and diversity of grasslands in landscape through their effects on plant community dynamics: Tschöpe et al. (2011) assessed the impact of red deer grazing on grasslands in Germany, concluding that it affected successional pathways and species composition and delayed woody encroachment of open habitats. Effects of grazing, treading, dunging and urination on plant community depend on the herbivore species and on the grazing pressure of its population. High herbivore pressure depresses species diversity in grasslands, while a moderate grazing may enhance it (van Wieren 1995; Olff H. & Ritchie M.E. 1998; Bugalho et al. 2011a). Herbivores may also act as important seed disperser (e.g. Malo & Suárez 1996; Shiponeni & Milton 2006), directly affecting plant succession. Local environmental conditions, specifically water availability and soil characteristics, also influence the final outcome of grazing effects: grasslands on drier and poorer soils are more prone to biodiversity loss (Olff H. & Ritchie M.E. 1998).

As land abandonment trends are likely to continue, especially in the more marginal areas of mountain systems, it is crucial to know how wild mammalian herbivores may interact with dynamics of land abandonment. In this thesis I addressed this issue, specifically considering how wildlife species (red and roe deer) are actually using the target vegetation types (semi-natural meadows), and which are the factors that most influence this use. In the following subchapters I present a brief description of the methodology used to characterize and classify the sampled meadows, together with the results obtained.

6.1.1 Vegetation surveys and meadows' characterization

When dealing with large mammalian herbivores, habitat selection at finer scales is ultimately affected by forage characteristics, like availability and quality (WallisDeVries, Laca, & Demment 1999; Illius et al. 2002; Moser et al. 2006), even though at coarser scales it may be constrained by other factors (e.g.: predation risk, if present; distance to water source; availability or distance to thermal shelter; etc.). To investigate fine scale use pattern a definition and classification of the "grain" of observation (Wiens 1989; Hobbs 2003 and see chapter 1.1) is necessary. Vegetation surveys are generally realized, with the objective of classifying vegetation "types" according to specific criteria that depend on the research aims. As the main objective of this thesis was evaluating whether phytosociology can be useful to wildlife management, we chose the scale of our investigation according to vegetation patterns as detected by phytosociological floristic relevé methodology.

I applied the methodology in a fine scale analysis of red deer spring use of meadows (chapter 8), as in Mediterranean areas deer behave as grazers during spring (Rodriguez-Berrocal 1978; Bugalho & Milne 2003; Lovari et al. 2007), when availability and nutritive quality of the herbaceous layer is higher. I aimed to assess how phytosociology contributed to explain deer use of meadows.

For this study (see details in chapter 8) I randomly selected 28 meadows from all those identified and mapped within the study area, and realized floristic records (i.e. relevé, see paragraph below) in each one, following the Zurich-Montpellier school methodology (Mueller-Dombois & Ellenberg 1974). Since the objective was to analyse deer use pattern of meadows patches, and not describing the range of occurring vegetation types, I used random sampling instead of the preferential sampling, which is generally used by phytosociologists for description and classification purposes (see discussion in subchapter 2.2.2.1).

The phytosociological relevé consists in recording all plant taxa occurring in the vegetation patch (that is, the visually identified community): generally the inventorying is constrained to a reduced portion of the patch, called minimal area, which includes the overall species diversity. Although standardized areas, or range values, have been proposed for the different vegetation types (Chytrý & Otýpková

2003), the usual procedure (adopted in our survey) consists in beginning the relevé in a chosen point/area and expanding it until no new species is found. An abundance-cover value is ascribed to each taxon, following the Braun-Blanquet scale (Braun-Blanquet 1932, see Table 4). Besides the floristic record, other data are gathered, typically: topographic variables, as slope, aspect, and elevation; lithology and soil apparent characteristics; physiognomic and structural traits of the sampled vegetation (see Braun-Blanquet 1932; Mueller-Dombois & Ellenberg 1974; Kent & Coker 1992; Capelo 2003, for details on the relevé procedure). The whole relevé process and its validity depend on the acquaintance of the researcher with the local flora and generally on his/her expertise.

Table 4 – Abundance-cover value scale adapted from Braun-Blanquet (1932).

Index	Description
5	Any numbers of individuals, with cover greater than 75%
4	Any numbers of individuals, with cover from 50 to 75%
3	Any numbers of individuals, with cover from 25 to 50%
2	Any numbers of individuals, with cover from 5 to 25%
1	Numerous individuals, with cover lesser than 5%
+	Few individuals, with small cover

The 50 relevés realized within the meadows-use research (chapter 8 and 9) followed the described procedure. Doubtful taxa were collected for posterior identification using national Floras (Franco 1971, 1984; Franco & Rocha Afonso 1994, 1998, 2003). The attribution of a phytosociological syntaxon to each of the relevés was attained through consultation of bibliographic records (Teles 1970; Aguiar 2001) and with assistance of phytosociology experts.

In Table 5 is given a summary of the main characteristics of the 28 sampled meadows, specifically: mean elevation, management situation (see 9.3.3.3 for details) and recorded vegetation communities (phytosociological classification). A brief description of the communities, together with the related relevés, is given in the following subchapters.

Table 5 – Characterization of the sampled meadows. Elevation data were retrieved from the SRTMv4 Digital Elevation Model (CGIAR-CSI 2008). In the Vegetation communities column: CYN = *Agrostio castellanae-Cynosuretum cristati*; JUNC = *Hyperico undulati-Juncetum acutiflori*; BRACHY = Community of *Brachypodium rupestre*; AVESU = Community of *Avenula sulcata*; NARD = Community of *Festuca rothmaleri* and *Nardus stricta*; ARRH = Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*.

Meadow	Elevation (m)	Management status	Relevé no.	Vegetation communities
1	819	used	1	CYN
2	803	used	2/3	CYN/JUN
3	822	recently abandoned	4/5	NARD/AVESU
4	811	abandoned	6/7	UNCLASS/JUN
5	758	used	8/9	CYN/UNCLASS
7	784	recently abandoned	10/11	AVESU/NARD
8	733	abandoned	12/13	AVESU/CYN
9	721	abandoned	14	AVESU
11	652	abandoned	15/16	UNCLASS/BRACHY
12	659	abandoned	17	BRACHY
14	660	abandoned	18/19	AVESU/BRACHY
16	687	used	20/21	CYN/NARD
17	708	recently abandoned	22	CYN
18	765	abandoned	23/24	AVESU/BRACHY
19	706	used	25/26	CYN/CYN
21	754	recently abandoned	27/28	AVESU/CYN
22	784	used	29/30	AVESU/CYN
23	783	used	31/32	CYN/AVESU
24	800	abandoned	33/34	BRACHY/AVESU
25	739	recently abandoned	35/36	AVESU/JUN
29	812	abandoned	37/38	ARRH
30	824	abandoned	39	ARRH
31	817	abandoned	40/41	ARRH
32	787	abandoned	42/43	CYN/AVESU
33	733	abandoned	44/45	NARD/AVESU
34	723	abandoned	46/47	AVESU/BRACHY
35	693	recently abandoned	48	CYN
39	828	abandoned	49/50	AVESU/BRACHY

6.1.1.1 Community of *Avenula sulcata*

The *Avenula sulcata* community was the most frequent in the sample. It typically occurs in marginal and steeper areas of managed meadows, not reached by the watering ditches, spreading its occupation area after management ceases, especially in meadows located further away from the watercourses, where lack of irrigation determines a substantial drop in the soil moisture balance, which is followed by a change in the floristic composition. I did not encounter a match in the existing literature with already classified community. I named it Community of *Avenula sulcata*, ascribing it to the *Agrostion castellanae* alliance of the *Stipo giganteae-Agrostietea castellanae* class, considering the characteristics of these meadows, the fidelity and dominance of *Avenula sulcata*, characteristic species of this alliance.

Table 6 – Community of *Avenula sulcata*.

Relevé no.	5	10	12	14	18	23	27	29	32	34	35	43	45	46	49
Cover (%)	90	95	100	85	100	100	90	95	95	100	100	95	100	100	100
Minimal area (m^2)	15	10	20	20	15	30	20	20	30	15	25	20	40	20	30
Avenula sulcata	4	5	3	3	3	5	3	4	4	3	4	3	4	3	5
Sanguisorba minor	2	+	.	2	+	+	2	3	1	2	.	3	1	+	3
Vicia sp.	.	1	1	+	.	.	3	+	1	.	+	2	+	.	+
Hieracium pilosella	.	+	.	.	.	+	2	.	2	1	1	.	1	.	1
Rumex angiocarpus	.	+	+	.	.	+	.	.	+	+	+	+	.	+	.
Hypericum perforatum	.	+	.	2	2	.	.	.	+	.	.	+	+	+	.
Agrostis x fouilladei/capillaris	.	.	.	2	1	5	.	.	3	.	.	.	3	.	3
Achillea millefolium	.	.	1	.	.	+	+	+	.	3	.	.	.	3	.
Trifolium dubium	.	.	.	.	.	.	1	2	+	+	+	.	.	.	1
Holcus lanatus	.	.	+	.	.	.	.	+	.	.	2	+	.	1	+
Dactylis glomerata	.	.	.	.	1	1	3	.	2	1	.	.	.	.	.
Galium sp.	.	.	.	.	2	.	1	.	.	.	.	2	3	+	.
Bromus hordeaceus	.	.	.	.	.	.	+	+	.	.	+	1	.	.	+
Jasione montana	.	.	.	.	.	+	.	.	1	+	.	+	+	.	.
Hypochaeris radicata	+	.	.	.	.	+	+	+	.	.	+	.	.	.	.
Plantago lanceolata	.	.	.	.	.	.	.	+	.	.	+	+	.	+	+
Trifolium pratense	+	.	.	.	.	.	.	.	+	.	1	.	.	.	+
Orchis sp.	.	+	.	.	.	.	.	.	+	+	.	.	+	.	.
Anthoxanthum odoratum	.	4	+	.	.	.	.	.	.	.	.	.	.	+	.
Nardus stricta	.	.	.	.	.	3	+	.	+	.	.	.	.	.	.
Briza media	.	.	.	1	.	.	.	+	+	.	.	.	.	.	.
Ranunculus bulbosus	.	.	1	.	.	.	.	.	.	.	.	.	.	+	+
Crepis capillaris	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.
Lotus corniculatus	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.
Chamaemelum nobile	.	+	.	.	.	.	.	.	.	.	+	+	.	.	.
Serapias lingua	.	.	+	.	.	.	.	.	.	+	.	.	.	.	+
Sherardia arvensis	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.
Trifolium campestre	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.
Anthoxanthum amarum	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Avena barbata	.	.	.	.	.	.	.	.	.	+	.	3	.	.	.
Cruciata glabra	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.
Vulpia bromoides	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.
Arrhenatherum bulbosum	.	.	.	.	.	.	.	.	.	.	+	2	.	.	.
Aristolochia paucinervis	.	.	.	.	1	.	.	.	.	.	.	.	+	.	.
Carex binervis	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1
Andryala integrifolia	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.
Danthonia decumbens	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+
Daucus maritimus	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.
Filipendula ulmaria	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.
Hypericum humifusum	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Luzula forsteri	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.
Myosotis discolor	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.
Poa pratensis	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.
Polygala vulgaris	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.
Festuca rothmaleri	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.
Aira cupaniana	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Hypericum undulatum	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.
Adenocarpus complicatus	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Euphorbia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Lotus pedunculatus	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Thymus pulegioides	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Agrostis castellanae	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Bellis perennis	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carex divisa	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Carex leporina	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Carum verticillatum	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Echium rosulatum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Hispidella hispanica	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Hyacinthoides hispanica	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Linaria elegans	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Narcissus bulbocodium	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Ornithogalum concinnum	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Poa bulbosa	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Quercus pyrenaica (frut.)	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Ranunculus olissiponensis	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Rubus sp.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Salix sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Stellaria graminea	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Viola sp.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.

see indexes description in Table 4; "." corresponds to species absence

6.1.1.2 Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*

The community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum* belongs to the *Arrhenatherion* alliance of the *Molinio-Arrhenatheretea* class. Normally these communities are found further away from the streambed, and are characterized by soil moisture deficit during summer (Aguiar 2001). In the sample, these communities were all included in abandoned meadows, meaning that management practices, characteristics of these anthropogenic alliance (above all hay harvesting and livestock grazing), ceased. Consequently, they might be regarded as transitional communities, differing from the typical floristic composition recorded by Aguiar (2001). The sample showed an overall abundance of legumes species (*Vicia* sp. and *Trifolium* sp.).

Table 7 – Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*.

Relevé no.	37	38	39	40	41
Cover (%)	100	95	95	95	100
Minimal area (m^2)	15	15	20	30	20
Vicia sp.	1	5	+	5	4
Arrhenatherum bulbosum	3	3	3	3	4
Agrostis x fouilladei/capillaris	4	1	3	.	3
Bromus hordeaceus	.	1	+	2	.
Rumex angiocarpus	+	.	2	.	+
Hypochaeris radicata	1	.	+	.	+
Sanguisorba minor	+	+	1	.	.
Jasione montana	.	+	+	.	+
Trifolium campestre	.	.	2	.	2
Avena barbata	.	2	.	.	1
Galium sp.	1	.	2	.	.
Trifolium pratense	2	.	1	.	.
Holcus lanatus	1	.	1	.	.
Ranunculus olissiponensis	1	.	1	.	.
Carduus carpetanus	.	.	+	+	.
Chamaemelum nobile	.	+	.	.	+
Achillea millefolium	2	.	.	.	.
Anthoxanthum aristatum	.	.	.	.	2
Lotus pedunculatus	.	.	.	.	2
Dactylis glomerata	.	1	.	.	.
Festuca rothmaleri	.	.	1	.	.
Hypericum perforatum	.	.	.	.	1
Anthoxanthum odoratum	.	.	+	.	.
Briza media	+	.	.	.	.
Carex divisa	.	.	.	+	.
Carum verticillatum	+	.	.	.	.
Crepis capillaris	.	+	.	.	.
Echium rosulatum	.	.	+	.	.
Mentha suaveolens	+	.	.	.	.
Myosotis discolor	+	.	.	.	.
Ornithopus compressus	.	.	.	.	+
Petrorhagia nanteuilii	.	+	.	.	.
Plantago lanceolata	+	.	.	.	.
Potentilla erecta	+	.	.	.	.
Ranunculus bulbosus	+	.	.	.	.
Trifolium dubium	.	.	+	.	.
Viola sp.	.	.	.	+	.
Vulpia bromoides	.	.	.	.	+

6.1.1.3 Community of *Brachypodium rupestre*

According to Aguiar (2001), these hygrophilous communities, also belonging to the *Molinio-Arrhenatheretea* class, are quite frequent in the study area, and are a consequence of abandonment or mismanagement: in the specific case, all samples are included in abandoned meadows (28% of the relevés realized in the sampled abandoned meadows). When management ceases, *Brachypodium rupestre* rapidly colonize the field, coming from the surrounding vegetation (black alder riparian forests, for instance). The frequency of this community is probably due to the fact that most meadows are concentrated in a narrow band along the watercourses, and surrounded by wooded fringe vegetation, where the colonizing *B. rupestre* comes from.

The further ecological succession of these communities is characterized by the entrance of the pre-forest vegetation of the de *Rhamno-Prunetea* class, followed by either ash or alder forests, according to the soil moisture balance (Aguiar 2001)

Table 8 – Community of *Brachypodium rupestre*.

Relevé no.	16	17	19	24	33	47	50
Cover (%)	100	100	100	100	100	100	100
Minimal area (m^2)	15	25	20	15	10	20	20
Brachypodium rupestre	5	4	3	5	4	5	3
Galium verum	3	3	+	+	1	+	.
Achillea millefolium	2	.	+	1	1	+	1
Avenula sulcata	.	.	1	2	+	+	.
Hypericum undulatum	.	1	+	+	.	+	.
Sanguisorba minor	.	+	.	+	+	+	.
Rubus sp.	.	.	.	+	+	+	.
Viola sp.	+	.	+	.	.	.	+
Carex hirta	.	2	3	.	.	.	.
Dactylis glomerata	.	1	+	.	.	.	.
Polygala vulgaris	.	.	.	+	1	.	.
Thymus pulegioides	.	.	+	1	.	.	.
Euphorbia sp.	+	.	+	.	.	.	.
Myosotis discolor	.	.	.	.	+	.	+
Ranunculus olissiponensis	+	.	.	.	+	.	.
Trifolium dubium	.	.	.	+	+	.	.
Vicia sp.	.	.	.	.	+	.	+
Agrostis x fouilladei/capillaris	3	.	.	.	.	.	.
Carex muricata	.	.	3	.	.	.	.
Festuca rothmaleri	.	.	.	.	3	.	.
Gaudinia fragilis	.	.	2	.	.	.	.
Holcus lanatus	.	.	.	.	.	.	2
Mentha suaveolens	.	.	.	.	.	.	2
Aristolochia paucinervis	.	.	.	.	1	.	.
Juncus effusus	.	.	.	.	.	.	1
Senecio sylvaticus	.	.	.	.	1	.	.
Stellaria holostea	1	.	.	.	.	.	.
Arrhenatherum bulbosum	+	.	.	.	.	.	.
Bromus hordeaceus	.	.	.	.	.	.	+
Carex leporina	.	.	.	.	.	.	+
Crepis capillaris	.	.	.	.	+	.	.
Cruciata glabra	.	.	+	.	.	.	.
Cytisus scoparius	.	+	.	.	.	.	.
Daucus maritimus	.	.	.	+	.	.	.
Festuca trichophylla	.	.	.	.	.	.	+
Filipendula ulmaria	.	.	+	.	.	.	.
Fumaria reuteri	.	.	.	.	+	.	.
Hieracium pilosella	.	.	.	+	.	.	.
Hypericum perforatum	.	.	.	.	+	.	.
Jasione montana	.	.	.	+	.	.	.
Lonicera hispanica	.	.	.	.	+	.	.

Luzula forsteri	.	.	.	.	.	.	+
Chamaemelum nobile	.	.	.	.	+	.	.
Nardus stricta	.	.	.	+	.	.	.
Omphalodes nitida	+	.	.	.	.	.	.
Ornithogalum baeticum	.	.	.	.	.	+	.
Poa pratensis	.	.	+	.	.	.	.
Pteridium aquilinum	.	.	.	+	.	.	.
Quercus pyrenaica (frut.)	.	.	.	+	.	.	.
Rhinanthus minor	.	.	.	.	.	.	+
Rumex acetosa	.	.	.	.	+	.	.
Rumex angiocarpus	.	.	.	.	.	+	.
Silene latifolia	+	.	.	.	.	.	.
Stellaria graminea	.	.	.	+	.	.	.
Taraxacum sp.	.	.	.	.	+	.	.

6.1.1.4 *Agrostio castellanae-Cynosuretum cristati*

The *Agrostio castellanae-Cynosuretum cristati* association, belonging to the *Cynosurion* alliance of the *Molinio-Arrhenatheretea* class, is typical of the more productive hygrophilous meadows, currently under traditional management, mainly grazing and hay harvesting (Aguiar 2001). Of the sampled communities, only two were found in abandoned meadows (relevés no. 13 and 42) and four in meadows only recently abandoned (relevés no. 22, 25, 26 and 48).

Table 9 - *Agrostio castellanae-Cynosuretum cristati.*

Relevé no.	1	2	8	13	20	22	25	26	28	30	31	42	48
Cover (%)	100	100	100	100	100	100	100	100	100	100	100	100	100
Minimal area (m^2)	40	20	20	10	20	10	20	25	15	20	20	10	10
Holcus lanatus	4	4	5	+	4	1	4	5	4	4	5	4	2
Trifolium pratense	1	2	+	.	3	+	1	+	4	2	1	+	1
Anthoxanthum odoratum	.	.	3	4	3	3	.	+	3	4	4	2	3
Sanguisorba minor	3	1	+	.	1	3	+	2	.	+	1	.	+
Cynosurus cristatus	3	.	3	.	1	.	.	4	3	3	2	2	3
Plantago lanceolata	3	3	.	.	+	.	+	+	+	1	.	+	2
Festuca rothmaleri	4	4	2	.	+	.	.	+	+	1	.	1	.
Ranunculus bulbosus	1	+	1	+	.	+	.	+	.	.	.	+	1
Carum verticillatum	.	.	+	1	+	+	.	+	+	.	.	2	.
Briza media	+	.	2	3	.	2	.	.	2	2	.	.	.
Trifolium dubium	+	4	+	.	3	.	.	3	+	.	.	.	.
Hypochaeris radicata	2	+	.	+	.	.	.	1	+	.	+	.	.
Rhinanthus minor	3	2	.	.	1	.	+	+	.	.	.	.	.
Serapias lingua	3	+	.	+	.	.	.	.	+	.	.	+	.
Rumex acetosa	+	+	1	.	+	.	.	.	.	+	.	.	.
Achillea millefolium	.	3	.	.	.	1	.	.	.	+	2	.	.
Galium sp.	.	.	.	.	+	.	.	.	.	+	2	+	.
Hyacinthoides hispanica	+	+	+	.	.	.	.	.	.	.	.	+	.
Bromus hordeaceus	.	.	+	.	.	.	5	1	.	.	.	.	.
Nardus stricta	.	.	3	+	.	.	.	.	.	3	.	.	.
Avenula sulcata	.	.	.	+	.	3	.	.	.	.	+	.	.
Mentha suaveolens	.	.	.	.	.	.	.	.	.	1	1	.	+
Poa pratensis	.	.	2	.	.	.	+	.	.	.	.	.	+
Vicia sp.	.	.	.	.	2	.	+	.	+	.	.	.	.
Vulpia bromoides	3	.	.	.	.	.	+	.	.	.	.	.	.
Cruciata glabra	.	.	.	.	.	2	.	.	+	.	.	.	.
Bellis perennis	+	+	.	.	.	.	.	.	.	.	.	.	.
Dactylis glomerata	.	.	.	+	.	.	.	.	.	.	+	.	.
Geranium sp.	.	.	.	.	.	.	+	+	.	.	.	.	.
Ornithogalum baeticum	.	.	+	.	.	+	.	.	.	.	.	.	.
Saxifraga granulata	+	.	.	.	.	.	.	.	.	+	.	.	.
Trifolium repens	.	.	+	.	.	.	.	+	.	.	.	.	.
Thymus pulegioides	.	.	.	.	.	2	.	.	.	.	.	.	.
Brachypodium rupestre	.	.	.	.	.	1	.	.	.	.	.	.	.
Holoschoenus romanum	1	.	.	.	.	.	.	.	.	.	.	.	.
Polygala vulgaris	.	.	.	.	.	1	.	.	.	.	.	.	.
Rubus sp.	.	.	.	.	.	.	.	.	.	.	1	.	.
Rumex angiocarpus	.	.	.	.	.	.	.	.	.	.	.	.	1

Anthoxanthum amarum	.	.	.	+	.	.	.	.	.	.	.	.	.
Aristolochia paucinervis	.	.	+	.	.	.	.	.	.	.	.	.	.
Carex divisa	.	.	+	.	.	.	.	.	.	.	.	.	.
Carex leporina	+	.	.	.	.	.	.	.	.	.	.	.	.
Carex muricata	.	.	.	.	.	.	.	+	.	.	.	.	.
Carex nigra	.	.	.	.	+	.	.	.	.	.	.	.	.
Cerastium vulgare	.	.	+	.	.	.	.	.	.	.	.	.	.
Crepis capillaris	.	.	.	.	.	.	+	.	.	.	.	.	.
Dactylorhiza maculata	.	.	.	.	.	.	.	.	+	.	.	.	.
Hypericum humifusum	.	.	+	.	.	.	.	.	.	.	.	.	.
Hypericum perforatum	.	.	.	.	.	.	.	.	.	+	.	.	.
Jasione montana	.	.	.	.	.	.	.	.	.	.	+	.	.
Lotus corniculatus	.	.	.	.	.	+	.	.	.	.	.	.	.
Lotus glaber	.	.	+	.	.	.	.	.	.	.	.	.	.
Chamaemelum nobile	.	.	.	.	.	.	+	.	.	.	.	.	.
Mentha pulegium	.	.	+	.	.	.	.	.	.	.	.	.	.
Myosotis discolor	.	.	+	.	.	.	.	.	.	.	.	.	.
Petrorhagia nanteuilii	.	.	.	.	.	.	+	.	.	.	.	.	.
Potentilla erecta	.	.	+	.	.	.	.	.	.	.	.	.	.
Ranunculus olissiponensis	.	.	.	.	.	.	.	.	.	+	.	.	.
Rumex crispus	.	.	.	.	.	.	.	+	.	.	.	.	.
Sherardia arvensis	.	.	.	.	.	.	+	.	.	.	.	.	.
Stellaria graminea	.	.	.	.	+	.	.	.	.	.	.	.	.
Stellaria holostea	.	.	.	.	.	.	+	.	.	.	.	.	.
Viola sp.	.	.	.	+	.	.	.	.	.	.	.	.	.

6.1.1.5 *Hyperico undulati-Juncetum acutiflori*

The community of *Hyperico undulati-Juncetum acutiflori* belongs to the *Juncion acutiflori* alliance of the *Molinio-Arrhenatheretea* class and occurs on oligotrophic permanently humid soils, either in the vicinity of permanent streams or in meadows' depressions (Aguiar 2001).

Table 10 – *Hyperico undulati-Juncetum acutiflori*.

Relevé no.	3	7	36
Cover (%)	100	100	100
Minimal area (m^2)	15	10	15
Juncus effusus	3	3	4
Juncus acutiflorus	2	2	.
Holcus lanatus	.	1	1
Hypochaeris radicata	.	+	1
Trifolium pratense	+	.	1
Briza media	+	.	+
Ranunculus bulbosus	+	.	+
Carex leporina	.	.	4
Plantago lanceolata	.	3	.
Agrostis x fouilladei/capillaris	.	2	.
Daucus maritimus	.	2	.
Festuca arundinacea	.	.	2
Hypericum perforatum	.	2	.
Lotus pedunculatus	.	2	.
Mentha suaveolens	.	.	2
Parentucellia viscosa	2	.	.
Trifolium dubium	2	.	.
Trifolium repens	.	2	.
Carex binervis	.	1	.
Carex hirta	1	.	.
Myosotis stolonifera	1	.	.
Nardus stricta	.	.	1
Poa pratensis	.	.	1
Rubus sp.	.	1	.
Achillea millefolium	.	.	+
Bromus hordeaceus	.	+	.
Carex muricata	+	.	.
Dactylis glomerata	.	+	.
Filipendula ulmaria	.	+	.
Galium sp.	+	.	.
Hypericum undulatum	+	.	.
Myosotis discolor	.	+	.

Oenanthe crocata	.	.	+
Ranunculus flammula	+	.	.
Sanguisorba minor	.	.	+
Serapias lingua	.	+	.

6.1.1.6 Community of *Festuca rothmaleri* and *Nardus stricta*

Nardus stricta communities (*Nardetea* class) occur on deep oligotrophic soils, generally humid during most of the year (Aguiar 2001). The Community of *Agrostis hesperica* and *Nardus stricta* (Aguiar 2001) was the more similar to the relevés, although without presence of *A. hesperica* and other species characteristic of the class. Consequently I named it Community of *Festuca rothmaleri* and *Nardus stricta*. From the four samples, only one (relevé no. 21) was currently grazed and specifically by sheep, whereas the others were abandoned or recently abandoned meadows.

Table 11 – Community of *Festuca rothmaleri* and *Nardus stricta*.

Relevé no.	4	11	21	44
Cover (%)	100	100	100	100
Minimal area (m^2)	20	20	10	15
Nardus stricta	4	5	5	4
Festuca rothmaleri	+	3	.	3
Holcus lanatus	3	2	1	.
Briza media	+	+	.	+
Hypochaeris radicata	1	+	.	.
Trifolium dubium	1	.	.	+
Carum verticillatum	.	+	.	+
Plantago lanceolata	+	.	+	.
Ranunculus bulbosus	.	+	+	.
Vicia sp.	.	.	+	+
Sanguisorba minor	4	.	.	.
Gaudinia fragilis	.	2	.	.
Carex leporina	.	.	1	.
Cruciata glabra	1	.	.	.
Aira cupaniana	.	.	.	+
Andryala integrifolia	.	.	.	+
Aristolochia paucinervis	.	+	.	.
Bellis perennis	+	.	.	.
Carex binervis	+	.	.	.
Hypericum perforatum	.	.	.	+
Jasione montana	.	.	.	+
Juncus acutiflorus	+	.	.	.

6.1.2 Forest communities

In the first half of the Holocene (about 10000 years ago), European landscape was dominated by forests, even though cover was interrupted by other vegetation types (different shrubs communities and grasslands) according to the disturbance regime and soil productivity. Canopy openness was probably related to abiotic disturbances, like fire, windstorms, and landslides, as well as to the foraging activity of large herbivores (van Wieren 1995; Vera 2000). Human impact on vegetation dynamic began to increase along the Neolithic, with the development of agriculture and itinerant farming. Both activities made large use of fire to obtain fields and pastures. The main result of human activities along the millennia has been the reduction of forest cover. Presently, only 9.4% of the territory in the Mediterranean basin is covered by forests (Marchand 1990 apud Blondel 2006). In Portugal, like in the rest of the Mediterranean basin, forest degradation, is also associated to millennia of anthropogenic fires and to the progressive deforestation connected to wood charcoal production and to the diverse uses of fire wood and timber that accompanied Portuguese history (Aguiar & Pinto 2007). Human use, however, have also contributed to create landscape diversity and have generated human-shaped systems of conservation value such as the cork oak montado (Blondel 2006; Bugalho et al. 2011) or the semi-natural meadow system addressed in the present thesis.

Deciduous oak forests were probably the dominant forest cover of central and northern Portugal in the past, with species variability related to biogeographic position and local bioclimatic and lithological characteristics. During the last millennia, sclerophyllous evergreen forests (for example, *Q. rotundifolia* forests in Portugal) have progressively replaced deciduous ones (as *Q. pyrenaica* forests) in great parts of their climatic domain in the northern Mediterranean basin, as a consequence of recurrent human use, such as clear- cutting, fires, and overgrazing (Blondel & Aronson 1999). This generalized replacement is related to ecological differences between the two forest types: deciduous oak forests require deeper forest soils and are more sensitive to water stress than evergreen ones, which instead are characterized by a greater resilience (recovery capacity after disturbance such as high re-sprouting capacity) and are better adapted to the low fertility and shallow soils resulting from the human-related long disturbance regime (Barbero et al. 1990), which characterized many Mediterranean mountains.

Considering the recent history of Portuguese forests, according to the Annex D of the National Plan for Forest Defence against Fire (PNDFCI, Resolution of the Ministry Council 2006), at the end of the nineteenth century forests covered only 7% of the mainland Portuguese territory. From the end of that century, through the first part of the following one, Portugal was involved in a huge re-forestation programme: by 1965, 33% of the territory was covered by forests, which consisted mainly of maritime pine stands (*Pinus pinaster*) (PNDFCI, Resolution of the Ministry Council 2006). In the first half of the past century, the landscape of the still populated rural areas was characterized by subsistence farming. Agriculture and pasture kept the land free of shrub vegetation while remnant forests were “cleaned” by livestock grazing.

The second half of the twentieth century, as previously said (Section 6.1), has been characterized by a continuous human migration fluxes from marginal rural areas towards the more productive coastal Portuguese cities and foreign countries. This progressive exodus has had conspicuous effects on vegetation landscape and dynamics in the abandoned areas. In subchapter 6.1 I have already debated on the semi-natural mountain meadows, the lameiros, and on the related impact of land abandonment. In this subchapter I focus on natural forest communities in the present rural situation of Portuguese central and northern mountainous areas.

The decline of rural activities that followed the demographic maximum in the fifties and sixties, began more than 50 years later than in central Europe mountains (Aguiar et al. 2009). Land abandonment has favoured the re-expansion of forests all over European mountains. In the Mediterranean area, the consequences of shrubs and trees colonization into old agricultural fields and meadows differ from central Europe: shrubs encroachment promotes landscape homogenization, structurally speaking, increasing connectivity among combustible patches and the risk of wildfires (MacDonald et al. 2000), especially were commercial pine stands are frequent (Gonzalez-Bernaldez 1991).

The study area in the Montesinho Natural Park is a good example of this situation. Observing the map of land use cover classes (Figure 5), the fragmentation and scarcity of natural forests is evident when compared to coniferous plantations or areas dominated by shrublands/grasslands matrix, which cover the majority of the territory. Crops and meadows are grouped together, but discerning the lameiros results easy thanks to their characteristic strip-like shape developed along waterlines. Undoubtedly the actual vegetation mosaic is currently different, as a gap of two decade has passed since the production of COS'90 land use cover maps (from which the mentioned map is adapted), and it is also more complex when observed at a finer scale (confront, for instance, with Figure 11).

Since the seventies and eighties wild range populations of red and roe deer have been re-colonizing the Montesinho Natural Park area, coming from the Spanish border (Salazar 2009). This trend results partly from land abandonment processes and consequent increase of favourable habitat for deer, particularly shrubland and wooded areas. It is therefore important understanding how these populations are using the present landscape vegetation mosaic, with special stress on the more vulnerable and less represented natural forests.

In this thesis I focused on three forest vegetation communities, pine plantations, deciduous oak forests and evergreen sclerophyllous oak forests, accounting for their representativeness at the landscape scale.

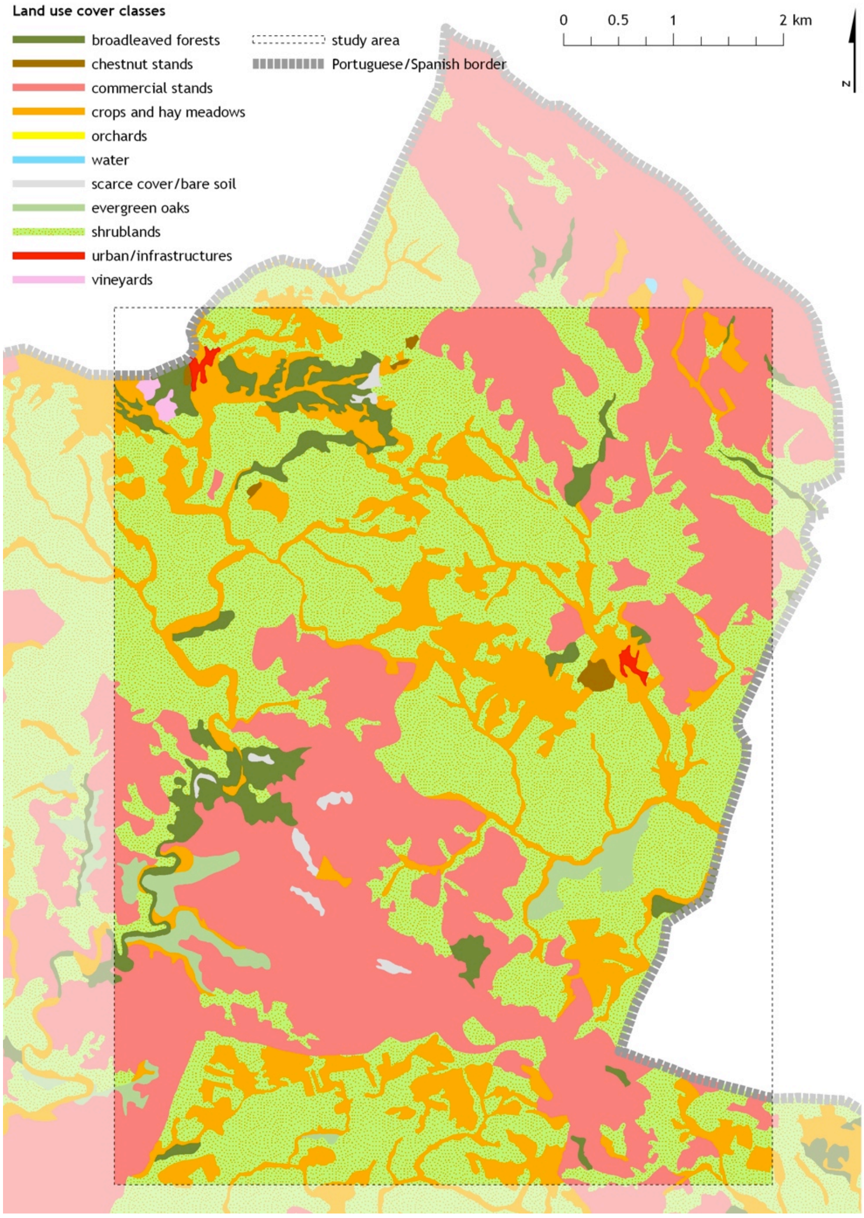

Figure 5 – Land use cover classes in the study area of Montesinho Natural Park. The map was based on COS'90 map (Instituto Geográfico Português) and related legend with adjustments derived from field surveys.

Pine plantations are a widespread reality in Montesinho Natural Park (30% of the study area, based on the COS '90 map data), as well as in the rest of the Portuguese territory, North of Tagus River, and they have substituted previous land uses in most of the marginal areas. I was interested in evaluating the deer use of pine commercial stands as compared to natural oak forests. This knowledge may promote a better understanding of deer population distribution in a Mediterranean mountain area such as NPM, and generate guidelines for forest and wildlife management. Furthermore, the information gathered can be valuable to enhance the accuracy of studies on the potentiality for deer reintroduction programmes in areas where pine stands coexist with natural forest communities comparable to NPM ones.

Deciduous (*Quercus pyrenaica*) and evergreen (*Q. rotundifolia*) oak forests are the final (climactic) stage of the two vegetation series with distribution in the area of NPM (see subchapter 5.5). Other forest communities occur in the area, as, for example, black alder (*Alnus glutinosa*) and willow (*Salix salviifolia*) riparian forest communities, but their distribution, which is confined to a narrow string along watercourses, is not as representative at the landscape scale. Altogether, broadleaved forests comprise only 3% of the study area.

Although land abandonment has favoured the re-colonization of old agricultural fields, forests are still fragmented and patches are dispersed in a matrix of shrub communities (see Figure 5), which are related to different soil development stages and to different climatic optima. Both deer species forage abundantly on shrub vegetation, as attested by other researches findings (see subchapter 3.4 for references) and by the frequent browsing indexes found during fieldwork (Bellu, personal observation).

Forest patches are an important landscape component for the target deer species in the Mediterranean area, acting as shelter habitat, especially for the roe deer, which is generally more associated to wooded areas. Considering the preference of this species for deciduous over sclerophyllous oak forests (subchapter 3.4), another of the research aims was to assess if the co-occurrence of red deer is displacing roes towards sub-optimal habitats or if habitat overlaps exist. A more detailed description of the three forest types analysed is given in chapter 10.

7. Fieldwork methodology

7.1 Relative use assessment

Habitat use by wildlife can be assessed by direct and indirect methods. The former includes direct observation of animals or radio-tracking, and the latter observation of indexes of animal presence such as dung or tracks counts, or, when dealing with herbivores, indexes of browsing. Indirect methodologies are useful when dealing with species hard to detect either because of their temperament or low visibility (Newey et al. 2003). In the present thesis I used faecal pellet (dung) counts to investigate deer use of habitat.

7.1.1 Dung counts

Dung counts consist in recording the number of faecal pellet groups over certain habitats. In relation to cervids, a faecal pellets group can be defined as a group of more than six (Mayle, Putman, & Wyllie 2000), ten (Palmer & Truscott 2003), or even 16 (Marques et al. 2001) pellets of similar size and colour. Different counting methods exist: Faecal Standing Crop (FSC) which is a simple counting of dung groups within the sampling plots, allowing the conversion of pellet counts into estimates of population density, by applying a daily defecation rate and a dung decaying rate; Faecal Accumulation Rate (FAR), consists in periodic counting of faecal pellets in sampling plots that were previously cleaned from faeces (Laing et al. 2003; Smart, Ward, & White 2004; Campbell, Swanson, & Sales 2004). Population density estimates are derived from the formula:

$$D = \frac{m}{tr}$$

where D is population density estimate per km^2; m is the mean number of dung groups per km^2; t is either faecal group decaying rate (FSC) or the accumulation period (FAR); r is the daily defecation rate.

Although data on decaying rates are available for different species and for various vegetation and climate types (Massei, Bacon, & Genov 1998; Laing et al. 2003; Hemami & Dolman 2004), trials on local disappearance rates would permit more precise estimates of deer populations. Although more labour intensive, FAR technique has the advantage of not needing information on dung decaying-rate. The accumulation period should, however, be short enough to prevent decaying or disappearance of pellet groups during the interval between counts, which would lead to underestimation of population size. Though criticized by some authors (Collins & Urness 1981), this methodology can also give insights about habitat relative use (Loft

& Kie 1988; Latham, Staines, & Gorman 1996; Palmer & Truscott 2003; Borkowski & Ukalska 2008), when a stratified sampling design is adopted.

Within the present thesis, I investigated deer relative use of semi-natural meadows and different forest cover types. I was interested in evaluating if deer were selective at fine scales (patch or vegetation community level) and how patterns of habitat use varied seasonally. In the researches sampling design I choose random permanent plots, and applied FAR counting methodology, in order to assess deer seasonal use.

When applying FAR I used circular plots (4 m diameter) for assessing deer use of meadows and belt transects (2 x 10 m) to assess use of forest cover types. I chose different plot shapes to simplify both re-location of the plots and dung search in the two structurally different physiognomic types. Faecal pellets of red and roe deer were discriminated based on size and appearance (roe deer droppings are smaller).

Detectability of faecal pellet groups may vary with animal species, vegetation or litter ground cover, and thus seasonally. Usually larger herbivore species such as red deer yield higher detectability values than smaller species such as roe deer (Theuerkauf, Rouys, & Jedrzejewski 2008). In the present thesis I searched exhaustively both circular plots and belt transects minimizing potential differences in faecal detectability between species and vegetation communities.

8. Habitat use at fine spatial scale: How does patch clustering criteria explain the use of meadows by red deer?

8.1 Abstract of the chapter

Context: Large mammalian herbivores are keystone species in different ecosystems. To mediate the effects of large mammalian herbivores on ecosystems it is crucial to understand their habitat selection pattern. At finer scales, herbivore patch selection depends strongly on plant community traits and therefore its understanding is constrained by patch definition criteria.

Aims: Our aim was to assess which criteria for patch definition best explained use of meadows by wild, free ranging, red deer (*Cervus elaphus hispanicus*) in a study area in Northeast Portugal.

Methods: We used two clustering criteria types based on floristic composition and gross forage classes, respectively. For the floristic criteria, phytosociological approach was used to classify plant communities, and its objectivity evaluated with a mathematical clustering of the floristic relevés. Cover of dominant plant species was tested as a proxy for the phytosociological method. For the gross forage classes, the graminoids/forbs ratio and the percentage cover of legumes were used. For assessing deer relative use of meadows we used faecal accumulation rates (FAR).

Key results: Patches clustered according to floristic classification better explained selection of patches by deer. Plant community classifications based on Phytosociology, or proxies of this, used for characterizing meadow patches resulted useful to understand herbivore selection pattern at fine scales and thus potentially suitable to assist wildlife management decisions.

8.2 Introduction

Deer populations are generally expanding, both in numbers and geographic range, across the northern hemisphere (Cote et al. 2004) affecting the biodiversity and functioning of ecosystems (Huntly 1991; Rooney & Waller 2003; Hester et al. 2006; Bugalho et al. 2011). When managing habitats for conservation it is crucial to understand herbivore selection pattern. Herbivore decisions operate at different spatial scales, varying from the regional to the plant community level (Senft et al. 1987; Bailey et al. 1996). At broader scales, topography (Boyce et al. 2003; Kie, Ager, & Bowyer 2005), human disturbances (Coulon et al. 2008; Fang et al. 2009), predation risk (Fortin et al. 2005; Hebblewhite, Merrill, & McDonald 2005) or thermal and hiding cover (Mysterud et al. 1999; Partl et al. 2002) are key factors affecting habitat selection. At finer scales (patch and feeding station, sensu Bailey et al. 1996), selection is better explained by forage availability (Johnson, Parker, & Heard

2001) and quality (WallisDeVries et al. 1999; Illius et al. 2002; Moser et al. 2006). The criteria used for patch definition may affect the observer interpretation of herbivore behaviour (Kie et al. 2002; Bowyer & Kie 2006). According to landscape ecologists, a patch can be defined as a discrete spatial unit distinguished by discontinuities in one or more environmental variables (Wiens 1976). For example, a wet grassland community can be classified as a patch if its plant species composition differs from the surrounding drier grassland area. According to animal ecologists a patch is better defined by a change in the rate of a process or behaviour (Senft et al. 1987; Bailey et al. 1996) as, for example, a change in the foraging sequence of the animal or when it moves or relocates itself to continue feeding (Bailey et al. 1996). However, feeding patches are frequently defined according to the availability and quality of the plant food and mostly based on plant species composition (Clutton-Brock et al. 1982; Gordon 1989a; b; c). Red deer (*Cervus elaphus*) hinds in the island of Rhum, Scotland, for example, selected nutritive rich *Agrostis tenuis-Festuca rubra* and poor *Agrostis* sp.*-Festuca vivipara* communities during spring, while stags fed more on herb rich heath and poor *Agrostis-Festuca* communities throughout the year and on marsh communities in all seasons but summer (Gordon 1989a).

Controlled experiments, dealing with captive animals and artificially created patches, have shown that the selectivity of herbivores depends largely on forage characteristics such as plant digestible protein content (Langvatn & Hanley 1993), plant abundance, spatial distribution of preferred plant species (Dumont, Carrère, & D'Hour 2002; Chapman et al. 2007) or sward structure (Griffiths, Hodgson, & Arnold 2003). However, in natural or semi-natural conditions, environmental variability and forage heterogeneity are more difficult to quantify. In these situations the way a patch is defined is crucial to understand herbivore selection: the classification methods employed should be considered themselves object of study (Loehle 2011).

In the present study we analysed red deer spring use of meadows at a fine scale. Our aim was to assess if the plant community level, or patch level, sensu Bailey et al. (1996), was useful to detect patterns in deer use, and which criteria for patch definition permitted a better understanding of red deer use of meadows. We clustered patches according to two different criteria types: floristic classification and gross forage class ratios. Among the floristic criteria we tested the phytosociological classification, following the Zurich-Montpellier school methodology. To evaluate the objectivity of this approach, we also tested patch classification resulting from mathematical clustering using the total cover of plant species. To assess the possibility of using less time consuming methods to discriminate among plant communities, we clustered meadow patches according to the cover of dominant plant species only. For the gross forage type we used the ratio of graminoids and forbs and the percentage cover of legumes. This may contribute to consolidate criteria for defining patches when investigating herbivore habitat use pattern at fine scales.

8.3 Methods

8.3.1 Study area

The study area is located in the Natural Park of Montesinho (NPM), Northeast Portugal (Figure 6 a, b). NPM is a 75 000 ha area, included in the Pan-European network of protected areas Natura 2000. NPM is under the influence of Mediterranean bioclimate (Rivas-Martínez 2007) and it is characterized by a mosaic of deciduous (*Quercus pyrenaica*) and evergreen (*Q. rotundifolia, Q. suber*) oak woodlands, coniferous plantations (*Pseudotsuga menziesii*, *Pinus pinaster*), shrublands (*Erica australis*, *Pterospartum tridentatum*, *Halimium alyssoides*, *Cistus ladanifer* and *Cytisus* spp.), and a variety of perennial grasslands mostly belonging to the phytosociological classes of *Molinio-Arrhenatheretea, Nardetea* and *Stipo-Agrostietea* (Aguiar 2001). Mostly the soils are cambisols derived from pre-Ordovician schists (Aguiar 2001).

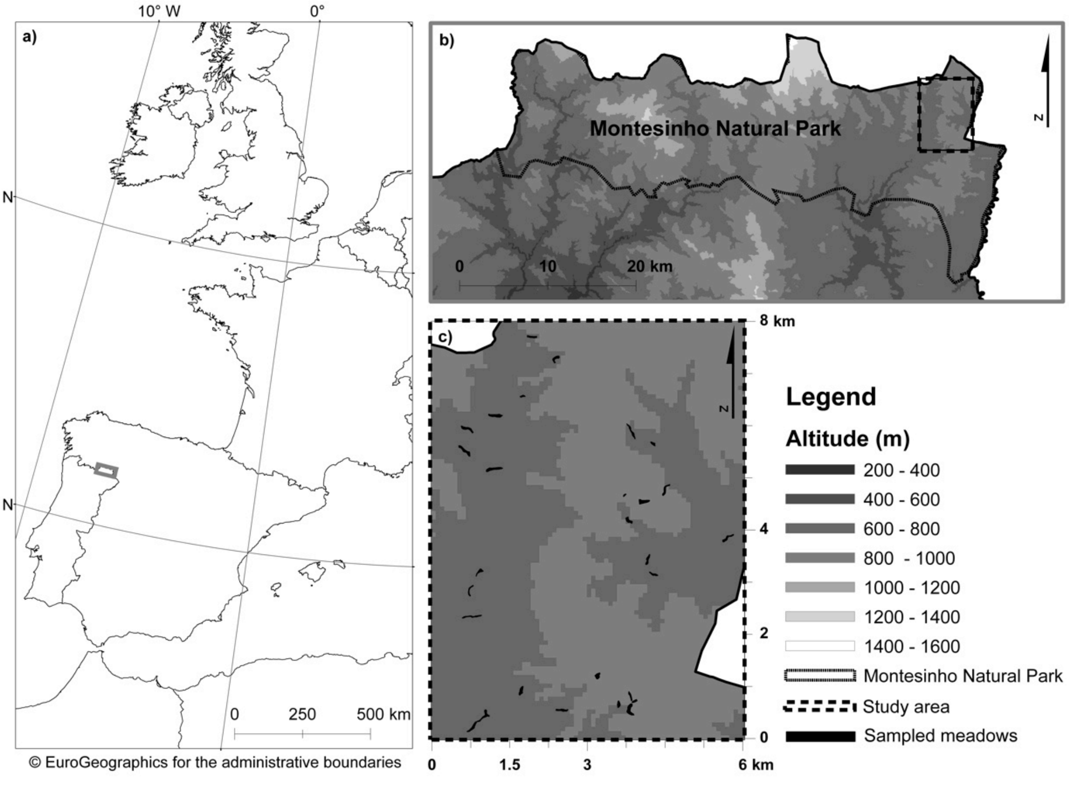

Figure 6 – Study area location: a) map of Western Europe highlighting the area of the research; b) Montesinho Natural Park boundaries (North-East of Portugal) and study area; c) sampled meadows location within the study area.

A system of semi-natural meadows occurs along watercourses and is maintained by local population through traditional irrigation techniques, extensive livestock grazing and hay harvesting. The plant species composition of these meadows varies with soil moisture (Aguiar 2001).

Red and roe deer (*Capreolus capreolus*) populations occur in the study area at 3 to 4 and 1 to 2 individuals/km^2, respectively (Paiva 2004). A stable population of wolves (*Canis lupus signatus*) is also present in the area.

8.3.2 Sampling units and sampling plots

We selected an area of 48 km^2 (6 x 8 km) in NPM using aerial photographs. All meadow units within this area were digitized using the ESRI ArcMap^{TM} 9.2 SP4 geographical information system software. A total of 192 polygons, each corresponding to a recognizable meadow unit, were identified and mapped (Figure 7a). From this, we randomly selected 28 polygons (Figure 6c).

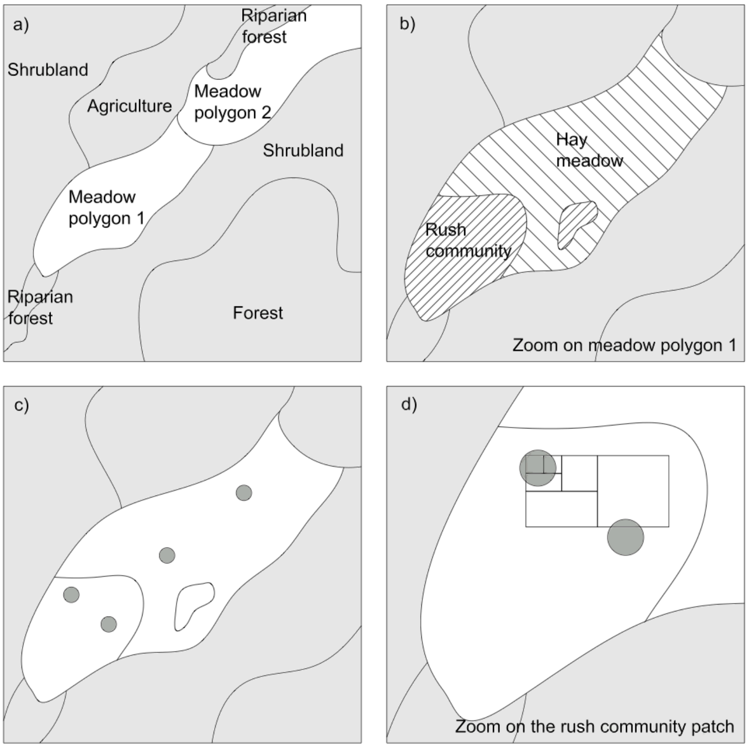

Figure 7 - Schematic representation of the sampling design steps: a) meadow polygons mapping; b) random selection of meadow polygons and visual recognition of plant communities; c) random positioning of FAR plots in each recognized vegetation patch; d) vegetation sampling (relevé minimal area schematized by squares and rectangles).

Within each of the sampled meadow polygons, the most spatially representative phytocoenosis (that is, a floristically and environmentally homogeneous community, sensu van der Maarel 2005a) were visually identified (Figure 7b). Four circular permanent plots (4 m diameter) for Faecal Accumulation Rate (FAR) sampling were randomly established in the field within each polygon; however when more than one phytocoenosis was present two permanent plots were randomly positioned in each of the two dominant ones (Figure 7c). All plots were geo-referenced by GPS and marked with a steel stick. We used circular plots for reducing the bias related to missing faecal pellet group (Neff 1968), and because they are easier to establish in the field as compared, for example, to belt transects (Noor, Habib, & Kumar 2010).

8.3.3 Vegetation sampling

Floristic relevés were conducted in each sampled phytocoenosis following the Zurich-Montpellier school methodology. All present vascular plant species were recorded, together with correspondent abundance-cover values (Braun-Blanquet 1932) relative to the minimal area, which comprised the floristic diversity of the plant community (see Mueller-Dombois & Ellenberg 1974 for details). Sampling was conducted in June (2008), when most plant species were flowering and easier to identify and because deer are dominantly grazers during this period (Bugalho & Milne 2003). The minimal area (Mueller-Dombois & Ellenberg 1974) of each relevé included at least one of the permanent plots and varied between 10 to 40 m^2 (Figure 7d).

8.3.4 Deer use of meadows

Faecal Accumulation Rate (FAR) was used as an indicator of spring use of meadow patches. FAR is a method commonly used to estimate deer abundances when data on dung decay is not available (Smart et al. 2004; Campbell et al. 2004) and can provide reliable information on relative habitat use (Palmer & Truscott 2003). All faecal pellet groups containing at least 10 identifiable pellets of similar size, colour and shape (Palmer & Truscott 2003) were counted in each of the circular permanent plots. Each of the 112 plots was visited twice, at the beginning and end of spring, and faecal pellets groups counted and removed in each visit.

8.3.5 Patch clustering criteria

The floristic relevés were clustered taking into consideration either floristic composition or gross forage types.

1) Floristic criteria

- Phytosociology

For the floristic criteria we used phytosociological classification: phytosociological units were attributed to each floristic relevé following mainly Aguiar (2001) but also expert knowledge.

- Total cover of plant species

To test the objectivity of the phytosociological approach, we also classified the floristic relevés adopting a common mathematical clustering procedure, considering the total cover of plant species.

We performed a k-means cluster analysis (KCA) (Hartigan & Wong 1979) on the 50 relevés using the function **kmeans** (package *stats*) in R Statistical Software (R Development Core Team 2010) with 10000 starts using random initial centres and k (number of partitions) from 2 to 25. To select the optimal number of clusters we used the indicator value index (IndVal), which is a measure of fidelity and relative abundance of a species in a specific cluster (Dufrêne & Legendre 1997). We applied the following cumulative criteria to select the optimal partition, using IndVal and the associated p-value obtained by a 10000 permutation test:

i) **max %:** select the partition(s) that maximizes the percentage of total clusters with at least one indicator species with p-value < 0.05;

ii) **min IndVal drop**: if more than one partition is selected in the previous step, the optimal partition is considered the one which minimizes the drop of IndVal.

IndVal was calculated in R Statistical Software (R Development Core Team 2010) using the function **indval** of package *labdsv* (Robert 2010). IndVal drop for each partition was calculated as follows:

$$1 - \frac{1}{n}\sum_{n=1}^{n} IndVal_{p-value<0.05}$$

where *n* is the number of indicator species with *p-value* < 0.05 in the partition and *IndVal* the respective indicator value of each species.

- Cover of dominant species

In order to test the possibility of discriminating among plant community using less labour intensive methodology, we clustered meadow patches using the same methodology as in the previous point, but considering only species with cover equal to or above 25% – Braun-Blanquet’s abundance-cover scale was converted into central cover percentage, following Monteiro-Henriques (2010), as shown in Table 12. The dominant species criteria relies on the assumption that grazers selectivity depends on the overall nutritive value of that patch, which is associated to the nutritive value of the dominant plant species in that patch (Dumont et al. 2002). Records of dominant plant species are also less time consuming which could optimize field sampling.

Table 12 – Central cover percentage of Braun-Blanquet's abundance-cover scale according to the proposal of Monteiro-Henriques (2010).

Index	Description	Central cover percentage
5	Any numbers of individuals, with cover greater than 75%	87,5 %
4	Any numbers of individuals, with cover from 50 to 75%	62,5 %
3	Any numbers of individuals, with cover from 25 to 50%	37,5 %
2	Any numbers of individuals, with cover from 5 to 25%	15,0 %
1	Numerous individuals, with cover lesser than 5%	3,0 %
+	Few individuals, with small cover	1,0 %

2) Gross forage types

- Graminoids/forbs ratio

Recorded species were divided into graminoids (including grasses, sedges and rushes) and forbs, which tend to differ in palatability and nutritive value (Shipley 1999; Clauss, Kaiser, & Hummel 2007). Forbs usually have higher digestibility value throughout the year, as compared to graminoids and heaths (Gordon 1989b).

The total cover of graminoids and forbs was estimated within each plant community and samples clustered according to the following range of graminoids/forbs ratios: group 1, less than 1; group 2, 1 to 2; group 3, 2 to 4; group 4, 4 to 10; group 5, more than 10.

- Cover of legumes

According to other researches, ruminants usually have higher voluntary intake rates for legumes as compared, for example, with grasses of similar digestibility (van Soest 1994; Fales & Fritz 2007). Therefore, the percentage cover of this forage class might affect deer use of meadow patches. Clusters were obtained by estimating total percentage cover of legumes within the sampled plant community and by applying the following threshold values for cover of legumes: group 1, 0; group 2, less than 2,5%; group 3, 2,5 to 10%; group 4, 10 to 25%, group 5, more than 25%.

8.3.6 Statistical analyses

We used Fisher exact tests (Fisher 1935, 1990) to assess if there were significant differences in FAR among patches defined by different criteria. We applied the **fisher.test** function (package *stats*) in R Statistical Software version 2.13.0 (R Development Core Team 2010). Means of faecal group counts within relevé plots were used. Because there was a high number of zero counts, as it frequently occurs when collecting such type of data (Gu & Swihart 2004), we firstly used presence-absence data and subsequently grouped the faecal data into three classes of abundance: 0; 0 to 1; and more than 1 faecal groups, in order to assess whether information relative to abundance was valuable.

Within each clustering criteria, patch type preference was evaluated using Jacobs modification of Ivlev's electivity index (Jacobs 1974).

For Jacobs index:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$$

r_i is the proportion of faecal pellets groups in patch type *i* within the total sum of occurrences, and p_i the proportion of patch type *i* within the existing meadows sample, which is assumed as representative of the study area. D_i varies from –1 (never used) to +1 (exclusively used) with values equal to or around zero meaning that patch type use can be considered random.

8.4 Results

8.4.1 Patch clustering criteria

A total of 50 relevés (available in the Online Resource 1 - Floristic relevés and information on the clusters according to the used criteria) were realized within the sampled meadows: 22 of them comprised two different phytocoenosis, whereas the remaining 6 were considered floristically homogeneous, and therefore were characterized by only one relevé.

Six different phytosociological units were ascribed to the floristic relevés while three of them had no clear phytosociological classification (Table 13) and were excluded from the statistical analyses.

Table 13 – Phytosociological units (associations and communities) attributed to the floristic relevés, relative abbreviations, number of relevés and plots in each cluster and corresponding groups according to the total cover of plant species and cover of dominant species criteria (K-m tot/dom).

Phytosociological unit	Abbreviation	no. relevés	no. plots	K-m tot/dom
Community of *Avenula sulcata*	AVESU	16	36	group1
Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*	ARRH	5	12	group2
Community of *Brachypodium rupestre*	BRACHY	7	16	group3
Agrostio castellanae-Cynosuretum cristati	CYN	12	28	group4
Hyperico undulati-Juncetum acutiflori	JUNC	3	6	group5
Community of *Festuca rothmaleri* and *Nardus stricta*	NARD	4	8	group6
Unclassified		3	6	group7

The groups generated using total cover of plant species and cover of dominant species (K-means clusters) were consistent with the phytosociological units; the three unclassified relevés were clustered in a single group (Table 13). Five patch clusters were obtained when considering the graminoids/forbs ratio and cover of legumes (Table 14).

Table 14 – Number of relevés and plots in each cluster of the graminoids/forbs ratio and cover of legumes criteria.

	gram/forb		% cover of legumes	
	no. relevés	no. plots	no. relevés	no. plots
group 1	8	18	9	18
group 2	12	32	18	44
group 3	14	30	11	24
group 4	6	12	5	12
group 5	10	20	7	14

8.4.2 Deer use of meadows

Red deer use of meadows patches, clustered according to the five criteria analysed is resumed in Table 15 (see raw data in Table 45 of the Appendix).

Table 15 – Red deer use of meadows patches clustered according to the five criteria (FPG: number of faecal pellet groups counted for each patch type).

Phytosociology, total cover of plant species and cover of dominant species

	AVESU	ARRH	BRACHY	CYN	JUNC	NARD	
	group1	group2	group3	group4	group5	group6	group7
presence	14	8	0	6	3	3	2
absence	22	4	16	22	3	5	4
tot FPG	18	19	0	10	4	3	5
mean FPG/relevé	1.1	3.8	0	0.8	1.3	0.8	1.7
mean FPG/plot	0.5	1.6	0	0.4	0.7	0.4	0.8

Graminoids/forbs ratio

	group1	group2	group3	group4	group5
presence	9	12	7	3	5
absence	9	20	23	9	15
tot FPG	17	20	11	4	7
mean FPG/relevé	2.1	1.7	0.8	0.7	0.7
mean FPG/plot	0.9	0.6	0.4	0.3	0.4

Cover of legumes

	group1	group2	group3	group4	group5
presence	5	14	3	6	8
absence	13	30	21	6	6
tot FPG	10	19	3	10	17
mean FPG/relevé	1.1	1.1	0.3	2	2.4
mean FPG/plot	0.6	0.4	0.1	0.8	1.2

There were significant differences among FAR considering patch clustered according to phytosociology (P-value$_{phyto}$=0.04, presence/absence data; P-value$_{phyto}$=0.05, with 0, 0-1 and >1 classes).

When considering phytosociological units, the patches belonging to the Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum* (ARRH) were selected more than randomly expected (D_{ARRH} = 0.64). Communities of *Hyperico undulati-Juncetum acutiflori* (JUNC) and *Avenula sulcata* (AVESU) were used randomly (D_{JUNC} = 0.08; D_{AVESU} = -0.02), whilst those of *Agrostio castellanae-Cynosuretum cristati* (CYN), and of *Festuca rothmaleri* and *Nardus stricta* (NARD) were selected less than randomly expected (D_{CYN} = -0.2; D_{NARD} = -0.23) and those of *Brachypodium rupestre* (BRACHY) were avoided (D_{BRACHY} = -1) (Table 16).

Similar results were obtained when considering clustering criteria based on both total and dominant plant species: the marginal differences were only due to the unclassified plots excluded from the phytosociological clusters (P-value$_{K\text{-}m}$=0.05, presence/absence data; P-value$_{K\text{-}m}$=0.06, with 0, 1 and >1 classes). Both clusters based on cover of legumes and ratio of graminoids/forbs did not explain red deer selection of feeding patches (P-value$_{leg\%}$=0.18, presence/absence data; P-value$_{leg\%}$=0.34, with 0, 1 and >1 classes; P-value$_{gram/forb}$=0.68, presence/absence data; P-value$_{gram/forb}$=0.82, with 0, 1 and >1 classes).

Table 16 – Jacobs's selectivity indexes (Di) for the clusters based on floristic criteria (total cover of plant species and cover of dominant species are consistent with phytosociological units, and the 7th group correspond to the three relevés not classified by phytosociology, as shown in Table 13), on graminoids/forbs ratio and on legumes cover.

Phytosociology	D_i	K-m tot/dom	D_i	gram/forbs	D_i	% legumes	D_i
AVESU	-0.02	group1	-0.03	group1	0.36	group1	-0.04
ARRH	0.64	group2	0.62	group2	0.24	group2	-0.08
BRACHY	-1	group3	-1	group3	-0.26	group3	-0.68
CYN	-0.2	group4	-0.21	group4	-0.3	group4	0.29
JUNC	0.08	group5	0.07	group5	-0.3	group5	0.43
NARD	-0.23	group6	-0.24				
		group7	0.18				

8.5 Discussion

Phytosociology has been commonly used to describe plant communities (but see Ewald 2003 for criticism) as, for example, the classified 'natural habitats' of the Natura 2000 network, a pan-European network of protected habitats (European Commission 2007), but less utilized in wildlife research (Putfarken et al. 2008). Most of the meadows patches (94%) analysed in this study could be ascribed to phytosociological units and there were significant differences in deer FAR among such units. Because sampling was random, floristic records were not expected to necessarily fall into "typical stands" (Roleček et al. 2007), hence including some marginal/recently-disturbed communities for which the identification of phytosociological units at the lower hierarchical level (i.e. association or "Community of") was not possible. The high classification power of phytosociology may have resulted from the physical characteristics of the analysed meadows, which are mostly "discrete" units, separated by traditional irrigation channels and natural waterlines, but also by stone walls or fences, and are characterized by a peculiar pattern of vegetation disturbance related to traditional management, which is distributed uniformly in space and regularly in time, namely: continuous irrigation (throughout the year), extensive livestock grazing from the end of summer to the beginning of spring, and hay harvesting in summer.

Patches defined by total cover of plant species or cover of the dominant ones were consistent with those based on phytosociology and produced similar results. Such findings showed the importance of dominant species in characterizing meadow plant communities particularly when the geographic domain is restricted, like in our survey. Results also suggested that less labour-intensive criteria, such as dominant species cover, might be used as proxies of phytosociological units. This is particularly useful in Mediterranean meadows, which usually have a high diversity of plant species (Puerto et al. 1990).

Red deer avoided *Brachypodium rupestre* dominated communities (BRACHY) and while selecting those dominated by *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum* (ARRH). *B. rupestre* is a grass species with a very low nutritive value (García 1992), which tends to form tall and thick tufts that are deterrent to grazing. ARRH communities are rich in species of medium to high nutritive value such as *Arrhenatherum bulbosum*, *Agrostis* x *fouilladei*, *A. capillaris*, and in our study area they were also rich in high quality legumes (e.g.: *Vicia* spp.). Additionally, patches of legumes shrubs, such as *Cytisus* spp. and *Adenocarpus* spp., heavily browsed by deer (Bellu, personal observation), occurred in the area surrounding ARRH patches. These factors may have also contributed to explain deer preference for these communities. Rush communities (*Hyperico undulati-Juncetum acutiflori* patches – JUNC) were used in proportion to availability (Table 16): red deer use of marshes, although random in our case, was shown to occur in temperate climate in the isle of Rhum, Scotland (Clutton-Brock et al. 1982). *Avenula sulcata* dominated communities (AVESU) were used also randomly. AVESU communities, although being the most frequent type in our sample, can be considered as marginal within the meadows system, meaning that they are usually confined farther from the water courses or irrigation ditches, frequently on the steeper sides of a meadow, i.e. on drier areas. These communities also tend to spread out when meadows located farther from the watercourses are abandoned, i.e. when management and above all irrigation ceases. *Agrostio castellanae-Cynosuretum cristati* patches (CYN) shown moderate avoidance. Most of the sampled CYN patches were within currently managed meadows, which, due to irrigation, have relatively constant soil moisture and consequently an extended vegetative season, both during summer and winter. Additionally, these communities are periodically grazed and manured by domestic cattle, generating high nutritive grazing lawns (Mládek et al. 2011): floristic composition comprises species such as the high quality grasses *Cynosurus cristatus*, *Holcus lanatus* or *Anthoxanthum odoratum*, forbs like *Plantago lanceolata*, *Sanguisorba minor*, and legumes such *Trifolium* spp. that are vey palatable for deer (Gordon 1988; Arsenault & Owen-Smith 2002; Vavra 2005), and thus would be expected to be preferred by deer. A possible explanation for this moderate avoidance could be the fact that the majority of CYN meadows are set aside during spring, i.e. they are not grazed, as part of the traditional grazing rotation. As a consequence the herb layer, rich in grass species, grows to maturity, and overall digestibility and palatability declines (Kilcher 1981). However, further experiments will be needed to test this hypothesis. In addition, the CYN type meadows which are not set aside are grazed by communitarian sheep flocks, which may act as a deterrent for deer grazing (Osborne 1984). Patches belonging to the Community of *Festuca rothmaleri* and *Nardus stricta* (NARD) were also used less than random expectation: NARD communities are characterized by dominance, or at least very abundant presence, of low palatable *Nardus stricta*.

There were no significant differences in FAR when using clusters based on graminoids/forbs ratio. The graminoids and forbs classes comprised a highly heterogeneous mixture of plant species, with different physical properties, chemical composition, and nutritional values (Hanley 1997). Oversimplification of the plant species diversity into broad categories such as graminoids/forbs may have prevented the evidence of patterns of selectivity, although patches with a higher proportion of forbs had higher selectivity indexes (groups 1 and 2, Table 16), as established by other authors (Dumont et al. 2005).

Similarly, no differences in deer FAR were found when using patches clustered according to cover of legumes, although those patches richer in legumes (groups 4 and 5, Table 16) were selected more than the others. Preference for patches with an increasing availability of nutritive species such as legumes has been recorded in different studies of ruminant nutritional ecology (Semiadil et al. 1995; Dumont et al. 2002).

Patch definition criteria affected results of deer meadow use pattern. Specifically, clusters based on floristic classification explained red deer use of meadow patches better than gross forage classes. Our results relate to a specific phenological season when meadow forage is growing and thus availability and nutritive quality of the herbaceous layer are higher. The richer and more abundant forage may have resulted in a higher selective ability at the patch level in our study. Possibly, deer perception of vegetation patches and thus their selective ability decrease with the declining of forage nutritional quality (Owen-Smith & Novellie 1982). Beyond plant species composition and abundances, patch selection by deer is affected by other factors, which were out of the scope of present study. For example, topography and associated elements as slope and aspect may affect plant phenological stages and forage nutritional value (Sharif & West 1968; Smallidge et al. 2010). Our results indicate that phytosociological classifications or proxy methodologies such as criteria based on cover of dominant plant species may prove useful in wildlife research, particularly at finer scales of analysis. However, given the hierarchical structure of foraging behaviour (Senft et al. 1987; Bailey et al. 1996), other factors operating at broader scales must be integrated when explaining the foraging behaviour of large mammalian herbivores.

9. Multiple scale factors affecting red and roe deer use of meadows in a Mediterranean environment

9.1 Abstract of the chapter

Context: Multi-scalar approaches are necessary to understand hierarchical ecological processes such as patterns of habitat use by wild herbivores that can be constrained by factors measured at different scales.

Aims: Our aim was to assess which factors influence red and roe deer use of semi-natural meadows, taking different scale features into account, from meadows characteristics, to landscape structure and composition, to larger scale variables.

Methods: As first step we took meso-scale landscape descriptors into account. Assuming that landscape scale features affect meadows use pattern, we have fixed the grain of the observation (sample unit) and changed the extent of the analysed neighbourhood (100, 250 and 500 m buffers), with the objective of assessing both the importance of the different landscape mosaic components and the more suitable size of the vicinity to be considered. In the second step, we introduced broader and finer scale variables to assess if they improved the understanding of meadow use pattern.

Key results: The composition of the neighbouring vegetation mosaic affected red and roe deer use of meadows. Red deer use was positively related to the area of grassland and meadow cover, and negatively related to cover of riparian forests. Roe deer use was negatively correlated to meadows cover and positively related to presence of cultivated patches and oak forest cover. While red deer preferred meadows surrounded by more open and lower vegetation, roe deer favoured those nearer to cover habitat. Both species preferred meadows located in more open topography. Red and roe deer response to landscape mosaic characteristics was stronger in the smallest and/or medium buffers. Macro scale variables did not affect sensibly meadows use, while micro-scale factors did.

9.2 Introduction

Considering the complexity of natural systems, it is important to use different scale of observation when analysing ecological processes, as the different variables that influence them operate at different spatial and temporal scales (Johnson 1980; Senft et al. 1987; Bailey et al. 1996).

Habitat use by wild herbivores varies with a number of factors affecting individual fitness at different spatial and temporal scales (Wiens 1989; Johnson et al. 2002). Variables like predation risk (Fortin et al. 2005; Hebblewhite et al. 2005; Dussault et al. 2005), distance to water sources (Weckerly 2005), or human disturbance (Jiang, Zhang, & Ma 2007; Jiang et al. 2008), affect habitat selection at broader scales, hence constraining individuals decision process at finer scales, where selection is more related to forage characteristics, such as availability (Johnson et al. 2001) palatability and nutritive value (WallisDeVries et al. 1999; Illius et al. 2002; Moser et al. 2006).

Choosing the right scale of observation is important to avoid misleading interpretations of the phenomenon in study, as it may happens when there is a mismatch between the researcher scale of observation and the animal perception of the environment (Wiens 1989; Levin 1992; Etzenhouser et al. 1998; Hobbs 2003). A multiple-scale approach allows better interpretation of habitat selection issues (Wiens, Rotenberry, & Van Horne 1987; Orians & Wittenberger 1991).

We investigated red and roe deer use of meadows in a mountainous Mediterranean environment in Northeast Portugal, using a multiple scale approach. Specifically, we assessed the influence on deer use of meadows of variables at different scales, spanning from meadows characteristics, namely management status and dominant phytosociological type, to landscape structure and composition, to broader scale variables related to human disturbance. In particular we aimed to reply to the following questions:

- How do landscape factors characterizing the area around meadows affect red and roe deer patterns of use? Which are the most significant factors affecting deer use of meadows? Do they differ between red and roe deer? Which scale of observation gives the best prediction?
- What is the influence of larger scale variables?
- What is the influence of finer scale variables?

To answer these questions, we used a multiple-scale approach, keeping constant the grain of our research (meadow unit) and varying the spatial extent of the variables assumed to affect deer response.

9.3 Methods

9.3.1 Study area

The study area is a rectangle of 48 km^2 (6 x 8 km) located in the Natural Park of Montesinho (NPM), Northeast Portugal (see Figure 8a, b). The Park is a 75 000 ha area, comprised within the Pan-European network of classified areas Natura 2000. Both red and roe deer populations occur in the park at densities of 3 to 4 and 1 to 2 individuals/km^2 respectively (Paiva 2004). A stable population of wolves (*Canis lupus signatus*) is also present in the study area, with an estimated density of 1.6 to 3.1 individuals/100km^2 (Moreira et al. 1997).

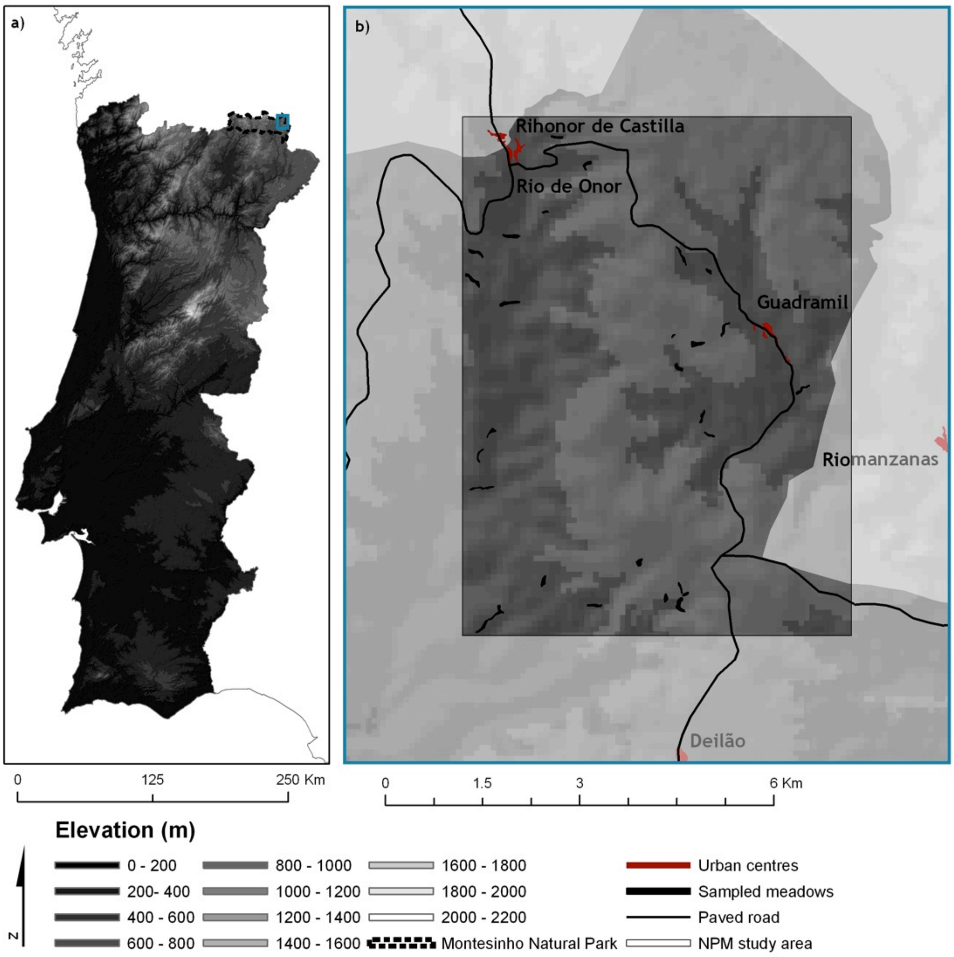

Figure 8 - Study area location: a) map of Portugal highlighting Natural Park of Montesinho boundaries and the area of the research; b) sampled meadows location within the study area.

The study area (Figure 8b) is characterized by a mosaic of deciduous (*Quercus pyrenaica*) and evergreen (*Q. rotundifolia, Q. suber*) oak woodlands, coniferous plantations (*Pseudotsuga menziesii*, *Pinus pinaster*), shrublands and grasslands. Natural and semi-natural plant communities have been classified following the phytosociological approach of the Zurich-Montpellier School (see Aguiar 2001). The area is under Mediterranean bioclimate (meso to supra-Mediterranean, sub-humid) according to the Rivas-Martínez's Bioclimatic Classification of the Earth (Rivas-Martínez 2007). Local soils are mainly cambisols derived from pre-Ordovician schists (Aguiar 2001).

Low density farming, agricultural and forestry activities occur in the area. The area is crossed by only one main road (N308, which links Portugal to Spain) but a well-developed network of forest trails allows motor vehicle access to great part of the territory.

9.3.2 Sampling units and sampling plots

The sampling areas were chosen within the traditional livestock farming system of meadows that, although declining, still occurs in the study area. This semi-natural meadow system develops typically along watercourses, and it is maintained by traditional management, comprising irrigation techniques, livestock grazing and hay harvesting. The plant species composition of these meadows depends on soil moisture gradients, which vary with water availability and microtopography (Aguiar 2001).

All meadow units within the study area were digitized using ESRI ArcMap 9.2 SP4 software and aerial photographs. A sample of 28 units (approx. 15% of the total), comprising both abandoned and still in use meadows, was randomly selected.

Within each of the selected meadows four permanent circular plots (4 m diameter) were randomly chosen and established in the field. Each plot centre was geo-referenced by GPS and marked with a steel stick and a coloured striped plastic band inserted into the ground, to overcome GPS resolution error and facilitate subsequent location. Circular plots were preferred over the belt transects because they are easier to establish in the field (Noor, Habib, & Kumar 2010), and a preliminary sampling revealed that faecal pellet search and cleaning was quicker.

Faecal Accumulation Rate (FAR) was used as an indicator of deer use of meadows, as it provides reliable information on relative habitat use (Palmer & Truscott 2003; Borkowski & Ukalska 2008). All faecal pellet groups, of red and roe deer, containing at least 10 identifiable pellets of similar size, colour and shape (Palmer & Truscott 2003) were counted in each plot. Red and roe deer pellets were discriminated according to size and appearance. To assess seasonal use of habitat by deer, plots were first cleared from deer faecal pellet groups, at the beginning of spring 2008, and subsequently sampled in June, September 2008 and February 2009, when faecal pellets groups were counted and removed during each visit.

9.3.3 Environmental descriptors

9.3.3.1 Landscape meso-scale descriptors

Buffers of 100, 250 and 500 m were marked around each meadow unit. Buffers of different radii were used to assess which size of the vicinity is more suitable to analyse the influence of landscape variables on deer use of meadows (Kie et al. 2002). Through aerial photo interpretation polygons corresponding to different vegetation types units were identified and digitized within each buffer area and subsequently ascribed to a cover type (Table 17) and a cover class (Table 18). Classification was based on photointerpretation and field surveys.

Table 17 – Cover types identified within the meadows buffers.

Cover type	Description	Abbreviation
agriculture	any crop	AGR
grasslands	perennial grasslands or long abandoned (more than 5 years) meadows	GRA
trails	unpaved country roads, mostly accessible by motor vehicles and other smaller tracks	TRA
commercial stands	generally pine stands – punctually other coniferous species or *Eucalyptus*	COM
fire bands	self explained	FBA
roads	paved road (N308, which links Portugal to Spain)	ROA
riparian	either alder or willow communities	RIP
meadows	managed or recently abandoned (less than 5 years) meadows	MEA
shrubland	different communities	SHR
burnt	different burnt vegetation communities	BUR
oak forests	either deciduous or sclerophyllous forests	OAK
bare soils	rock outcrops or exposed soils	BSO
urban	population centres	URB
water	artificial small water ponds	WAT

Cover types considered the main vegetation type of each digitized polygon, whereas cover classes were defined considering vegetation height and canopy cover, which provide both obstruction to visibility and thermal shelter.

Table 18 – Canopy cover classes.

Cover class	Description
class a	herbaceous vegetation; low shrubland (< 1.5 m) with tall shrub (> 1.5 m) or tree cover under 25%
class b	young or recent commercial stands (pine and eucalyptus); low shrubland with tall shrub or tree cover between 25 and 50 %
class c	tall shrubland; natural forests and commercial stands; shrubs or tree cover between 50 to 75%
class d	tall shrubland; natural forests and commercial stands; shrubs or tree cover over 75%

We also considered the topographic characteristics of the buffers. Using the SRTM digital terrain model (CGIAR-CSI 2008) we computed the mean slope of the 500, 250 and 100 m buffers (mean_slope) and an elevation index (Δ_elev), computed as the difference between the meadow mean elevation and each buffer mean elevation. Slope and elevation index give an approximation of the meadow position and of the physiography of the surrounding landscape (e.g.: bottom of a narrow valley; broad valley; plateau), which can influence deer selection, as they may interfere, for example, with the target species assessment of both predation risk and escape possibility (Dill & Lima 1990; Ripple & Beschta 2003; Fortin et al. 2005).

9.3.3.2 Landscape macro-scale descriptors

Both red and roe deer habitat selection is affected by human-related disturbance (Adrados et al. 2008; Puddu et al. 2009; Torres et al. 2011). In this research the proxies used for human disturbance were “distance to the nearest main paved road” (road_dist) and “distance to the nearest urban centre” (urb_dist). These distance indexes are not related to the more restricted spatial scales of the buffers but are associated to the study area spatial extent.

9.3.3.3 Micro-scale descriptors

Among the micro-scale descriptors, we included two features of the sampled meadows (which represent the grain of the different scales of observation considered): i) the phytosociological unit with greater spatial representativeness of each sampled meadow (domin_phyto), in order to account for the effect of finer scale selection process (see chapter, 6.1.1. and 8, for details on vegetation survey, phytosociological relevés and fine scale use of meadow patches); ii) the current (at the time of the field data collection) management status (manag_status), according to three classes: used (currently grazed and/or cut yearly); recently abandoned (up to five years); abandoned (more than five years) (see Table 19). As classification criteria for assessing the management status we considered the presence of water in the irrigation ditches, presence of livestock and/or their dejections and resident confirmation, for currently used meadows. For the abandoned ones, we relied on absence of mentioned indexes. Additionally, the time of management cease was assessed via either inquiries to local residents or visual evaluation of the meadow vegetation characteristics (e.g.: shrub colonization).

Table 19 – Management status and prevalent phytosociological unit of the sampled meadows. In Management status: used = currently managed; rec.ab = recently abandoned; ab = abandoned. For the vegetation communities: CYN = *Agrostio castellanae-Cynosuretum cristati*; BRACHY = Community of *Brachypodium rupestre*; AVESU = Community of *Avenula sulcata*; ARRH = Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*.

Meadow	Management status	Vegetation communities
1	used	CYN
2	used	CYN
3	rec.ab	AVESU
4	ab	JUN
5	used	CYN
7	rec.ab	AVESU
8	ab	CYN
9	ab	AVESU
11	ab	BRACHY
12	ab	BRACHY
14	ab	BRACHY
16	used	CYN
17	rec.ab	CYN
18	ab	BRACHY
19	used	CYN
21	rec.ab	CYN
22	used	CYN
23	used	CYN
24	ab	BRACHY
25	rec.ab	AVESU
29	ab	ARRH
30	ab	ARRH
31	ab	ARRH
32	ab	CYN
33	ab	AVESU
34	ab	BRACHY
35	rec.ab	CYN
39	ab	AVESU

9.3.4 Statistical analyses

To analyse our data we used generalized linear models (GLMs) (Nelder & Wedderburn 1972). For red deer we assumed a Poisson distribution of the faecal pellet counts. Overdispersion was checked fitting a quasipoisson model: whenever the dispersion parameter was larger than 1 and the residual deviance goodness of fit test was significant (bad fit for the Poisson model), we fitted the GLM with a negative binomial distribution (log link-function in both cases). As roe deer pellet count data had a high percentage of nil counts (over 70% in the three seasons), and very low percentage of counts greater than 1 (max 10%), we used a logistic regression (logit link-function) for analysing the data. We transformed roe FAR into presence/absence data, and bulked the three seasonal counts together, thus employing the cumulative use of roe deer. Red deer data were analysed taking also season into account. In the analysis we considered each buffer separately, to account for the effect of scale.

Analyses were executed in R (R Development Core Team 2010), using package *glmulti* (Calcagno 2011), which provides a wrapper for **glm** and other similar R functions. *glmulti* has the advantage of performing automated model selection which allows managing large candidate model sets, as can happen when the number of variables to be tested is large, like in our case. Considering the small sample size (28 meadows), we constrained the number of terms in the candidate model formula to 3 (Maroco 2007), to reduce overfitting. The modelling was conducted in two steps. We firstly analysed deer use of meadows considering the meso-scale variables as predictors, to assess the effect, if any, of the different spatial extents considered (buffer analysis).

We introduced percentage cover types and cover classes into the models separately, modelling each group with topographic indexes. Selection of the best model(s) in the *glmulti* procedure uses, as a default, the AIC_c (Burnham & Anderson 2004), which is a correction for Akaike Information Criteria (Akaike 1974) for small sample size:

$$AIC_c = AIC + \frac{2k(k+1)}{n-k-1}$$

where k is the number of parameters (predictors) and n the sample size.

After testing their goodness of fit (Chi-squared test using the residual deviance and the residual degrees of freedom (Statistical Consulting Group 2011)), we retained the best models, i.e. the one with lowest AIC_c and any other with $\Delta\ AIC_c$ from the lowest < 2, provided that models did not present numerical problems (e.g.: artefactual perfect separation of the dependent variable by one or more predictors (Maroco 2007)), or the null model was not included. To support model selection we also computed pairwise Pearson correlations among the independent variables that were included in the candidate formula, to check for multicollinearity, which can result in weaker individual effect (Calcagno 2011) or unstable coefficients, and refused models with variables correlation $|r| > 0.5$.

Final selected models (lowest AIC_c plus models with $\Delta\ AIC_c < 2$) of the three buffers were therefore compared to assess the effect of meso-scale extents.

In the second step analysis, we assessed whether the introduction of macro and micro-scales descriptors (see above), together with the meso-scale ones, affected model performance, and helped explaining deer use of meadows.

Variables overall performance was assessed considering the importance of each one across all models, computed as summed AIC_c weight of all the models in which the specific variable appears (Calcagno 2011). Following Calcagno (2011), considering the small sample size ($n = 28$) we used an importance threshold of 20%, aiming to minimize the probability of type II error (drop of an important term). For the same reasons, among the important variables we considered those with likelihood ratio test p-values lower than 0.25 (Hosmer & Lemeshow 2000).

In Table 20, a resuming scheme of the modelling procedure is given.

Table 20 – Resuming table of the procedure followed, with the variables used in each step of the analysis.

Analysis steps and corresponding scales	**Candidate model formula**		
	Cover types	**+**	**Topographic indexes**
First step: buffer analysis (meso-scale)	AGR_(buffer*) MEA_(buffer) OAK_(buffer) RIP_(buffer) COM_(buffer) SHR_(buffer) TRA_(buffer) GRA_(buffer)		Δ_elev_(buffer) mean_slope_(buffer)
	Cover classes	**+**	**Topographic indexes**
	a_(buffer) b_(buffer) c_(buffer) d_(buffer)		Δ_elev_(buffer) mean_slope_(buffer)

		Candidate model formula		
Second step: introduction of macro and micro scale variables:	**meso + macro**	**Cover types (or classes), topographic indexes**	**+**	**Distance** urb_dist road_dist source_dist
	meso + micro	**Cover types (or classes), topographic indexes**	**+**	**Meadows characteristics** manag_status domin_phyto

* (buffer) = 100, 250 or 500 m buffer

9.4 Results

9.4.1 Buffers characterization

Figure 9 to Figure 14 show the results of the buffers classification according to the cover types and cover classes. Of the cover types summarized in Table 17, only RIP, AGR, GRA, TRA, COM, MEA, SHR and OAK, were employed in the analysis, as the remaining (ROA, BUR, BSO and FBA) were scarcely represented at the landscape scale (occurring in less than 40% of the buffers).

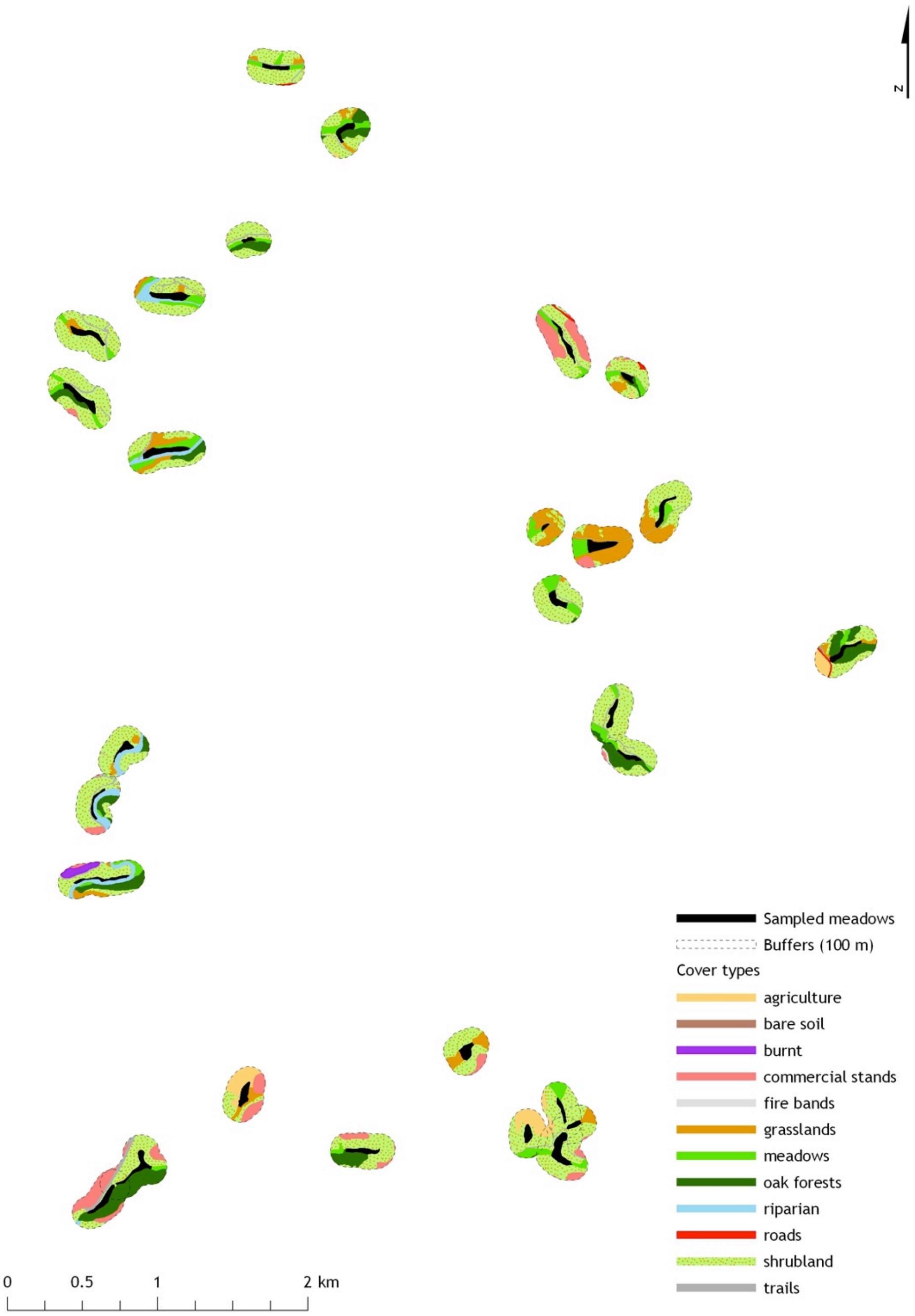

Figure 9 – Cover types' map of the 100 m buffers. See Table 17 for details.

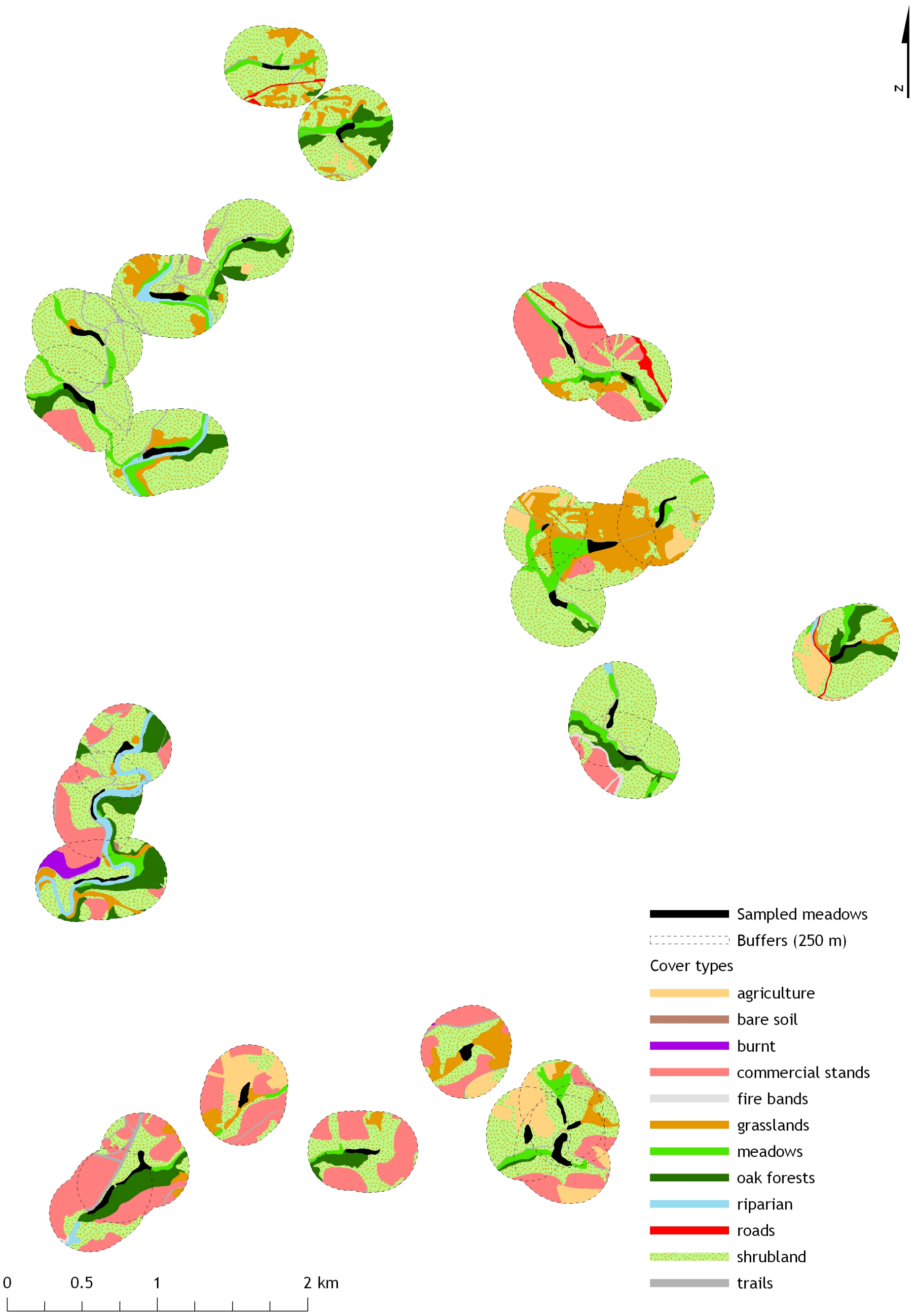

Figure 10 - Cover types' map of the 100 m buffers. See Table 17 for details.

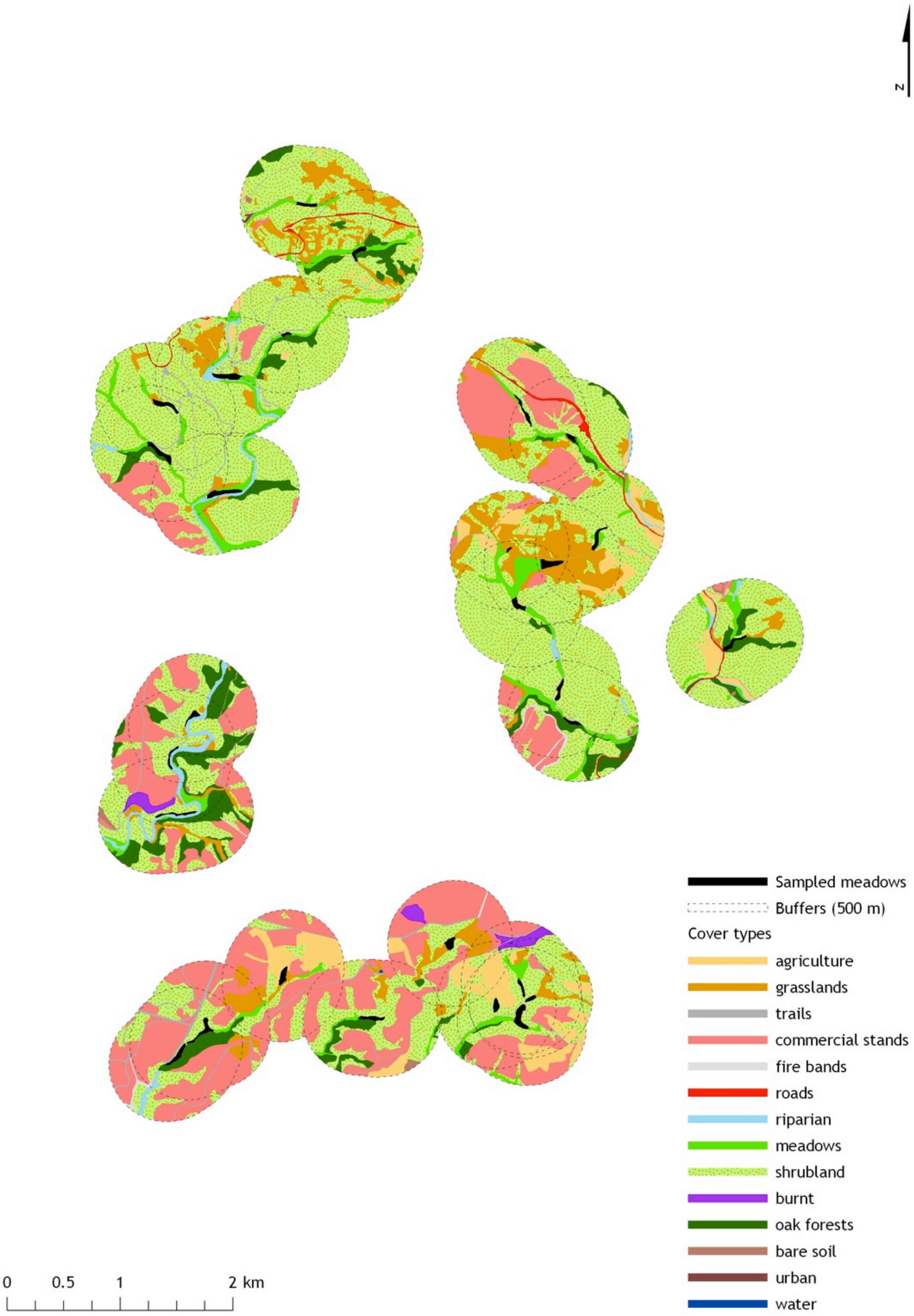

Figure 11 - Cover types' map of the 500 m buffers. See Table 17 for details.

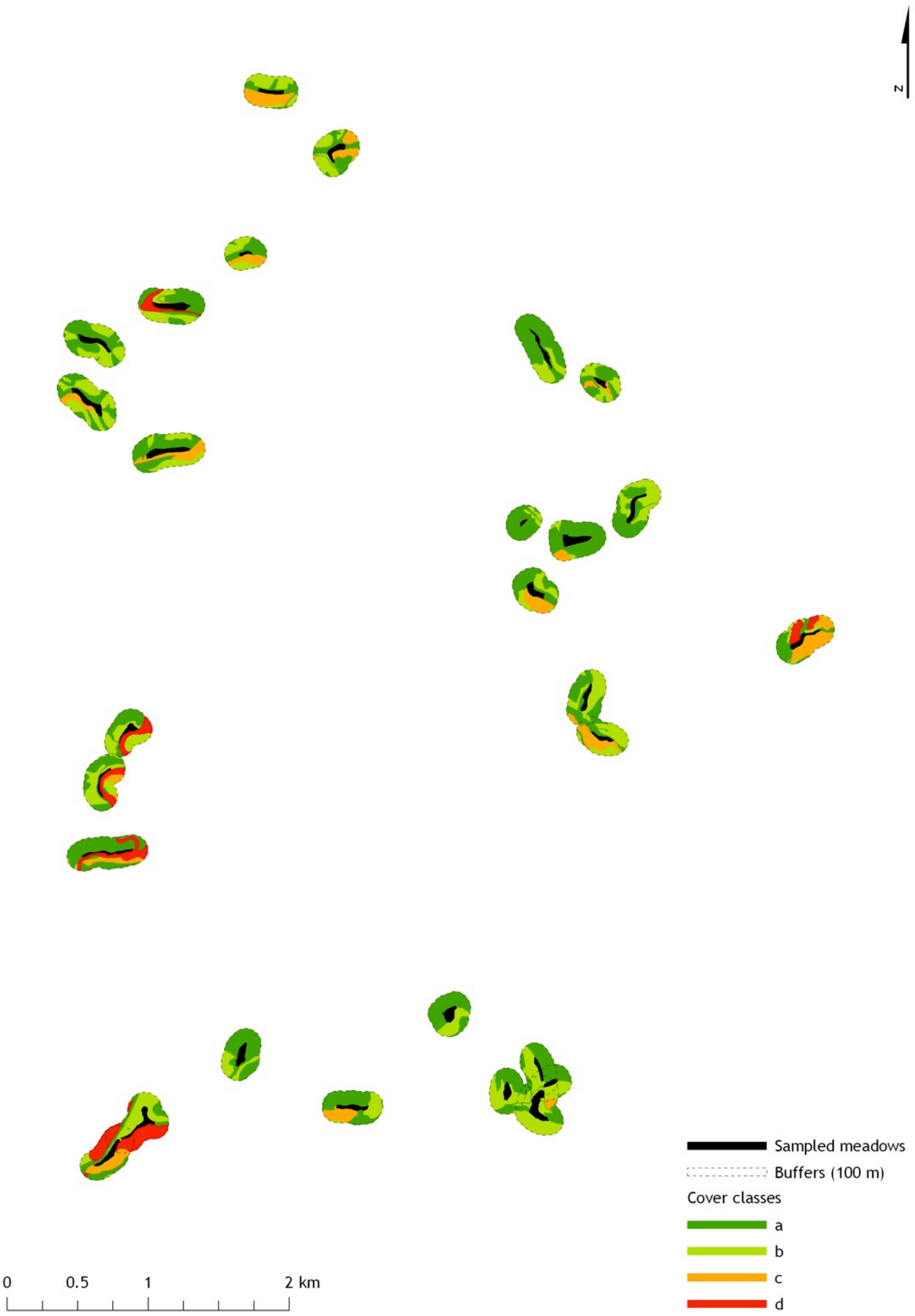

Figure 12 – Cover classes' map of the 100 m buffers. See Table 18 for details.

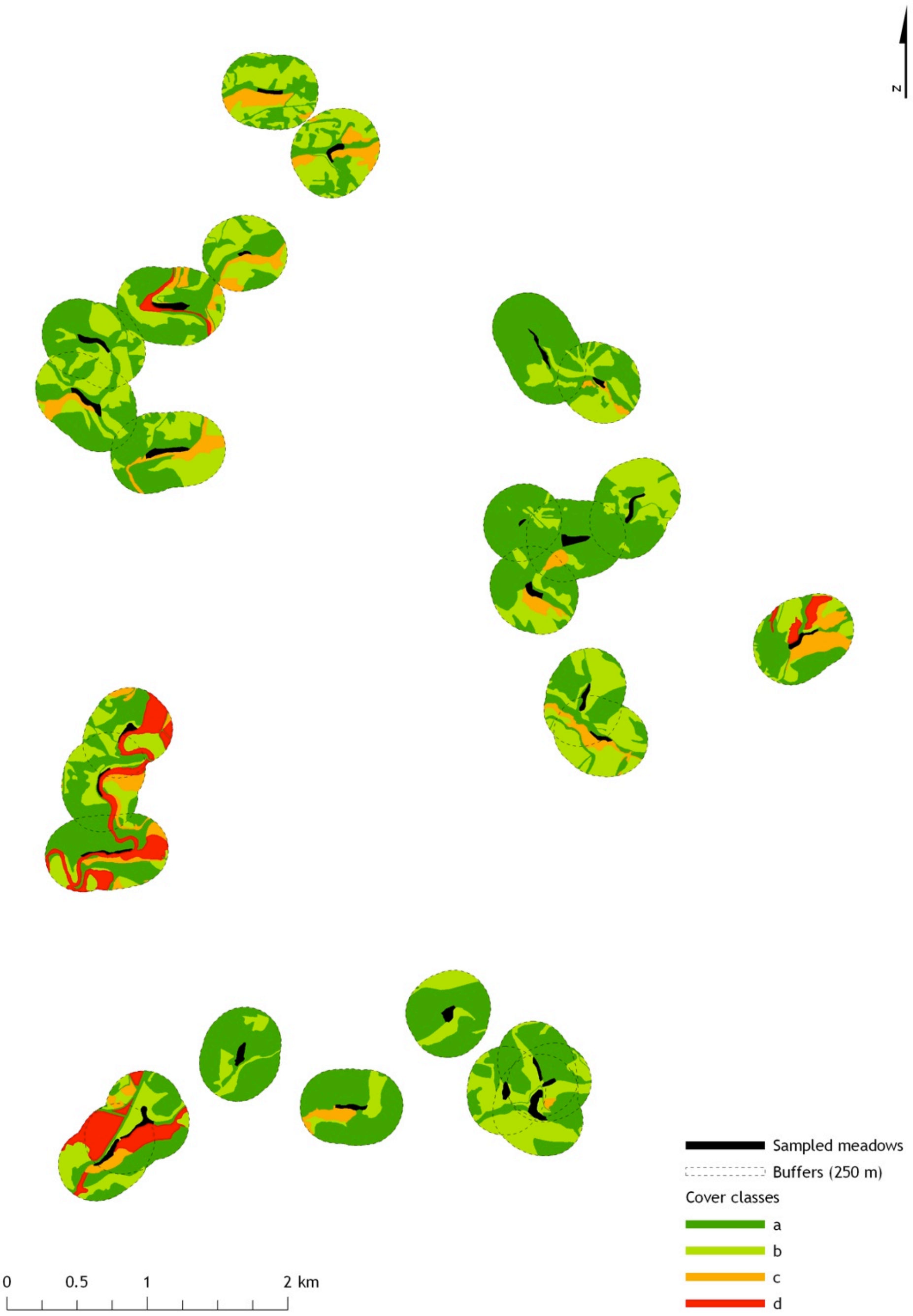

Figure 13 - Cover classes' map of the 250 m buffers. See Table 18 for details.

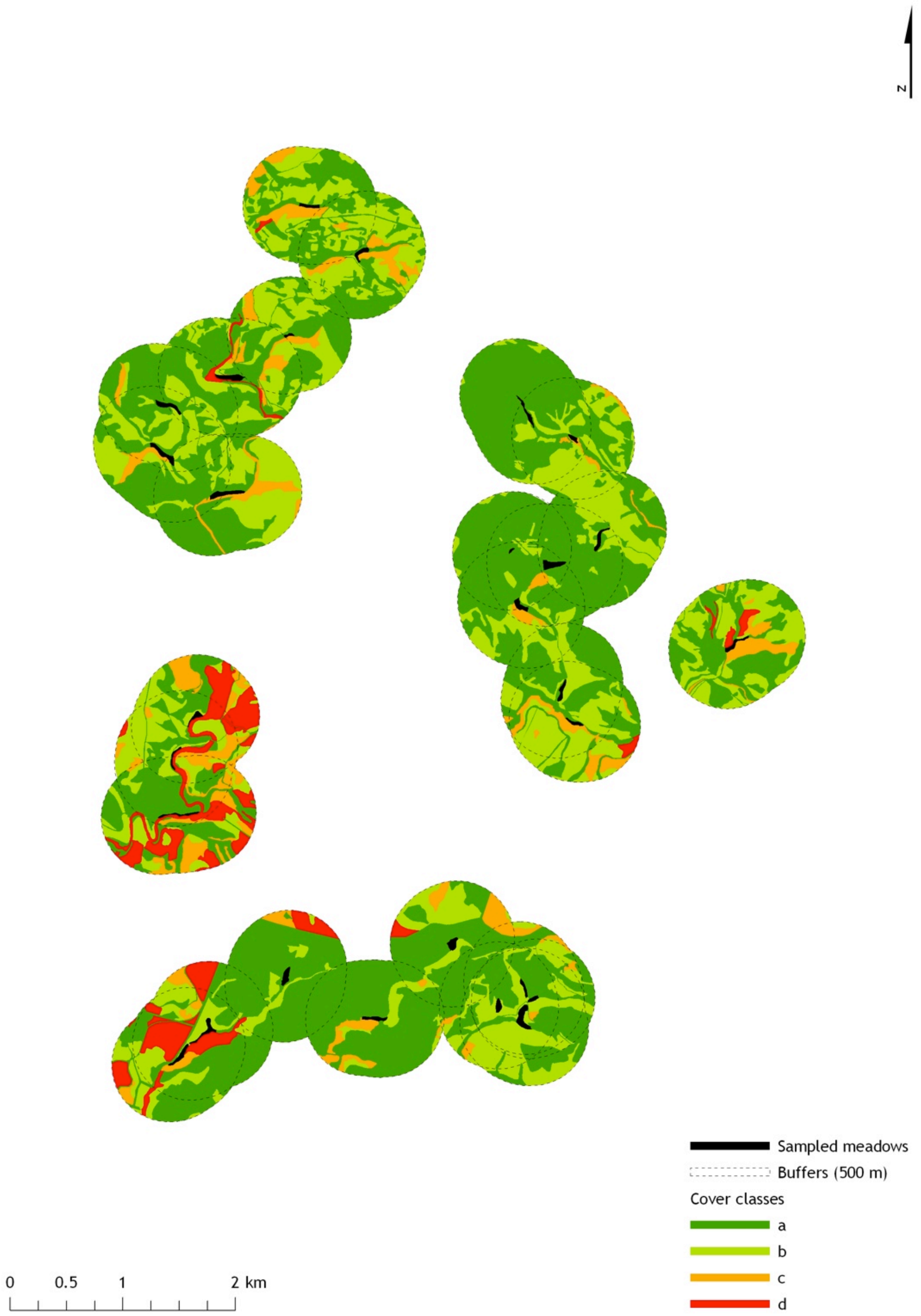

Figure 14 - Cover classes' map of the 500 m buffers. See Table 18 for details.

9.4.2 Use of meadows by red deer

Figure 15 shows red deer seasonal and pooled FAR frequencies. For each meadow, the sum of plots faecal groups was used (a summary of the seasonal count data is given in Table 47, chapter 2 of the Appendix).

The results of the univariate explorative analysis plots are displayed in the Appendix (chapter 2 Figure 33 to Figure 56). Count data were log-transformed for visualization purposes in the boxplots (Zeileis, Kleiber, & Jackman 2008). Boxplots display FAR distribution in 20% quantile classes.

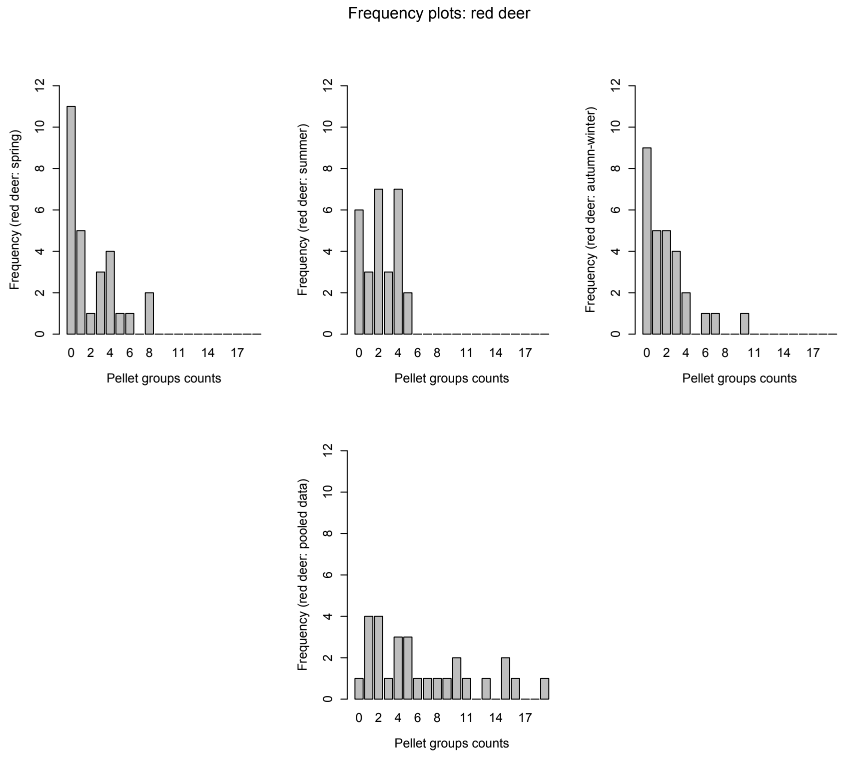

Figure 15 – Frequency distribution of red deer seasonal and pooled count data.

9.4.2.1 First step: buffer analysis

The plot displayed in Figure 16, shows the pairwise correlations related to cover types and topographic indexes. Models that included collinear variables (|r| > 0.5) were not considered.

Considering spring use, the variables that performed better were Δ_elev_100 GRA_100, RIP_100, COM_100 within the best models for the 100 m buffer analysis. In the 250 m buffer analysis the selected variables were COM_250, Δ_elev_250, MEA_250 and RIP_250, whereas OAK_500, MEA_500, Δ_elev_500 and RIP_500 were the best performing in the 500 m buffer analysis (see Table 48, in chapter 3 of the Appendix)

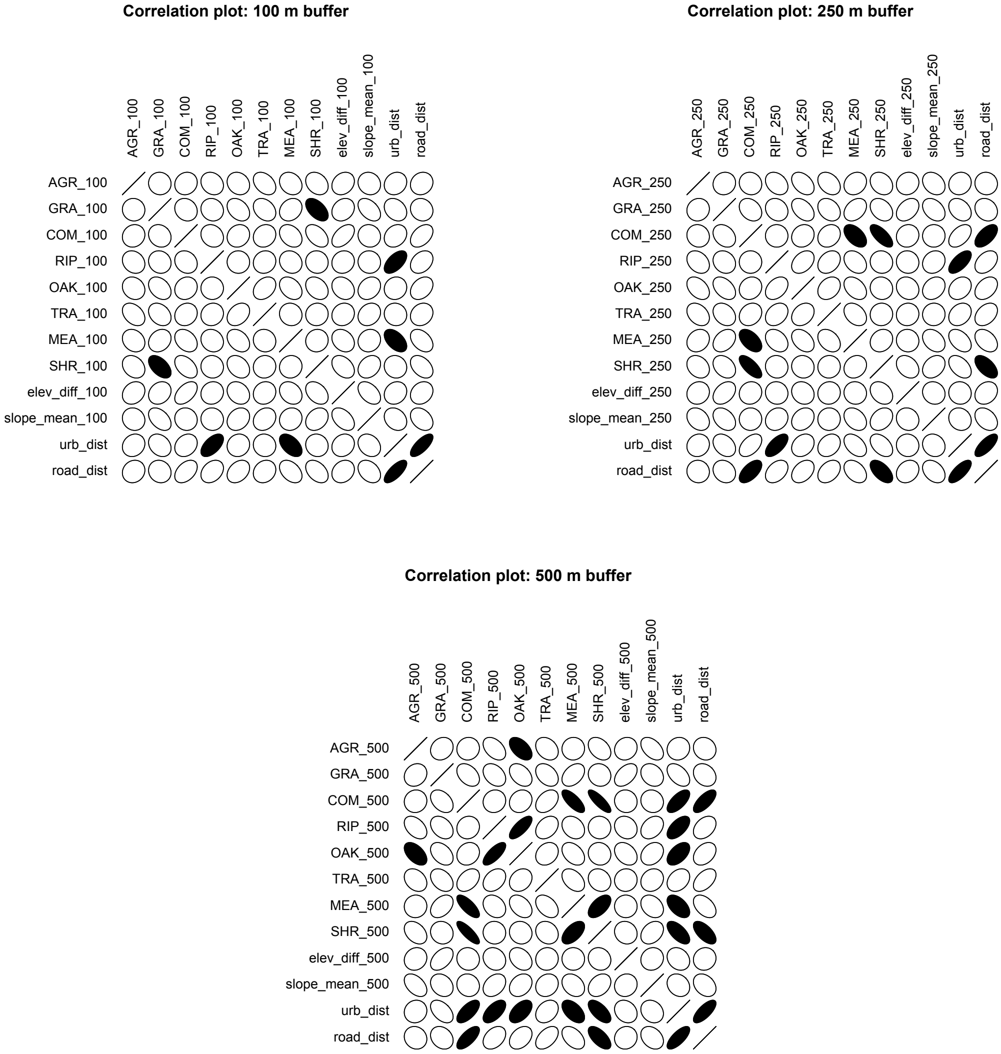

Figure 16 – Pearson correlation plots of cover type variables, topographic and distance indexes corresponding to the three buffers. Black ellipses correspond to |r| > 0.5; ellipses' width vary with r-value, r = 0 corresponds to a circle; inclination reflects correlation sign.

Spring use models related to the 100 m buffer performed better than those related to the 250 m buffer (AIC_c = 104.16 to 105.72), or to the 500 m buffer (AIC_c = 106.67 to 108.54). A summary of the selected models is displayed in Table 21.

Table 21 –Summary of the best and alternative models selected for red deer spring use of meadows, considering percentage of cover types and topographic indexes as variables.

Best models (spring)	**Res.d**	**Df**	**GOF**	**AIC_c**	
1 + RIP_100 + COM_100 + Δ_elev_100	29.6241	24	0.1975	101.24	
1 + RIP_100 + COM_100 + SHR_100	27.9975	24	0.2601	102.13	
1 + GRA_100 + RIP_100	27.8907	25	0.3129	103.17	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + RIP_100 + COM_100 + Δ_elev_100					
(Intercept)	1.5798	0.2468	6.4009	<0.0001***	
COM_100	-0.0524	0.0194	-2.6993	0.0069**	0.0054**
RIP_100	-0.3887	0.2817	-1.3797	0.1677	<0.0001***
Δ_elev_100	0.0665	0.024	2.7724	0.0056**	0.004**
1 + RIP_100 + COM_100 + SHR_100					
(Intercept)	2.4181	0.5534	4.3694	<0.0001***	
COM_100	-0.0595	0.0246	-2.4244	0.0153*	0.0076**
RIP_100	-0.409	0.2838	-1.441	0.1496	<0.0001***
SHR_100	-0.0242	0.0097	-2.4976	0.0125*	0.0113*
1 + GRA_100 + RIP_100					
(Intercept)	0.6856	0.238	2.8807	0.004**	
GRA_100	0.0195	0.0104	1.8701	0.0615	0.0436*
RIP_100	-0.4484	0.4414	-1.0157	0.3098	0.0002***

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AIC_c = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

As for the summer use models for the 100 m buffer analysis, GRA_100 and RIP_100 were the best performing variables; mean_slope_250, GRA_250 and RIP_250 were selected within the 250 m buffer models; and GRA_500, Δ_elev_500, mean_slope_500 and RIP_500 were chosen within the 500 m buffers models (see Table 49, in chapter 3 of the Appendix). Summer models related to the 250 m buffer yielded lower AIC_c than those related to the other two buffers (100 m buffer: AIC_c = 97.83 to 99.74; 500 m buffer: AIC_c = 97.35 to 99.2) and the best set is reported in Table 22.

Table 22 –Summary of the best and alternative models selected for red deer summer use of meadows, considering percentage of cover types and topographic indexes as variables.

Best models (summer)	**Res.d**	**Df**	**GOF**	**AIC_c**	
1 + GRA_250 + RIP_250 + mean_slope_250	22.2575	24	0.5639	95.09	
1 + GRA_250 + RIP_250	25.6281	25	0.4277	95.72	
1 + RIP_250	28.2679	26	0.3454	95.84	
1 + RIP_250 + Δ_elev_250	26.7919	25	0.3664	96.88	
1 + GRA_250 + RIP_250 + TRA_250	24.1752	24	0.4516	97.01	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + GRA_250 + RIP_250 + mean_slope_250					
(Intercept)	-0.1337	0.5716	-0.2339	0.8151	
GRA_250	0.02	0.0089	2.2563	0.0241*	0.0309*
RIP_250	-0.2261	0.0865	-2.6143	0.0089**	0.0002***
mean_slope_250	0.0584	0.0315	1.8552	0.0636	0.0664
1 + GRA_250 + RIP_250					
(Intercept)	0.8634	0.1693	5.1011	<0.0001***	
GRA_250	0.0135	0.0079	1.7106	0.0872	0.1042
RIP_250	-0.2205	0.0867	-2.5427	0.011*	0.0004***
1 + RIP_250					
(Intercept)	1.0294	0.1291	7.9724	<0.0001***	

RIP_250	-0.2348	0.0882	-2.6626	0.0078**	0.0001***
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + RIP_250 + Δ_elev_250					
(Intercept)	1.2438	0.2101	5.9189	<0.0001***	
RIP_250	-0.2339	0.0884	-2.6446	0.0082**	0.0001***
Δ_elev_250	0.0133	0.0109	1.2215	0.2219	0.2244
1 + GRA_250 + RIP_250 + TRA_250					
(Intercept)	0.6083	0.275	2.2122	0.027*	
GRA_250	0.0165	0.0083	1.9971	0.0458*	0.0581
RIP_250	-0.2334	0.088	-2.652	0.008**	0.0002***
TRA_250	0.1101	0.0879	1.2518	0.2107	0.2281
1 + RIP_250 + mean_slope_250					
(Intercept)	0.4257	0.5533	0.7694	0.4417	
RIP_250	-0.2421	0.0886	-2.7319	0.0063**	0.0001***
mean_slope_250	0.0385	0.0337	1.1428	0.2531	0.2454

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AIC$_c$ = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Autumn-winter use models indicated, for the 100 m buffer, five cover types as best performing variables: SHR_100, RIP_100, OAK_100, TRA_100 and GRA_100. Within the 250 m buffer, SHR_250, GRA_250 and OAK_250 were the selected variables, and COM_500, SHR_500, GRA_500 and OAK_500 were chosen within the 500 m models set. No topographic index was selected. Though there were no relevant differences among the AIC$_c$, models related to the 250 m buffer showed an overall better fit (see Table 50, in chapter 3 of the Appendix). Selected models summaries are showed in Table 23.

Table 23 –Summary of the best and alternative models selected for red deer autumn-winter use of meadows, considering percentage of cover types and topographic indexes as variables.

Best models (autumn-winter)	**Res.d**	**Df**	**GOF**	**AIC$_c$**	
1 + OAK_250 + SHR_250	31.2927	25	0.1795	105.41	
1 + GRA_250 + OAK_250	32.5428	25	0.1429	106.49	
1 + OAK_250	31.411	26	0.2133	106.83	
1 + GRA_250 + COM_250 + OAK_250	32.8018	24	0.1083	107.3	
1 + GRA_250 + OAK_250 + SHR_250	32.6148	24	0.1125	107.39	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + OAK_250 + SHR_250					
(Intercept)	2.1067	0.4801	4.3884	<0.0001***	
OAK_250	-0.0998	0.0316	-3.1593	0.0016**	0.0006***
SHR_250	-0.0204	0.0097	-2.0984	0.0359*	0.0335*
1 + GRA_250 + OAK_250					
(Intercept)	0.7477	0.3146	2.3768	0.0175*	
GRA_250	0.0233	0.0124	1.8845	0.0595	0.0625
OAK_250	-0.0736	0.0347	-2.1198	0.034*	0.0265*
1 + OAK_250					
(Intercept)	1.186	0.2357	5.0325	<0.0001***	
OAK_250	-0.1029	0.0346	-2.9712	0.003**	0.0012**
1 + GRA_250 + COM_250 + OAK_250					
(Intercept)	0.4428	0.3711	1.193	0.2329	
GRA_250	0.0281	0.0122	2.3148	0.0206*	0.0207*
COM_250	0.015	0.0097	1.5441	0.1226	0.1294
OAK_250	-0.076	0.0338	-2.2459	0.0247*	0.0179*
1 + GRA_250 + OAK_250 + SHR_250					
(Intercept)	1.6077	0.6095	2.6375	0.0084**	
GRA_250	0.0141	0.0126	1.1264	0.26	0.2874
OAK_250	-0.0819	0.0335	-2.4433	0.0146*	0.0108*

SHR_250	-0.0153	0.01	-1.5276	0.1266	0.1392

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AIC_c = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

Among the best pooled annual model set the best performing variables were: Δ_elev_100, GRA_100, OAK_100 and RIP_100, within the 100 m buffer models; GRA_250 and RIP_250, for the 250 m buffer; and Δ_elev_500, GRA_500, OAK_500 and RIP_500 in the 500 m buffer analysis. Lower AIC_c were recorded for the 100 m buffer models, summarized in Table 24 (250 m buffer: AIC_c = 151.62 to 153.59; 500 m buffer: AIC_c = 154.75 to 156.57, see Table 51, in chapter 3 of the Appendix).

Table 24 –Summary of the best and alternative models selected for red deer annual use of meadows, considering percentage of cover types and topographic indexes as variables.

Best models (annual)	**Res.d**	**Df**	**GOF test**	**AICc**	
1 + GRA_100 + RIP_100	29.6906	25	0.2361	149.01	
1 + GRA_100 + RIP_100 + Δ_elev_100	29.7176	24	0.1943	150.15	
1 + GRA_100+ RIP_100 + OAK_100	29.8121	24	0.1910	150.21	
1 + GRA_100+ RIP_100 + SHR_100	29.8021	24	0.1913	150.64	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + GRA_100 + RIP_100					
(Intercept)	1.7681	0.1349	13.107	<0.0001***	
GRA_100	0.0194	0.0059	3.3023	0.001**	0.0007***
RIP_100	-0.1235	0.0328	-3.7698	0.0002***	<0.0001***
1 + GRA_100 + RIP_100 + Δ_elev_100					
(Intercept)	1.9054	0.1588	11.9984	<0.0001***	
GRA_100	0.0173	0.0057	3.0152	0.0026**	0.0024**
RIP_100	-0.126	0.0325	-3.8771	0.0001***	<0.0001***
Δ_elev_100	0.0189	0.0131	1.445	0.1484	0.1662
1 + GRA_100+ RIP_100 + OAK_100					
(Intercept)	1.911	0.1644	11.6269	<0.0001***	
GRA_100	0.0164	0.006	2.7296	0.0063**	0.0057**
RIP_100	-0.1234	0.0322	-3.8282	0.0001***	<0.0001***
OAK_100	-0.0136	0.0099	-1.3796	0.1677	0.1727
1 + GRA_100+ RIP_100 + SHR_100					
(Intercept)	1.2918	0.4216	3.0639	0.0022**	
GRA_100	0.0248	0.0073	3.382	0.0007***	0.0005***
RIP_100	-0.1198	0.0324	-3.6936	0.0002***	<0.0001***
SHR_100	0.0082	0.0068	1.2001	0.2301	0.2363

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AIC_c = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

The modelling of red deer counts using percentage of cover classes and topographic indexes as predicting variables gave poorer results, that is, the AIC_c were higher than those yielded by cover types plus topographic indexes of the corresponding buffer and count data.

In Figure 17 pairwise correlation between cover class variables and topographic indexes are displayed, highlighting those with |r| above 0.5.

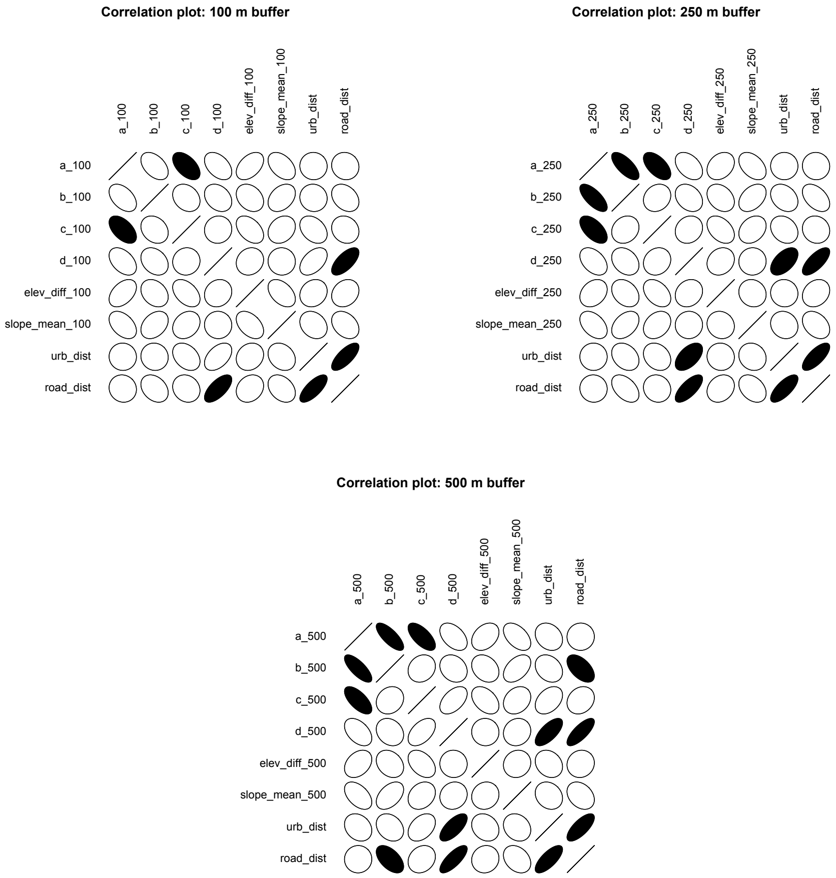

Figure 17 – Pearson correlation plots of cover class variables and topographic indexes corresponding to the three buffers. Black ellipses correspond to |r| > 0.5.

Spring use models for 100 and 250 m buffers were discarded, as the null model was among the best set (see Table 52, in chapter 3 of the Appendix). For the 500 m buffer, c_500 was the best performing variable: best and alternative models are summarized in Table 25.

Table 25 - Summary of the best and alternative models selected for red deer spring use of meadows, considering percentage of cover classes and topographic indexes as variables.

Best models (spring)	**Res.d**	**Df**	**GOF test**	**AICc**	
1 + c_500	29.692	26	0.2806	108.75	
1 + c_500 + mean_slope_500	30.288	25	0.2137	110.50	
1 + c_500 + Δ_elev_500	30.0956	25	0.2207	110.69	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + c_500					
(Intercept)	1.6446	0.3764	4.3699	<0.0001***	
c_500	-0.1811	0.0624	-2.9035	0.0037**	0.0041**
1 + c_500 + mean_slope_500					
(Intercept)	2.4662	0.9667	2.5511	0.0107	
c_500	-0.1657	0.0621	-2.6665	0.0077**	0.0074**
mean_slope_500	-0.0576	0.0604	-0.9549	0.3396	0.3077
1 + c_500 + Δ_elev_500					
(Intercept)	1.6735	0.3701	4.522	<0.0001***	
c_500	-0.1494	0.0651	-2.2929	0.0219*	0.0306*
Δ_elev_500	0.0113	0.0115	0.9856	0.3243	0.3605

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Summer use models for 100 and 250 m buffers were also dropped (identical reason as above, see Table 53, in chapter 3 of the Appendix). In the 500 m buffers analysis d_500 and Δ_elev_500 were selected as best performing variables: related models are displayed and summarized respectively in and Table 26.

Table 26 - Summary of the best and alternative models selected for red deer summer use of meadows, considering percentage of cover classes and topographic indexes as variables.

Best models (summer)	**Res.d**	**Df**	**GOF test**	**AICc**	
1 + d_500 + Δ_elev_500	33.1025	25	0.1285	103.2	
1 + Δ_elev_500	37.56	26	0.0665	105.13	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + d_500 + Δ_elev_500					
(Intercept)	1.1866	0.1533	7.7382	<0.0001***	
d_500	-0.0436	0.0232	-1.8799	0.0601*	0.0347*
Δ_elev_500	0.0127	0.0053	2.4157	0.0157*	0.0236*
1 + Δ_elev _500					
(Intercept)	1.0686	0.1472	7.2591	<0.0001***	
Δ_elev_500	0.0137	0.0054	2.5458	0.0109*	0.0177*

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

In relation to autumn-winter use models, class a was selected in the three buffers, and c for the 250 m buffer only. Neither of the two topographic indexes was selected. Autumn-winter models related to the 250 m buffer had lower AIC_c (100 m buffer: AIC_c = 101.35 and 103.23; 500 m buffer: AIC_c = 104.5, see Table 54, in chapter 3 of the Appendix) and are summarized in Table 27.

Table 27 - Summary of the best model selected for red deer autumn-winter use of meadows, considering percentage of cover classes and topographic indexes as variables.

Best models (autumn-winter)	Res.d	Df	GOF	AICc	
1 + a_250	30.3088	26	0.255	101.16	
1 + b_250 + c_250	29.8288	25	0.2308	102.89	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + a_250					
(Intercept)	-1.9341	0.6658	-2.9048	0.0037**	
a_250	0.0425	0.0099	4.2823	<0.0001***	<0.0001***
1 + b_250 + c_250					
(Intercept)	2.1314	0.4064	5.2447	<0.0001***	
b_250	-0.0291	0.0127	-2.2837	0.0224*	0.0203*
c_250	-0.1211	0.0381	-3.18	0.0015**	0.0004***

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Within the annual use models, the best performing variables were class cover a, for the three buffers, Δ_elev_500 for the 500 m buffers and cover class c and d for the 250 m buffers (Table 55). The models related to the 500 m buffer yielded lower AIC_c (100 m buffer: AIC_c = 162.6 and 164.26; 250 m buffer: AIC_c = 162.95 to 164.38, see Table 55, in chapter 3 of the Appendix) and are summarized in Table 28.

Table 28 - Summary of the best and alternative models selected for red deer annual use of meadows, considering percentage of cover classes and topographic indexes as variables.

Best models	Res.d	Df	GOF	AICc	
1 + a_500	29.7147	26	0.2796	159.39	
1 + a_500 + Δ_elev_500	29.9357	25	0.2267	160.04	
1 + a_500 + d_500	29.742	25	0.2341	161.26	
1 + a_500	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	-0.021	0.5441	-0.0386	0.9692	
a_500	0.0308	0.0087	3.5245	0.0004***	0.0008***
1 + a_500 + Δ_elev_500					
(Intercept)	0.4329	0.6016	0.7195	0.4718	
a_500	0.0263	0.0088	2.9743	0.0029*	0.0042*
Δ_elev_500	0.0102	0.0071	1.4374	0.1506	0.1384
1 + a_500 + d_500					
(Intercept)	0.2863	0.6196	0.462	0.6441	
a_500	0.0268	0.0095	2.8288	0.0047**	0.0071**
d_500	-0.0204	0.0224	-0.9122	0.3617	0.3465

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

9.4.2.2 Second step: introduction of macro and micro scale descriptors

Taking into account the best performing buffer for each season, the introduction of macro-scale variables (urb_dist and road_dist) did not improved the best model set (with cover types and topographic indexes), except for autumn-winter models (best model formula: GRA_250 + RIP_250 + urb_dist; $AIC_c = 105.29$; GOF = 0.0670; see Table 29 for summary).

Table 29 – Best model summary for red deer autumn-winter use of meadows, considering percentage of cover classes, topographic indexes and macro-scale descriptors as variables.

	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
GRA_250 + RIP_250 + urb_dist					
(Intercept)	-0.6977	0.4883	-1.4287	0.1531	
GRA_250	0.041	0.0096	4.2555	<0.0001***	<0.0001***
RIP_250	-0.1931	0.07	-2.7594	0.0058**	0.0017**
urb_dist	0.0005	0.0002	2.735	0.0062**	0.0053**

SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

When the distance indexes were introduced together with cover classes and topographic indexes, the resulting models did improve (lower AIC_c), for spring use models (Table 30) related to the best performing buffer (500 m).

Table 30 - Best models and corresponding summaries for red deer spring use of meadows with cover classes, topographic and distance indexes as predictors.

Best models (spring - 500 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + c_500 + urb_dist	28.8706	25	0.2694	108.54	0.0006
1 + c_500 + mean_slope_500 + urb_dist	30.3281	24	0.1741	108.66	0.0154
1 + Δ_elev_500 + mean_slope_500 + urb_dist	32.8877	24	0.1065	108.73	0.0435
1 + c_500 + urb_dist	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	2.4401	0.6152	3.9667	0.0001***	
c_500	-0.1697	0.0637	-2.666	0.0077**	0.0091**
urb_dist	-0.0004	0.0003	-1.6984	0.0894	0.0807
1 + c_500 + mean_slope_500 + urb_dist					
(Intercept)	4.0692	1.1542	3.5255	0.0004***	
c_500	-0.1389	0.0609	-2.2828	0.0224*	0.0226*
mean_slope_500	-0.0987	0.0561	-1.7599	0.0784	0.0707
urb_dist	-0.0006	0.0002	-2.2019	0.0277*	0.021*
1 + Δ_elev_500 + mean_slope_500 + urb_dist					
(Intercept)	4.3278	1.0195	4.2451	<0.0001***	
Δ_elev_500	0.0213	0.0092	2.3229	0.0202*	0.0172*
mean_slope_500	-0.1435	0.0511	-2.8063	0.005**	0.0042**
urb_dist	-0.0005	0.0002	-2.367	0.0179*	0.0159*

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test.
SE = standard error Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

Summer use models (500 m buffer) were also improved by distance indexes (Table 31), whereas autumn-winter (250 m buffer) and pooled annual ones (500 m buffer) were not enhanced.

Table 31 - Best models and corresponding summaries for red deer summer use of meadows with cover classes, topographic and distance indexes as predictors.

Best models (summer - 500 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**DPqpoisson**
1 + Δ_elev_500 + urb_dist	33.0425	25	0.1300	103.13	1.0987
1 + urb_dist	35.9218	26	0.0931	103.50	1.1209
1 + Δ_elev_500 + road_dist	33.6039	25	0.1166	103.70	1.0680
1 + a_500 + urb_dist	33.7149	25	0.1141	103.81	1.0944
1 + c_500 + urb_dist	33.7901	25	0.1125	103.88	1.1324
1 + b_500 + urb_dist	34.6610	25	0.0945	104.75	1.1421
1 + a_500 + road_dist	34.9823	25	0.0885	105.07	1.1060
1 + Δ_elev_500 + urb_dist	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	1.5546	0.2677	5.8073	<0.0001***	
Δ_elev_500	0.0097	0.0055	1.762	0.0781	0.0897
urb_dist	-0.0003	0.0001	-2.033	0.0421*	0.0336*
1 + urb_dist					
(Intercept)	1.5097	0.2759	5.4725	<0.0001***	
urb_dist	-0.0003	0.0001	-2.5465	0.0109*	0.007**
1 + Δ_elev_500 + road_dist					
(Intercept)	1.3505	0.1972	6.8471	<0.0001***	
Δ_elev_500	0.0128	0.0052	2.4923	0.0127*	0.0196*
road_dist	-0.0003	0.0002	-1.8811	0.06	0.0467*
1 + a_500 + urb_dist					
(Intercept)	0.755	0.583	1.2949	0.1954	
a_500	0.012	0.0079	1.5081	0.1315	0.1374
urb_dist	-0.0003	0.0001	-2.3363	0.0195*	0.0146*
1 + c_500 + urb_dist					
(Intercept)	1.7254	0.3225	5.3501	<0.0001***	
c_500	-0.0483	0.0338	-1.4289	0.153	0.1443
urb_dist	-0.0003	0.0001	-2.2073	0.0273*	0.0232*
1 + b_500 + urb_dist					
(Intercept)	1.9263	0.4511	4.2705	<0.0001***	
b_500	-0.0112	0.0099	-1.139	0.2547	0.2615
urb_dist	-0.0004	0.0001	-2.7295	0.0063**	0.0039**
1 + a_500 + road_dist					
(Intercept)	0.1762	0.5146	0.3425	0.732	
a_500	0.0165	0.0081	2.0455	0.0408*	0.0437*
road_dist	-0.0004	0.0002	-2.0406	0.0413*	0.0303*

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; DPqpoisson = dispersion parameter fitting a quasipoisson.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

Taking the 250 m buffers into account, the introduction of distance indexes produced alternative models (considering $\Delta AIC_c < 2$) for spring, summer and annual use.

Table 32 - Best models and corresponding summaries for red deer spring, summer and annual use of meadows, with cover classes corresponding to the 250 m buffer, and distance indexes as predictors.

Best models (spring)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + c_250 + urb_dist	30.1501	25	0.2187	110.32	0.0006
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	2.5276	0.6216	4.0664	<0.0001***	
c_250	-0.0898	0.0388	-2.3138	0.0207*	0.0267*
urb_dist	-0.0006	0.0002	-2.6161	0.0089**	0.0076**
Best models (summer)	**Res.d**	**Df**	**GOF**	**AICc**	**DPqpoisson**
1 + c_250 + urb_dist	30.7306	25	0.1981	100.82	0.9683
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	1.9684	0.3345	5.8837	<0.0001***	
c_250	-0.0486	0.022	-2.2139	0.0268*	0.0227*
urb_dist	-0.0004	0.0001	-2.9658	0.003**	0.0016**
Best models (annual)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + c_250 + urb_dist	29.7640	25	0.2332	158.10	<0.0001
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	3.118	0.3567	8.7408	<0.0001***	
c_250	-0.0815	0.0232	-3.5113	0.0004***	0.0004***
urb_dist	-0.0004	0.0001	-2.9256	0.0034**	0.0034**

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; odTest = overdispersion test; DPqpoisson = dispersion parameter fitting a quasipoisson.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

The introduction of micro-scale variables (manag_status and domin_phyto) in the model candidate formula enhanced the results (lower AIC$_c$): in the analysis of spring use, both management status and dominant phytosociology helped explaining deer use of meadows (Table 33).

Table 33 - Best models and corresponding summaries for red deer spring use of meadows, with cover types, topographic indexes and micro-scale variables as predictors.

Best models (spring - 100 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**DPqpoisson**
1 + manag_status + domin_phyto	23.2244	21	0.3321	92.49	0.9158
1 + manag_status + domin_phyto + RIP_100	20.0499	20	0.4548	93.29	0.7142
1 + domin_phyto + RIP_100	27.8479	22	0.1808	93.51	1.0302
1 + manag_status + domin_phyto + Δ_elev_100	20.5911	20	0.4215	93.84	0.8822
1 + domin_phyto + RIP_100 + TRA_100	24.6082	21	0.2645	93.87	0.9807
1 + manag_status + domin_phyto	Estimate	Std. Error	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	1.7492	0.2085	8.3889	<0.0001***	
manag_status(rec_ab)	0.1054	0.4216	0.2499	0.8027	0.0025**
manag_status(used)	-1.8124	0.6886	-2.6319	0.0085**	
AVESU	-1.1206	0.4614	-2.4285	0.0152*	<0.0001***
BRACHY	-3.541	1.0214	-3.4669	0.0005***	
CYN	-0.7841	0.4294	-1.8262	0.0678	
JUNC	0.3302	0.4105	0.8046	0.4211	
1 + manag_status + domin_phyto + RIP_100					
(Intercept)	1.7492	0.2085	8.3889	<0.0001***	
manag_status(rec_ab)	0.0519	0.4265	0.1216	0.9032	0.0203*
manag_status(used)	-1.5175	0.6867	-2.21	0.0271*	
AVESU	-1.0392	0.4755	-2.1854	0.0289*	<0.0001***
BRACHY	-2.8549	1.0225	-2.7921	0.0052**	

CYN	-0.751	0.4279	-1.755	0.0793	
JUNC	0.3302	0.4105	0.8046	0.4211	
RIP_100	-0.3132	0.4027	-0.7778	0.4367	0.0748
1 + domin_phyto + RIP_100					
(Intercept)	1.7492	0.2085	8.3889	<0.0001***	
AVESU	-0.9972	0.3826	-2.6062	0.0092**	<0.0001***
BRACHY	-2.8504	1.0216	-2.79	0.0053**	
CYN	-1.2206	0.32	-3.8145	0.0001***	
JUNC	0.3302	0.4105	0.8046	0.4211	
RIP_100	-0.3787	0.4007	-0.9451	0.3446	0.0067**
1 + manag_status + domin_phyto + Δ_elev_100					
(Intercept)	1.9104	0.2235	8.5479	<0.0001***	
manag_status(rec_ab)	0.397	0.456	0.8707	0.3839	0.0015**
manag_status(used)	-1.6905	0.6894	-2.4522	0.0142*	
AVESU	-1.3483	0.4849	-2.7804	0.0054**	<0.0001***
BRACHY	-3.7201	1.0301	-3.6115	0.0003***	
CYN	-0.5686	0.4495	-1.265	0.2059	
JUNC	-0.0558	0.4651	-0.1199	0.9046	
Δ_elev_100	0.0449	0.0276	1.626	0.104	0.1046
1 + domin_phyto + RIP_100 + TRA_100					
(Intercept)	1.3236	0.3251	4.0714	<0.0001***	
AVESU	-0.7885	0.4374	-1.8029	0.0714	<0.0001***
BRACHY	-3.0093	1.0252	-2.9355	0.0033**	
CYN	-1.3061	0.3284	-3.9767	0.0001***	
JUNC	0.4804	0.421	1.1411	0.2538	
RIP_100	-0.9983	1.0461	-0.9543	0.3399	0.0719
TRA_100	0.158	0.0893	1.7681	0.077	0.0035

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; DPqpoisson = dispersion parameter fitting a quasipoisson
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Summer use models were not improved by micro-scale predictors. As to autumn-winter and pooled annual use analysis, management status improved both (Table 34).

Table 34 - Best models and corresponding summaries for red deer autumn-winter and annual use of meadows, with cover types and topographic indexes, corresponding to the 250 m buffer, and micro-scale variables as predictors.

Best models (autumn-winter - 250 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**DPqpoisson**
1 + manag_status + GRA_250 + OAK_250	31.1070	23	0.1202	97.02	1.4649
1 + manag_status + OAK_250 + SHR_250	31.2629	23	0.1165	97.18	1.3480
1 + manag_status + OAK_250	34.6434	24	0.0739	97.57	1.5476
1 + manag_status + GRA_250 + OAK_250	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	1.1275	0.282	3.9987	0.0001***	
manag_status(rec_ab)	0.005	0.3396	0.0148	0.9882	0.0004***
manag_status(used)	-1.7967	0.6046	-2.9718	0.003**	
GRA_250	0.0164	0.0085	1.9193	0.0549	0.06
OAK_250	-0.0841	0.0302	-2.7843	0.0054**	0.0024**
1 + manag_status + OAK_250 + SHR_250					
(Intercept)	2.0727	0.3406	6.0847	<0.0001***	
manag_status(rec_ab)	-0.2552	0.3192	-0.7995	0.424	0.0006***
manag_status(used)	-1.8162	0.6032	-3.0112	0.0026**	
OAK_250	-0.1038	0.0267	-3.8852	0.0001***	<0.0001***
SHR_250	-0.0127	0.0071	-1.788	0.0738	0.066
1 + manag_status + OAK_250					
(Intercept)	1.5166	0.1723	8.804	<0.0001***	
manag_status(rec_ab)	-0.1843	0.3179	-0.5799	0.562	0.0001***
manag_status(used)	-1.9386	0.5976	-3.2438	0.0012**	
OAK_250	-0.1099	0.0278	-3.9572	0.0001***	<0.0001***
Best models (annual - 250 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + manag_status + GRA_250 + RIP_250	28.5413	23	0.1960	143.82	0.16200

	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	2.0439	0.153	13.3553	<0.0001***	
manag_status(rec_ab)	-0.1793	0.2228	-0.8048	0.421	0.0002***
manag_status(used)	-1.0602	0.277	-3.8275	0.0001***	
GRA_250	0.0175	0.0057	3.0955	0.002**	0.0026**
RIP_250	-0.1932	0.0504	-3.8351	0.0001***	<0.0001***

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; DPqpoisson = dispersion parameter fitting a quasipoisson; odTest = overdispersion test.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

When using cover classes instead of cover types, micro-scale variables did not enhance either spring or summer use models, whereas autumn-winter and annual use models were improved (lower AIC$_c$) by the inclusion of management status.

Table 35 - Best models and corresponding summaries for red deer autumn-winter and annual use of meadows, with cover classes, topographic indexes and micro-scale variables as predictors.

Best models (autumn-winter - 250 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + manag_status + a_250	25.7959	24	0.3636	96.72	0.1734
1 + manag_status + a_250 + Δ_elev_250	27.1472	23	0.2497	98.50	0.3523
1 + manag_status + a_250	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	-1.357	0.5998	-2.2625	0.0237*	
manag_status(rec_ab)	-0.1783	0.3596	-0.4959	0.62	0.0041**
manag_status(used)	-1.6983	0.6292	-2.699	0.007**	
a_250	0.0375	0.0085	4.4307	<0.0001***	<0.0001***
1 + manag_status + a_250 + Δ_elev_250					
(Intercept)	-1.8983	0.7796	-2.4349	0.0149*	
manag_status(rec_ab)	-0.4233	0.3743	-1.1309	0.2581	0.0011**
manag_status(used)	-1.9563	0.646	-3.0283	0.0025**	
a_250	0.0416	0.0092	4.5103	<0.0001***	<0.0001***
Δ_elev_250	-0.0235	0.0181	-1.2951	0.1953	0.1841
Best models (annual - 500 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + manag_status + a_500 + d_500	30.7013	23	0.1303	155.50	0.0077
1 + manag_status + b_500 + d_500	30.9282	23	0.1246	156.37	0.0068
1 + manag_status + d_500	30.2994	24	0.1750	156.41	0.0005
1 + manag_status + a_500	30.0874	24	0.1819	156.92	0.0003
1 + manag_status + a_500 + d_500	Estimate	Std. Error	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	1.1979	0.5397	2.2195	0.0265*	
manag_status(rec_ab)	-0.2232	0.2667	-0.8368	0.4027	0.0004***
manag_status(used)	-1.236	0.3217	-3.8422	0.0001***	
a_500	0.0173	0.0076	2.2858	0.0223*	0.032*
d_500	-0.0442	0.0196	-2.2507	0.0244*	0.0217*
1 + manag_status + b_500 + d_500					
(Intercept)	2.8623	0.2903	9.8604	<0.0001***	
manag_status(rec_ab)	-0.2449	0.2698	-0.9075	0.3641	0.0002***
manag_status(used)	-1.2844	0.3231	-3.9754	0.0001***	
b_500	-0.0172	0.0086	-1.9956	0.046*	0.0573
d_500	-0.0664	0.0177	-3.7485	0.0002***	0.0001***
1 + manag_status + d_500					
(Intercept)	2.3972	0.173	13.8545	<0.0001***	
manag_status(rec_ab)	-0.4074	0.2903	-1.4034	0.1605	0.0001***
manag_status(used)	-1.4241	0.3355	-4.2447	<0.0001***	
d_500	-0.0643	0.0186	-3.4545	0.0006***	0.0003***
1 + manag_status + a_500					
(Intercept)	0.3539	0.4788	0.7393	0.4597	
manag_status(rec_ab)	0.0119	0.2871	0.0413	0.967	0.0075**

manag_status(used)	-0.9923	0.3324	-2.9852	0.0028**	
a_500	0.0273	0.0073	3.7214	0.0002***	0.0005***

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; odTest = over dispersion test.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

9.4.3 Roe deer use of meadows

Seasonal and pooled frequency distribution of roe deer presence/absence data is displayed in Figure 18 (a summary of the seasonal count data is given in Table 56, chapter 4 of the Appendix).

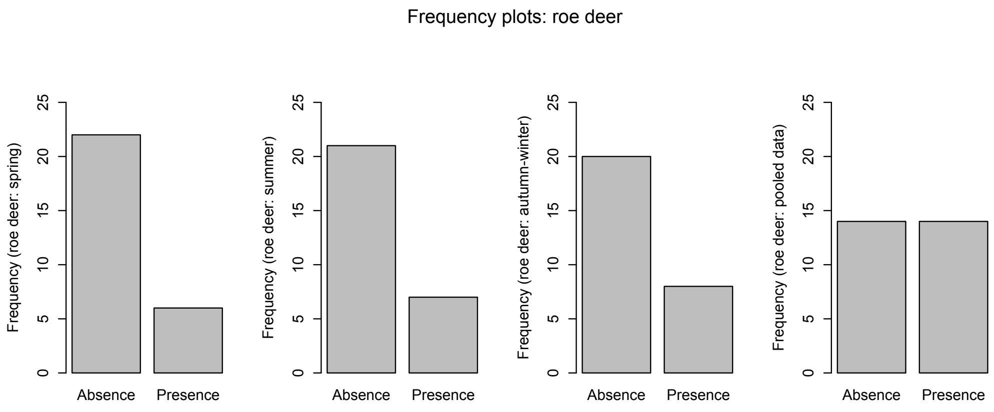

Figure 18 – Frequency distribution of seasonal and pooled roe deer data (transformed into presence/absence).

In the explorative analysis (see Figure 58 to Figure 64) we plotted roe deer presence/absence against each predictor (first and third lines) and the probability of presence associated to each decile class of each independent variable (second and fourth lines). All plots are displayed in chapter 4 of the Appendix.

9.4.3.1 First step: buffer analysis

In Table 36, the results of the first step analysis using cover types variables and topographic indexes as predictors are displayed.

Models relating to the 100 m buffer yielded lower AIC_c than the other two buffers (250 m buffer: AIC_c = 35.68 to 37.56; 500 m buffer: AIC_c = 38.46 to 40.35). MEA cover was the most significant variable included in the models, together with Δ_elev, mean_slope and AGR cover. Considering the other two buffers (see a resuming table of the models in Table 59, chapter 5 of the Appendix), the variables selected for the 250 m buffer were Δ_elev_250, AGR_250 and MEA_250. Finally, AGR_500, SHR_500, Δ_elev_500, MEA_500 and OAK_500 were the best performing variables within the 500 m buffer models.

Table 36 – Summary of the best and alternative models selected for roe deer annual use of meadows, considering cover types percentage cover and topographic indexes as variables.

Best models (100 m buffers)	Res.d	Df	GOF test	AICc	
1 + AGR_100 + MEA_100	27.0038	25	0.3557	34	
1 + AGR_100 + MEA_100 + Δ_elev_100	24.5845	24	0.4286	34.32	
1 + AGR_100 + MEA_100 + mean_slope_100	25.0212	24	0.4046	34.76	
1 + MEA_100	30.9370	26	0.2306	35.42	
	Estimate	**SE**	**z value**	**Pr(>|z|)**	**Pr(Chi)**
1 + AGR_100 + MEA_100					
(Intercept)	3.3385	1.6755	1.9925	0.0463*	
AGR_100	0.3626	0.2636	1.3752	0.1691	0.0473*
MEA_100	-0.2542	0.1188	-2.1392	0.0324*	0.0047**
1 + AGR_100 + MEA_100 + Δ_elev_100					
(Intercept)	3.6236	1.7063	2.1236	0.0337*	
AGR_100	0.4026	0.2664	1.5117	0.1306	0.0312*
MEA_100	-0.2315	0.1179	-1.9641	0.0495*	0.0117*
Δ_elev_100	0.1036	0.0745	1.39	0.1645	0.1199
1 + AGR_100 + MEA_100 + mean_slope_100					
(Intercept)	6.4972	3.165	2.0528	0.0401*	
AGR_100	0.3753	0.2757	1.3613	0.1734	0.0393*
MEA_100	-0.2725	0.1262	-2.1586	0.0309*	0.0041**
mean_slope_100	-0.2012	0.1523	-1.3214	0.1864	0.1591
1 + MEA_100					
(Intercept)	3.1526	1.3565	2.324	0.0201*	
MEA_100	-0.2078	0.087	-2.3891	0.0169*	0.005**

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05.

In relation to cover classes and topographic indexes, modelling effort did not provide interesting candidates: the null model is included within the best set in the analysis of the three buffers (see Table 60, chapter 5 of the Appendix).

9.4.3.2 Second step: introduction of macro and micro scale descriptors

In the second step, we introduced macro-scale (urb_dist and road_dist) and micro-scale variables (manag_status and domin_phyto) in the model candidate formula, together with the meso-scale variables (cover types and topographic indexes) related to the 100 m buffers (best performer in the first step analysis, yielding lower AIC_c).

Macro-scale variables did not prove significant in cover types models, and the final set of best models (model with lowest AIC_c plus any other with $\Delta AIC_c < 2$) was the same of the buffer analysis. Cover classes models were instead improved, as displayed in Table 37.

Table 37 - Best models and corresponding summaries for roe deer annual use of meadows, with cover classes and topographic indexes, corresponding to the 250 and 500 m buffer, and distance indexes as predictors.

Best model (250 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	
1 + Δ_elev_250 + urb_dist	31.6036	25	0.1698	38.60	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	-0.7015	1.1569	-0.6063	0.5443	
Δ_elev_250	0.0689	0.0416	1.6582	0.0973	0.08
urb_dist	0.0008	0.0004	1.9004	0.0574	0.0316*
Best models (500 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	
1 + urb_dist	34.6681	26	0.1190	39.15	
1 + c_500 + Δ_elev_500 + urb_dist	29.5717	24	0.1993	39.31	
1 + Δ_elev_500 + urb_dist	32.4923	25	0.1442	39.49	
1 + urb_dist	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	-1.6873	0.9816	-1.719	0.0856	
urb_dist	0.0008	0.0004	1.8344	0.0666	0.0417*
1 + c_500 + Δ_elev_500 + urb_dist					
(Intercept)	-2.3583	1.4476	-1.6291	0.1033	
c_500	0.2268	0.146	1.553	0.1204	0.0875
Δ_elev_500	0.0513	0.027	1.9015	0.0572	0.0413*
urb_dist	0.001	0.0006	1.7248	0.0846	0.0461*
1 + Δ_elev_500 + urb_dist					
(Intercept)	-1.3729	1.0447	-1.3142	0.1888	
Δ_elev_500	0.0329	0.0233	1.4118	0.158	0.1402
urb_dist	0.0009	0.0005	2.0263	0.0427*	0.0201*

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Introducing micro-scale variables did not enhance 100 m buffer models (AIC_c higher than the first step models), but was significant for the 250 and 500 m buffer analysis (Table 38). We excluded dominant phytosociology from this analysis as one of the phytosociological groups (namely, *Brachypodium rupestre* communities) had only roe presences, probably consequence of the small sample size, which prevented an interpretable modelling. Models with cover classes instead of cover types were not considered, as the best set included the null model.

Table 38 - Best models and corresponding summaries for roe deer annual use of meadows, with cover types and topographic indexes, corresponding to the 250 and 500 m buffer, and micro-scale variable management status as predictors.

Best model (250 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	
1 + manag_status + AGR_250 + MEA_250	22.5091	23	0.4898	35.24	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	3.3226	1.4991	2.2164	0.0267*	
manag_status(rec_ab)	-2.1749	1.4957	-1.4541	0.1459	0.0434*
manag_status(used)	-3.0565	1.4975	-2.0411	0.0412*	
AGR_250	0.1747	0.0902	1.938	0.0526	0.0157*
MEA_250	-0.3557	0.158	-2.2513	0.0244*	0.0051**

Best model (500 m buffer)	**Res.d**	**Df**	**GOF**	**AICc**	
1 + manag_status + AGR_500 + OAK_500	23.7170	23	0.4196	36.44	
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
(Intercept)	-1.9681	1.2259	-1.6054	0.1084	
manag_status(rec_ab)	-1.3271	1.3239	-1.0024	0.3161	0.0116*
manag_status(used)	-4.1934	1.8359	-2.2841	0.0224*	
AGR_500	0.212	0.1021	2.0775	0.0378*	0.0119*
OAK_500	0.456	0.2346	1.9436	0.0519	0.004**

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria.
SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

9.5 Discussion

Multi scalar approaches have been increasingly adopted to analyse wildlife habitat use (Rettie & Messier 2000; Mayor et al. 2009), allowing accounting for its hierarchical structure (Senft et al. 1987; Wiens 1989; Bailey et al. 1996).

The abundance of tall and dense vegetation (cover classes c and d) in the proximity of meadows, especially of riparian (most seasons) and oak forests (autumn-winter) discouraged red deer use of meadows. Conversely, large areas of herbaceous vegetation (natural grasslands and/or semi-natural meadows) correlated positively with red deer use of sampled meadows during all year, as found by other authors (Weckerly 2005). Red deer is an intermediate feeder (Hofmann 1989), changing its feeding behaviour with forage availability and quality. In the Mediterranean area, when the herbaceous vegetation is at its best nutritional value (i.e. spring and autumn, in the study area), red deer forage largely as a grazer (Bugalho & Milne 2003). Red deer seem also to prefer meadows in plateaus or wider valleys rather than in narrow and steeper valleys (positive correlation with Δ_elev) and surrounded by greater proportion of open and low vegetation cover (cover class a). This pattern of use is typical of large grazing herbivores that avoid predation risk and increase flee speed in such areas (Ripple & Beschta 2003; Fortin et al. 2005).

Roe deer is a typical browser (Tixier & Duncan 1996; Cornelis, Casaer, & Hermy 1999), using wooded landscapes frequently (Putman 1986), although it has shown a great plasticity in foraging behaviour and habitat use, like feeding on agriculture patches (Hewison et al. 2001). In our study area, roes selected more isolated meadows (presence negatively correlated to the percentage cover of meadows in the neighbourhood), preferably with presence of cultivated land in the proximity and oak forest patches within the 500 m buffer. This pattern of use reflects the need for more concealing habitat, as wood cover, in the proximity of feeding areas. Similarly to red deer, roe deer also preferred meadows in plateaus and wider valleys.

The buffer analysis permitted to compare the variability associated to vegetation mosaic composition and landscape topography across the three neighbourhood extents. Scale differences did not generate significant changes in the species response (comparable models across the three buffer), but the models fit varied: for roe deer use modelling, the 100 m buffer analysis yielded better results. Red deer results varied with season: for spring use, 100 m buffer models were the better fitted, for summer use the 250 m buffer models had lower AIC_c, whereas autumn-winter models yielded similar AIC_c in the three buffers.

The performance of the cover class variables was generally poorer (worse explicative power of the predictors and higher AIC_c values). A possible explanation could be that this category of variables (cover classes) averaged out vegetation heterogeneity (cover types), which might be important in the understanding of meadows use at these scales. In general, buffer analysis showed better results (lower AIC_c) in the models related to the larger neighbourhood, which might be related to the cover classes being coarser descriptors of the landscape mosaic.

In the second step of the analysis we aimed to assess whether the introduction of either broader or finer scale variables improved our models, thus helping describing deer use of meadows. Macro-scale variables, namely distance to urban centres and to paved road, which had been included to account for human-related disturbance, did not enhanced modelling results for either red deer or roe deer, when considering models with cover type variables. Cover classes models were instead improved, though slightly, with both distance indexes negatively correlated to red deer abundance in all the seasons. Roe deer presence was instead positively correlated to distance to villages. If we consider that the two variables (urb_dist and road_dist) are correlated, our results are in line with the findings of Torres et al. (2011), who concluded, for the same area, that roe occurrence is positively affected by distance to paved road, which reveals the shy temper of this species.

The introduction of micro-scale variables increased explanation of meadow use by deer. The dominant phytosociology of meadows explained abundance of red deer during spring. A similar result had been obtained in the patch-scale analysis of red deer spring use of meadow (see chapter 8). Phytosociology affected only red deer spring response: as underlined in chapter 8, in the Mediterranean area during spring meadow's vegetation is in the growing season, which means that its nutritional value and palatability is at its best. Red deer higher selective ability in spring may be related to this richer and more abundant forage.

Management status, that is, whether the sample meadow was currently managed (irrigated, harvested and/or grazed by livestock), recently or long abandoned, significantly improved models in both spring and autumn-winter use analysis (see Table 33 and Table 34 for red deer and Table 38, for roe deer use models). Both red and roe deer avoided particularly managed hay meadows, preferring the long abandoned ones. Concerning red deer use, this pattern can be related to the difference in forage characteristics: currently managed meadows are dominated by *Agrostio castellanae-Cynosuretum cristati* (CYN), which is moderately avoided by red deer, while the *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum* communities (ARRH), which patches are selected more than randomly (see Discussion in chapter 8), figure among the long abandoned ones. Managed meadows are also characterized, as a rule, by a greater cover of meadows in the proximity, which seems to deter roe presence. *Brachypodium rupestre* communities, which, in our sample, were always associated to roe deer presence (considering pooled annual data), occur instead as dominant type only of abandoned hay meadows: considering the low quality value of the dominant species of this vegetation type (García 1992), we should not infer that roe preference for these meadows is related to forage characteristics, but rather to the incidence of other factors, as greater distance to the villages, greater presence of concealing vegetation in the surrounding area (Mysterud et al. 1999).

In conclusion, we assessed that deer use of semi natural meadows is affected by the composition of the vegetation mosaic in the neighbourhood (above all 100 m and 250 m buffers) and it is constrained especially by micro-scale characteristics, namely, floristic composition, as described by phytosociology, and management status.

This study, considering the relatively small sample size, should be considered as a preliminary analysis of the factors affecting deer use of semi-natural meadows. However, our results showed consistency considering both seasonal patterns and buffer analysis.

10. Comparative use of Mediterranean forest habitat types by sympatric red and roe deer

10.1 Abstract of the chapter

Context: Wildlife habitat use is influenced by numerous factors, including coexistence with sympatric species that may generate competition for resources and niche segregation.

Aims: We compared deer use of pine plantations, deciduous Pyrenean oak and evergreen holm oak forests in a Mediterranean mountain range, where red and roe deer populations coexist.

Methods: Relative habitat use was assessed using faecal accumulation rate methodology. Deer use of habitat was modelled considering forest types, local topography, and relative use of the sympatric cervid. Pianka index was used to evaluate habitat use overlap.

Key results: Roe and red deer favoured autochthonous oak forests over pine plantations. Holm oak forests were preferred by red deer, whereas roe deer used deciduous oak forests more. Presence of the sympatric species was not a constraint and a substantial overlap in spatial use of habitat was observed between red and roe deer in both periods.

Conclusions: Although the two sympatric ungulates showed differences in their use of different forest types, no segregation was detected in the area, with instead a substantial overlap in habitat use. The observed lack of segregation in our opinion might be related to the low density at which red and roe deer populations occur.

10.2 Introduction

There are several determinants of habitat use by large mammalian herbivores, related to resource availability, especially forage and shelter. When sympatric ungulates co-occur in the same territory the characteristics of the available resources may lead to competition, when resources are limited, or coexistence between species. For example, studies on diet overlaps have confirmed that, in a number of cases, coexistence of herbivores sharing foraging habits is achieved by actual differential feeding behaviours, or niche partial segregation (Heroldová 1996; Storms et al. 2008; Bertolino, di Montezemolo, & Bassano 2009).

Beyond forage availability and quality, other factors constrain deer habitat selection, such as hiding and thermal cover (protection from extreme weather conditions). Roe deer habitat selection, for instance, may be more related to cover availability than forage availability (Mysterud et al. 1999). Hiding cover, measured as obstruction to visibility, and thermal cover, measured as stand canopy density and development, increase the probability of browsing and of habitat use by roe deer (Partl et al. 2002). The strength of these correlations may even increase in the case of female roe deer, because of their need for shelter to improve offspring survival (Cimino & Lovari 2003).

We focus our research on co-occurring red deer (*Cervus elaphus hispanicus*) and roe deer (*Capreolus capreolus*) in a Mediterranean environment. Red deer is an intermediate or mixed feeder (Hofmann 1989), switching from herbaceous vegetation to browse (and vice versa), depending on availability and forage nutritional quality. Anyway, particularly in winter, red deer has shown a foraging behaviour more similar to that of a concentrate selector, implying potential competition with sympatric browsers (see Gebert & Verheyden-Tixier 2001 for a review on European red deer diets). Roe deer is considered a selective browser (concentrate selector) (see Tixier & Duncan 1996; Cornelis et al. 1999 for a review) generally linked to wooded patches (Putman 1986), although some studies proved that its distribution is expanding on more open areas, like agricultural lands (Hewison et al. 2001), showing some plasticity in relation to feeding behaviour. Both species are expanding in Portugal, due to land use abandonment and increased favourable habitat and because of reintroduction programmes mainly for hunting and conservation purpose. Red and roe deer co-occurs naturally in the study area (Natural Park of Montesinho), and Peneda-Gerês National Park: both areas are located on the Portuguese frontier with Spain. The populations co-occurring in the Serra da Lousã derive from a reintroduction programme. According to previous studies in the Mediterranean area, sympatry among ungulates is often unfavourable for roe deer. For example, Focardi et al. (2006) pointed out high fallow deer density as a possible cause for roe deer population declining in the preserve of Castelporziano (near Rome). Ferretti et al. (2010) found that fallow deer directly interfered with roe deer feeding activity, displacing roe deer, and Torres (2011) established that roe deer distribution is negatively affected by red deer presence while the opposite is not true. In temperate areas roe deer populations can be outcompeted by red deer (Latham, Staines, & Gorman 1997) and muntjac deer (*Muntiacus reevesi*) (Chapman et al. 1993; Hemami et al. 2004). Generally the detrimental effect is linked to high population densities of the co-occurring species (Chapman et al. 1993; but cf. Prokešová, Barančeková, & Homolka 2006). Moreover, the outcome of ungulates coexistence and the magnitude of resource use overlapping can be related with the scale of observation: scaling up may show an increase of the overlap, as the resource heterogeneity is averaged out (Wiens 1989), masking finer scale resource partitioning. Ferretti et al. (2011) found that fallow and roe deer exhibited high spatial overlap at broad scale but low at a finer scale and similar results were found by Hemami, Watkinson, & Dolman (2004) for roe deer and muntjac. We investigated habitat use by red and roe deer in a Mediterranean mountain environment, where the two species occur at low densities. We assessed deer relative use of the three most representative forest habitat types occurring in the study area, and investigated if there was evidence of habitat use overlap or segregation at a fine spatial scale. We also considered the potential effect of topography on deer use of forest habitats.

Agricultural abandonment is a driving force in landscape vegetation dynamic (Chauchard et al. 2007). Abandonment has favoured natural regeneration and forest expansion in most Mediterranean marginal mountainous areas (but see Acácio et al. 2007, for a case of arrested succession); however, these autochthonous forest communities are still very fragmented in Portugal (Pôças et al. 2011). Evaluating how deer populations use these natural habitats in comparison with commercial plantations is important for both deer and forest management purposes. Although there is abundant research on deer ecology and habitat use in Mediterranean environments (Garcia-Gonzales & Cuartas 1992; San José et al. 1997; Tellería & Virgós 1997; Virgós & Tellería 1998; Garin et al. 2001; Paiva 2004; Lamberti et al. 2006; Acevedo & Cassinello 2009; Torres et al. 2011), less is known on fine scale habitat selection particularly in areas where red and roe deer may co-occur.

10.3 Methods

10.3.1 Study area

The study area is located in the Natural Park of Montesinho (NPM), Northeast Portugal (Figure 1a,b). NPM is a 75 000 ha area, included in the Pan-European network of protected areas Natura 2000. A mosaic of deciduous (*Quercus pyrenaica*) and evergreen (*Q. rotundifolia, Q. suber*) oak woodlands, commercial coniferous stands (above all *Pinus pinaster*), different shrublands (dominant species of the different communities: *Erica australis, Pterospartum tridentatum*, *Halimium alyssoides*, *Cistus ladanifer* and. *Cytisus* sps), and both annual and perennial grasslands, characterize NPM area. Natural and semi-natural plant communities of the Park have been classified by Aguiar (2001) following the phytosociological approach of the Zurich-Montpellier School. The study area is under Mediterranean bioclimate (meso to supra-Mediterranean, sub-humid) according to the Rivas-Martínez’s Bioclimatic Classification of the Earth (Rivas-Martínez 2007).

Both red and roe deer populations occur in the park at low densities (respectively 3 to 4 and 1 to 2 individuals/km^2 according to Paiva 2004), when compared to other non-fenced Mediterranean areas (roe deer: 8.5/km^2 (Focardi et al. 2002) and 13.3/km^2 (Fattorini et al. 2010) in Italy; red deer: 13/km^2 in Spain (Smit et al. 2009); 26/ km^2 in Sardinia (Lovari et al. 2007)). A stable population of wolves (*Canis lupus signatus*) is also present (density: 1,6 to 3,1 individuals/100km^2 according to Moreira et al. 1997).

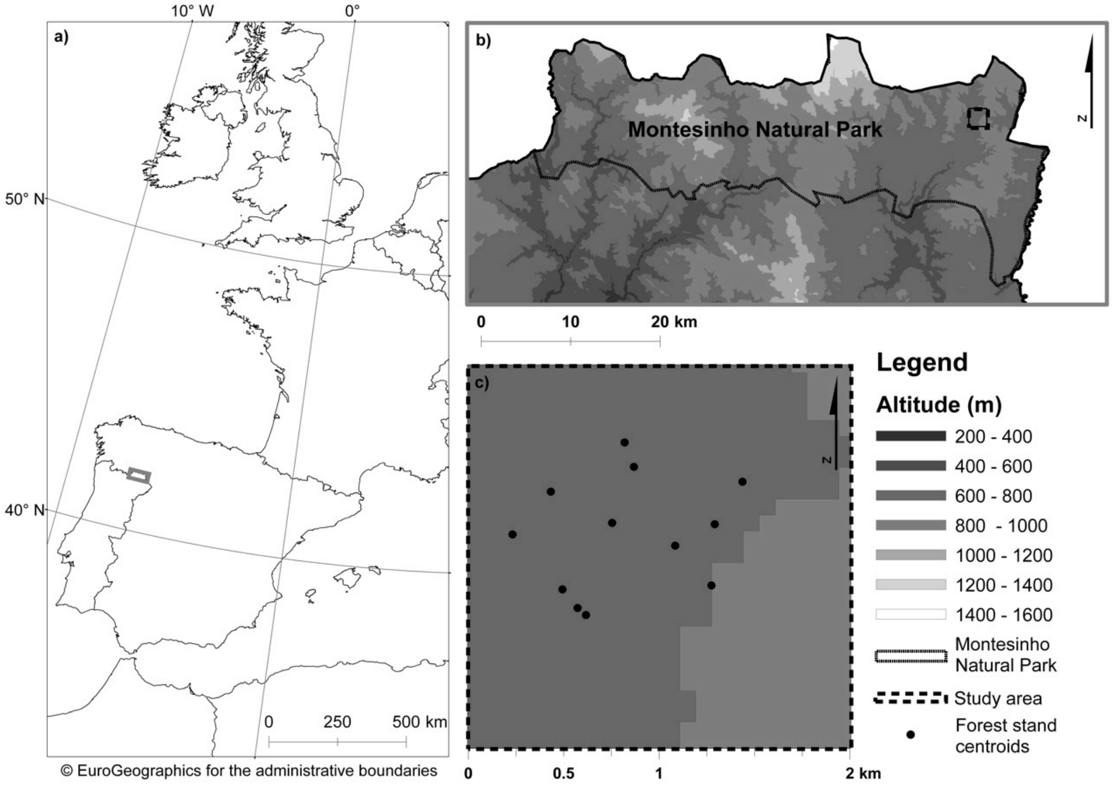

Figure 19 – Study area location: a) map of Western Europe highlighting the area of the research; b) Montesinho Natural Park boundaries (North-East of Portugal) and study area; c) location of the forest stand centroids within the study area.

The study area is a 2x2 km square (see Figure 19b) which was selected taking into account the following criteria: 1) similar distance from the three nearest villages (Rio de Onor, Varge and Guadramil); 2) inclusion of a segment of the Rio de Onor river; 3) fair distance from the main road (N308, which links Portugal to Spain); 4) good representation of the different vegetation communities in analysis and of the typical vegetation mosaic of this part of the Montesinho Natural Park.

Vegetation patches were digitized in using the ESRI ArcMap^{TM} 9.2 SP4 geographical information system software, aerial photographs and field recognition. The vegetation communities represented in the area are shown in Table 39 and Figure 20.

Table 39 – Vegetation communities occurring in the study area.

Vegetation units	Corresponding associations or communities
Deciduous oak forests	*Genisto falcatae-Quercetum pyrenaicae*
Evergreen oak forests	*Genisto hystrix-Quercetum rotundifoliae*
Mixed oak forests	Mosaic of *Genisto falcatae-Quercetum pyrenaicae* and *Genisto hystrix-Quercetum rotundifoliae*
Commercial stands	Commercial stands of *Pinus pinaster*
Riparian forests	Both Com. of *Salix x pseudosalviifolia* and *Galio broteriani-Alnetum glutinosae*
Grasslands	Correspond to abandoned semi-natural meadows and natural perennial grasslands
Meadows	Semi-natural meadows, still managed or very recently abandoned
Low shrubland	*Cistus ladaniferi-Genistetum hystricis*; *Genistello tridentate-Ericetum aragonensis* var. of *Cistus ladanifer*;
Tall shrubland	*Lavandulo sampaioanae-Cytisetum multiflori*

Three different forest habitat types were considered, being the most representative at the landscape scale. A brief description of the communities is given in Table 40.

Four stands were randomly chosen for each of the three forest types, and three 2x10 m transects marked in situ in each stand (Figure 19 and Figure 20). Belt transects were favoured over circular plots because they resulted easier to establish in the field, also facilitating the search effort. Transects were geo-referenced by GPS and nearest tree marked with a striped coloured plastic band to overcome GPS resolution error and assist the subsequent locating.

Figure 20 - Vegetation and land cover types of the study area.

We computed the mean slope of an area with 100 m radius, surrounding the centroid of the triangle formed by the central points of each stand transects, (mean_slope), using the SRTM digital terrain model (CGIAR-CSI 2008). Slope gives an approximation of the physiography of the surrounding landscape, which can influence deer selection, for example affecting energy expenditure (Kie et al. 2005).

Table 40 – Characterization of the forest communities considered in the study.

Pine stands	Commercial stands with high tree densities (> 80%), poor undergrowth, extremely rare to moderately dense (0 to 20%), mainly composed of *Erica* sp.
Deciduous oak forests	*Genisto falcatae-Quercetum pyrenaicae* association. Moderate (80 to 90% cover) to high (100% cover) tree density which affects the undergrowth and the presence of renovation: *Quercus rotundifolia* often present, as well as well developed renovation patches of *Q. pyrenaica*. In the older and denser stands, renovation is poorer and smaller.
Evergreen oak forests	*Genisto hystrix-Quercetum rotundifoliae* association. Either secondary communities that have been colonizing abandoned agricultural land in the past 30 years and are in slow transition towards the climactic *Genisto falcatae-Quercetum pyrenaicae*, (Aguiar 2001), or edaphoxerophilous communities on shallow schistic soils on steeper slopes. Canopy cover is generally lower than deciduous forests (60 to 75%), with greater presence of understory shrubs.

10.3.2 Deer use assessment

Faecal pellets groups were counted in December 2008 and June 2009 in transects that were cleared of pellets groups in June 2008. Faecal pellet groups found on the boundary of transects were alternately counted and ignored (Marques et al. 2001). The resulting faecal count accumulation was used to assess relative use of forest patch types by deer during summer/autumn and winter/spring. Faecal accumulation rate (FAR) is normally used to estimate deer relative use of habitat (Loft & Kie 1988; Latham et al. 1996; Palmer & Truscott 2003; Borkowski & Ukalska 2008).

Following Palmer & Truscott (2003), any faecal pellet group containing at least 10 identifiable pellets of similar size, colour and shape was counted. Pellets were discriminated between the two deer species according to their size.

10.3.3 Statistical analyses

We used generalized linear models (GLMs) to analyse FAR in different forest types. We assumed a Poisson distribution for faecal counts of red and roe deer and checked for overdispersion fitting a quasipoisson model: whenever the dispersion parameter was considerably larger than 1 and the residual deviance goodness of fit test was significant (bad fit for the Poisson model), we fitted the GLM with a negative binomial distribution (Zeileis et al. 2008). For both cases we used a log link-function. We modelled the response variable (deer faecal count data (within stand mean)) against forest types (three levels factor), mean slope of the surrounding area, and sympatric deer abundance (faecal counts in the same stand).

Analyses were executed in R (R Development Core Team 2010), using package *glmulti* (Calcagno 2011), which provides a wrapper for *glm* and other similar R functions. Considering the small sample size, we constrained the models candidate formula to only two variables, to reduce the risk of overfitting (Maroco 2007). Best model was selected considering the lowest AIC_c (Burnham & Anderson 2004), which is the correction for Akaike Information Criteria (Akaike 1974) for small sample size. Models with Δ AIC$_c$ (from the lowest) under 2 scores were also considered as alternative ones.

The degree of habitat use overlap was assessed with the Pianka index (Pianka 1974):

$$O_{red-roe} = \frac{\sum_i^n p_{i(red)} p_{i(roe)}}{\sqrt{\sum_i^n p_{i(red)}^2 \sum_i^n p_{i(roe)}^2}}$$

where $p_{i(red)}$ and $p_{i(roe)}$ represent the proportion of the resource ith (either forest type or forest stand) used by, respectively, red and roe deer. The index ranges from 0 (complete segregation) to 1 (complete overlap).

10.4 Results

Faecal counts were similar for red and roe deer with 34 and 42 pellets groups respectively, during summer/autumn and 32 and 29 in winter/spring, respectively (see raw data in Table 61, chapter 6 of the Appendix). There were differences in use of forest types by red and roe deer as shown in the models presented below.

During summer and autumn, roe deer use of forests was influenced by forest type (likelihood ratio test p-value = 0.0007), with pine plantations used significantly less than deciduous oak forests (estimate coefficient = -3.3673; Wald test p-value = 0.0032). Roe deer use of evergreen and deciduous oak woodlands did not differ significantly, although holm oak forests were used less than deciduous oak ones (estimate coefficient = -0.8824; Wald test p-value = 0.1498). Roe deer abundance was also positively related to red deer FAR counts (red_FAR Wald test p-value = 0.0148).

Table 41 - Roe deer seasonal use models.

Best and alternative models (summer-autumn)	**Res.d**	**Df**	**GOF**	**AICc**	**odTest**
1 + forest type (best)	12.0271	9	0.2118	60.33	0.0060
1 + red_FAR (alternative)	12.1684	10	0.2739	62.06	<0.0001
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + forest type					
(Intercept)	1.981	0.404	4.903	0<0.0001***	
scler_oak	-0.8824	0.6127	-1.4403	0.1498	0.0007***
pine	-3.3673	1.1367	-2.9624	0.0031**	
1 + red_FAR					
(Intercept)	-0.3281	0.744	-0.441	0.6592	
red_FAR	0.4766	0.1955	2.4384	0.0148*	0.0716
Best model (winter-spring)	**Res.d**	**Df**	**GOF**	**AICc**	**DPqpois**
1 + forest type (best)	10.0156	9	0.3492	46.45	0.9753

	Estimate	SE	z value	Pr((>|z|)	Pr(Chi)
1 + forest type					
(Intercept)	1.5041	0.2357	6.3813	<0.0001***	
scler_oak	-0.6931	0.4082	-1.6979	0.0895	0.0006***
pine	-2.1972	0.7454	-2.9479	0.0032**	

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; DPqpois = dispersion parameter.
SE = standard error Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

A similar pattern was found for winter and spring use models (Table 41), (forest type likelihood ratio test p-values = 0.0006): again, roe deer log counts in pine plantations were significantly lower than counts in deciduous oak forests (estimate coefficient = -2.1972, Wald test p-value = 0.0032). Evergreen forests were also used less than deciduous ones, with results marginally significant at the 0.05 level (estimate coefficient = -0.6931, Wald test p-value = 0.0895). Mean slope did not influence roe deer abundance.

Analysing red deer use models, again, forest type significantly influenced red deer use (likelihood ratio test p-value (summer-autumn) = 0.0306; likelihood ratio test p-value (winter-spring) = 0.0018). Pine plantations were significantly less used than evergreen oak forests (Wald test p-values (summer-autumn) = 0.0162; Wald test p-values (winter-spring) = 0.0033). In winter and spring red deer use of deciduous oak forests was significantly lower than their use of evergreen oak forests (estimate coefficient = -0.9163; Wald test p-value = 0.0285; see Table 42). The introduction of mean slope and abundance of sympatric roe deer into the model formula was not relevant.

Table 42 - Red deer seasonal use models.

Best model (summer-autumn)	**Res.d**	**Df**	**GOF**	**AICc**	**Dpqpois**
1 + forest type (best)	14.9412	9	0.0926	53.59	1.1434
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + forest type					
(Intercept)	1.4469	0.2425	5.9658	<0.0001***	
dec_oak	-0.3483	0.377	-0.9238	0.3556	0.0306*
pine	-1.2238	0.5087	-2.4055	0.0162*	
Best model (winter-spring)	**Res.d**	**Df**	**GOF**	**AICc**	**Dpqpois**
1 + forest type (best)	12.5976	9	0.1817	50.03	1.3112
	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + forest type					
(Intercept)	1.6094	0.2236	7.1976	<0.0001***	
dec_oak	-0.9163	0.4183	-2.1904	0.0285*	0.0018**
pine	-1.6094	0.5477	-2.9385	0.0033**	

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria; AIC = Akaike information criteria; DPqpois = dispersion parameter.
SE = standard error Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05

Pianka indexes showed the existence of habitat use overlap, greater for summer-autumn period than for winter-spring. Overlap was greater at the habitat type level than at the finer scale of stands (forest type level: summer-autumn $O_{red\text{-}roe} = 0.83$; winter-spring $O_{red\text{-}roe} = 0.75$; stand level: summer-autumn $O_{red\text{-}roe} = 0.70$; winter-spring $O_{red\text{-}roe} = 0.66$).

10.5 Discussion

According to the results, both roe and red deer showed an overall scarce use of pine plantations. Commercial pine stands in the area are generally characterized by high tree density and close canopy cover, which prevent the development of a shrub layer, thus they hardly serve as foraging habitat. The low use indexes encountered in pine plantations, may be related to the species preference, when the alternative is locally present, (as in the study area) for comparably smaller and more diverse stands, like oak forest patches, which can provide cover and forage, in the openings and the ecotone.

Roe deer use of deciduous oak forests during winter and spring was greater than use of evergreen oak forests, though marginally significant. Other authors found that in Mediterranean mountains roe deer is particularly linked to mesic forests and that its distribution in the more xeric ones (like holm oak stands) is constrained by scarcity of nutritive forage, above all during the drier seasons (San José et al. 1997; Tellería & Virgós 1997; Virgós & Tellería 1998). In our study area, unlike the mentioned studies, the distribution of the two oak forests is not related to an altitudinal or climatic gradient. Both forest types are interspersed in a fine scale mosaic (see Figure 20), and their occurrence depends on local topography, soil characteristics and past land management history (see chapter 6.1.2). Roe deer preference for the Pyrenean oak forests might be related to the presence of meso-hygrophilous species, like *Rubus* spp. and *Rosa* spp. in the openings and fringes, which are typically selected by roe deer (Tixier & Duncan 1996), and are infrequent in the dryer holm oak forests (Aguiar 2001). The more concealing habitat of deciduous oak forests, which have higher tree density in the study area, might be preferred as anti-predator strategy (Bongi et al. 2008).

In winter and spring, red deer used holm oak forests significantly more than deciduous ones, possibly because, in our study area, these stands have a more open structure than that of deciduous oak stands (see Table 40), and larger shrub cover (mostly leguminous shrubs and *Erica* sp.) that may be an important source of food.

Habitat use by one deer species was not negatively affected by the presence of the sympatric deer species, unlike other authors' findings (Torres 2011). The apparent lack of segregation, further confirmed by the Pianka indexes, could be related to the low population density of both deer species occurring in the area.

Despite differences in patterns, red and roe deer showed substantial overlap in their use of forest types. Similar findings were reported by other studies in the area (Vingada 1991, apud Valente e Santos 2009). Overlapping was greater during summer and autumn, which might be related to the fact that red deer switches from a grazing to a browsing foraging strategy during the dry season, and herbaceous vegetation declines in nutritive quality (Bugalho & Milne 2003). Additionally, autumn overlap can be related to availability of alternative food, such as oak acorns, which are selected by both deer species (Tixier & Duncan 1996; Gebert & Verheyden-Tixier 2001). Although still considerable, overlap at the stand level, that is, at a finer scale, is lower than at the forest type level, as reported by other researches on sympatric ungulates (Hemami et al. 2004; Ferretti et al. 2011).

Our results, as mentioned before, should be considered a preliminary interpretation of the comparative use of forest types of the two coexisting cervids: extending the study approach to a larger area is needed to confirm the assessed trends.

III. Potential distribution of roe deer in the Montemuro-Freita-Arada mountain range: suitability and constraints

11. Study area

11.1 Location

The study area is located in the mountainous complex of Montemuro-Freita-Arada (MFA), in the north-central mainland Portugal (between 40º 48’ N and 41º 10’ N parallels and 7º 32’ W e 8º 17’ W (ETRS89) meridians (Figure 21). The area includes two sites of community interest (SCI, PTCON0025 Serra de Montemuro and PTCON0047 Serras da Freita e da Arada).

The study area contains different classified habitats described in Natura 2000 Network Sectorial Plan (ICN 2006), including alder and ash alluvial wood (91E0 - *Alnus glutinosa* e *Fraxinus excelsior* alluvial woods, *Alno-Padion*, *Alnion incanae*, *Salicion albae*, priority habitat), relatively well preserved; oak woods (9230 – *Quercus robur* and *Q. pyrenaica* Galician-Portuguese forests), whose major examples are in the Serra de Montemuro site. In relation to shrublands, the temperate Atlantic wet heaths with *Erica ciliaris* and *Erica tetralix (priority habitat 4020*) and bogs (7140), occur in both Montemuro and Arada-Freita sites. In Arada-Freita *Ulex* dominated shrub communities (4030 – with *Ulex europaeus* subsp. *latebracteatus* and/or *U. minor*) are also frequent. With regard to wildlife, the two Natura 2000 sites comprise an important portion of the distribution area of some of the few Iberian wolf packs that still endure South of the Douro River (Pimenta et al. 2003).

The aim of this chapter was to assess the probability of use of the semi-natural meadow of MFA for cervids, considering patterns of use by deer investigated in the Natural Park of Montesinho.

I constrained the study area to the potential distribution area of the *pyrenaica* oak series (*Holcus mollis-Querco pyrenaicae* Sigmetum), as modelled and validated by Monteiro-Henriques (2010). I decided for this limit for two orders of reasons:

I. Montemuro-Freita-Arada lower mountain range (above all the Montemuro portion) is characterized by a greater anthropic presence than the area studied in the Montesinho Natural Park (NPM), that is, by both a greater number of urban centres and population density, which constitute an important source of disturbance for cervids populations. Thus, in order to find condition of human-related disturbance similar to the one in the NPM area, I considered only the upper mountain range.

II. Although the *pyrenaica* oak series occurring in the NPM area is not represented in the Montemuro-Freita-Arada area, the climactic mesic forest vegetation of the upper mountain range is also dominated by *Quercus pyrenaica*. Other *pyrenaica* oak dominated forests, namely the *Arbutus unedonis-Quercetum pyrenaicae*, were not consider because they occur at lower altitudes. Holm oak forests (9340 – *Quercus rotundifolia* forests) occur in the Freita-Arada site, but only on very localized steep slopes and crests without cartographic expression at the landscape scale and were also not considered.

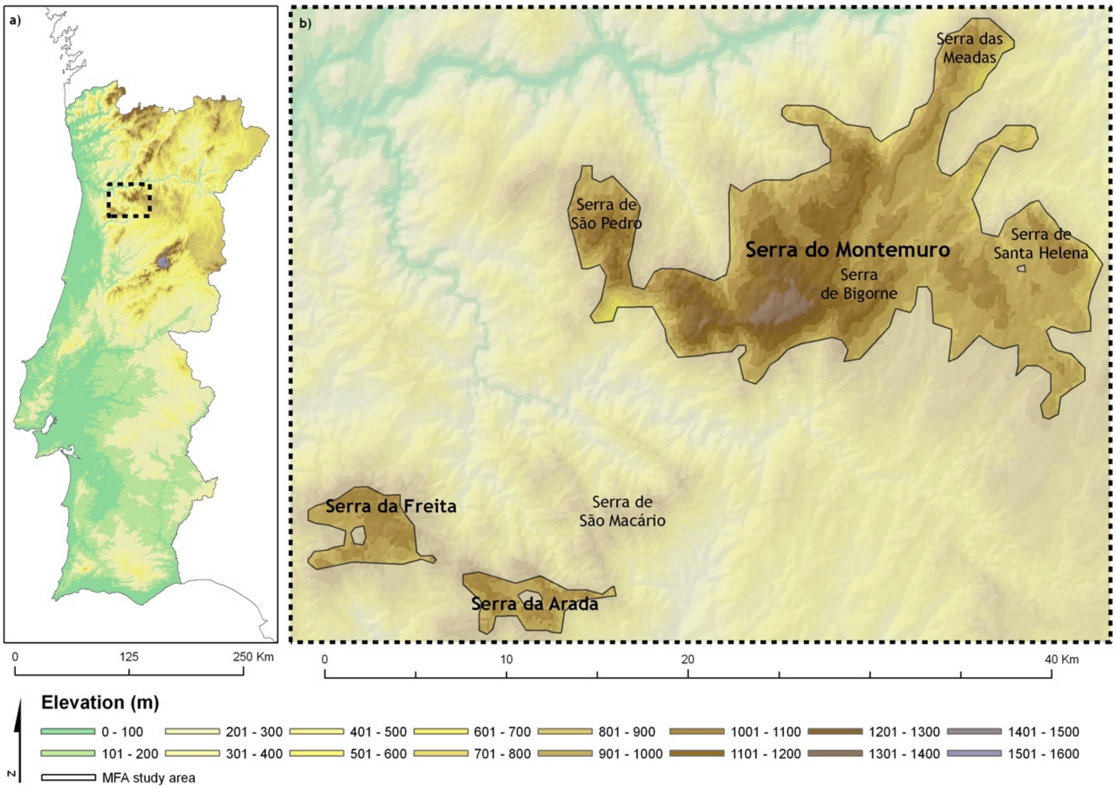

Figure 21 – Location of the study area, with reference to hypsometry: a) Montemuro-Freita-Arada (MFA) area (dotted line); c) study area within the MFA mountain range.

11.2 Geology and hydrology

The lithology of the study area can be summarized in five main rock groups: i) granitoid rocks (particularly monzonitic, muscovitic and/or biotitic Hercynian granites); ii) Douro's Group metasediments (Dúrico-Beirão Supergroup, or schist-greywacke pre-Ordovician Complex); iii) Beiras' Group metasediments (Dúrico-Beirão Supergroup, or schist-greywacke pre-Ordovician Complex); iv) granitoid rocks with higher base and mafic minerals tenor (especially granodiorites); v) Ordovician, Silurian and Carboniferous metasediments.

A lithological synthesis of the study area, based on the Geologic Map of Portugal 1:500 000, is displayed in Figure 22, adapted from Monteiro-Henriques (2010).

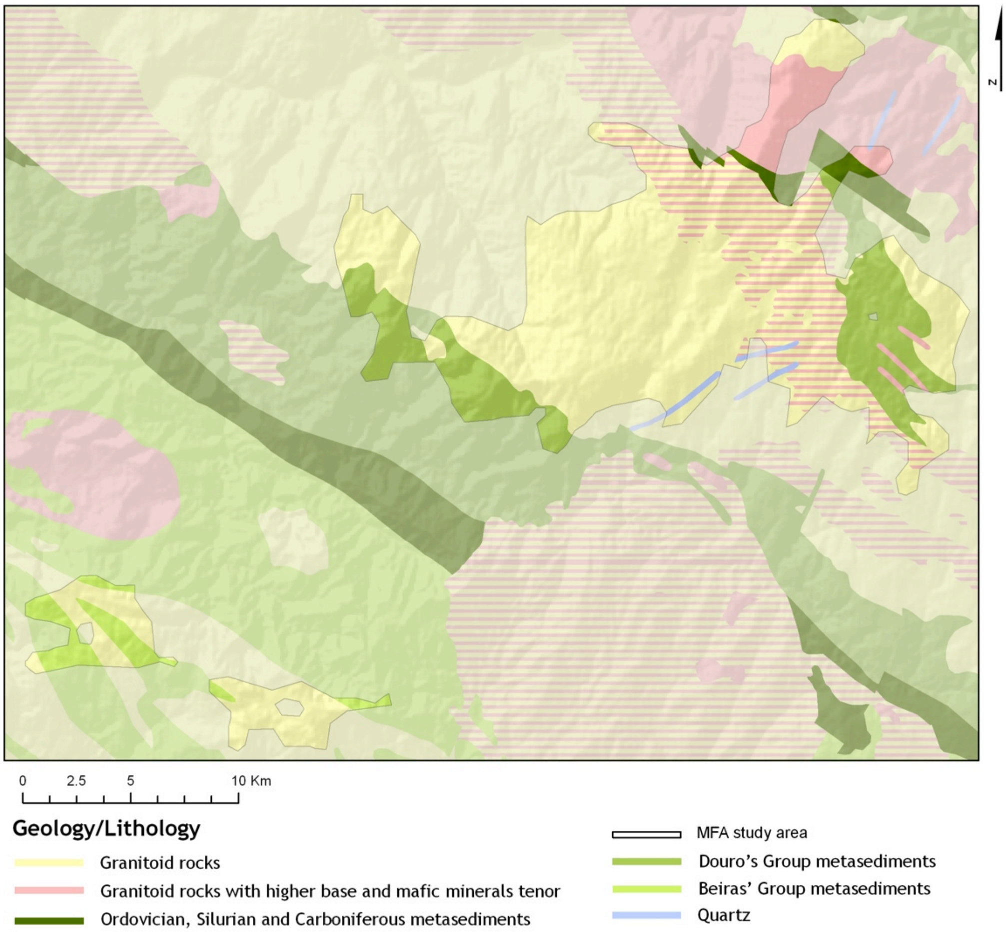

Figure 22 – Geologic map of the Montemuro-Freita-Arada study area.

The watercourses of the MFA are more rectilinear on granitoid rocks and more sinuous on metasediments. In the Montemuro massif, the granitoid rocks occur at the highest elevations, corresponding to the extensive polygenic planation surface of the Meseta. The streams' meanders in this higher portion of the massif resulted from a first erosion cycle (Schermerhorn 1980).

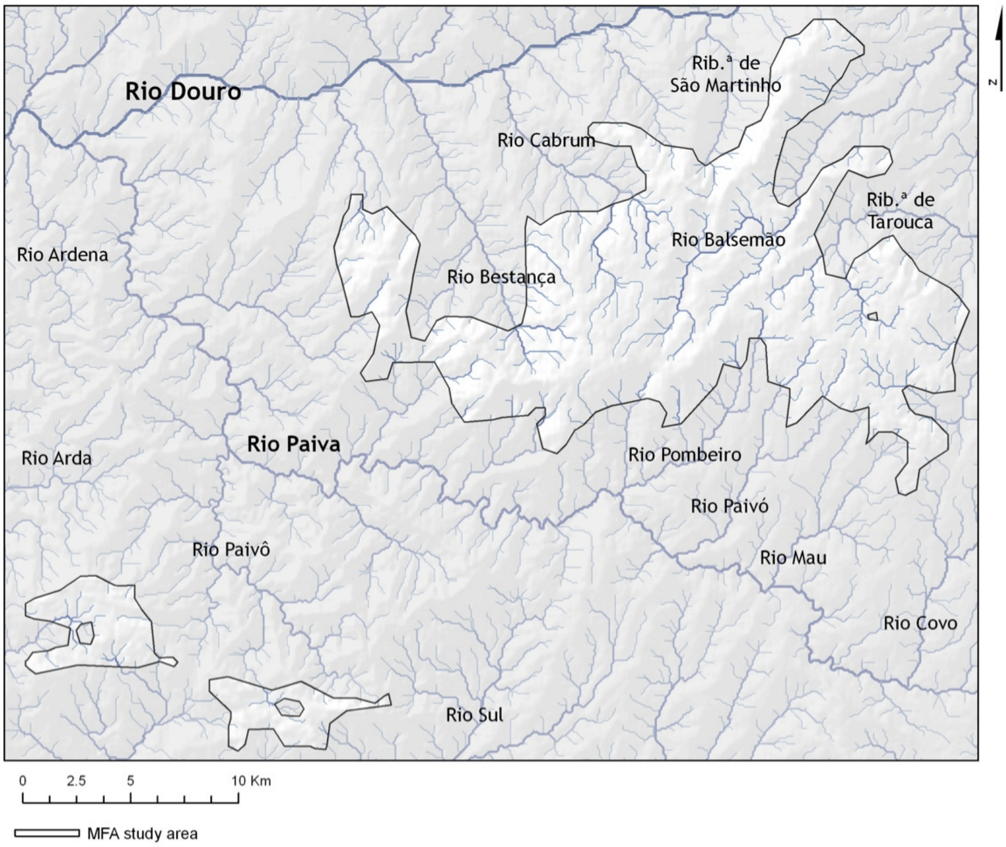

Figure 23 – Hydrological map with reference to the main watercourses of the MFA area.

11.3 Bioclimatology

The bioclimatic maps of the MFA massif (Monteiro-Henriques 2010) have been constructed following Rivas-Martínez (2005b). According to thermotypes map (Figure 24), the highest elevations are supra-temperate sub-Mediterranean while the mid-range altitudes present meso-temperate sub-Mediterranean thermotype; the bottom of the valleys is meso-Mediterranean/thermo-temperate. The ombrotypes map (Figure 24) shows that the humidity varies from ultra-hyper-humid on the mountaintops to sub-humid in the bottom of the valleys. The supra-temperate area corresponds with high accuracy to the climactic domain of *Quercus pyrenaica* forests (*Holco mollis-Quercetum pyrenaicae*), occurring in the mountaintops of Serra do Montemuro and Serra da Arada-Freita (see Monteiro-Henriques 2010), consequently the study area is constrained to the supra-temperate thermotype.

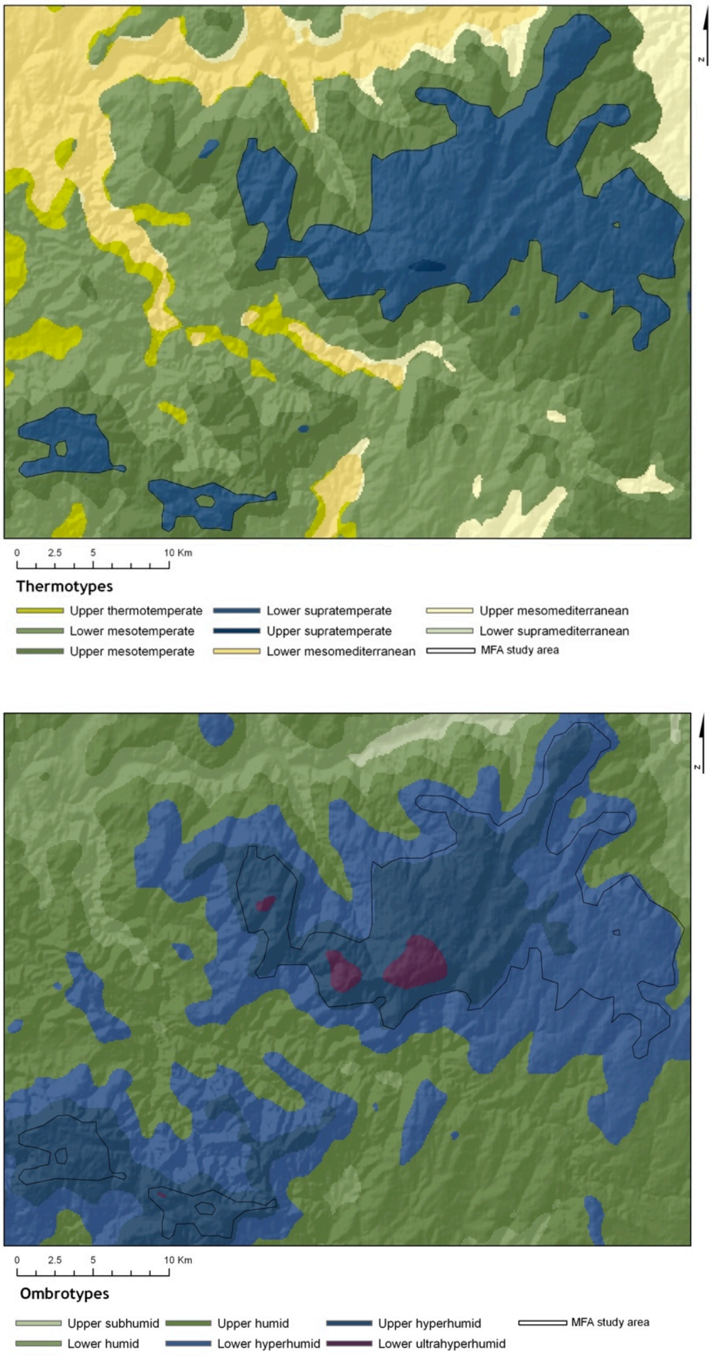

Figure 24 – Bioclimatic maps of the Montemuro-Freita-Arada mountain range.

11.4 Human presence and activities

The prehistoric human presence in the highlands of MFA massif is attested by the presence of megalithic structures from the Neolithic. In fact, if the vestiges from Palaeolithic are less frequent in Iberia compared to Central Europe, the Neolithic structures are extremely frequent in the centre of Portugal, especially those dated from the Copper Age, 5200-2200 BC (Milisauskas 2011). Since then, human presence in the region has been practically constant and agriculture has been undoubtedly the greater moulding factor of the landscape, particularly in the MFA. It is possible that in the middle of the XX century the maximal extension of territory use and population were reached (Aguiar et al. 2009). Presently, MFA mountain range, likewise Montesinho range, is interested by a progressive demographic decline, which reflects on the landscape mosaic: the abandonment of the cultivated lands and semi-natural meadows is advancing from the marginal areas towards the urban centres, followed by the expansion of shrubs and eventually forest patches. Wildfires have become very frequent (Figure 25), mainly set by residents, primarily to control shrub vegetation growth, to preserve pastures and to keep trails and paths open.

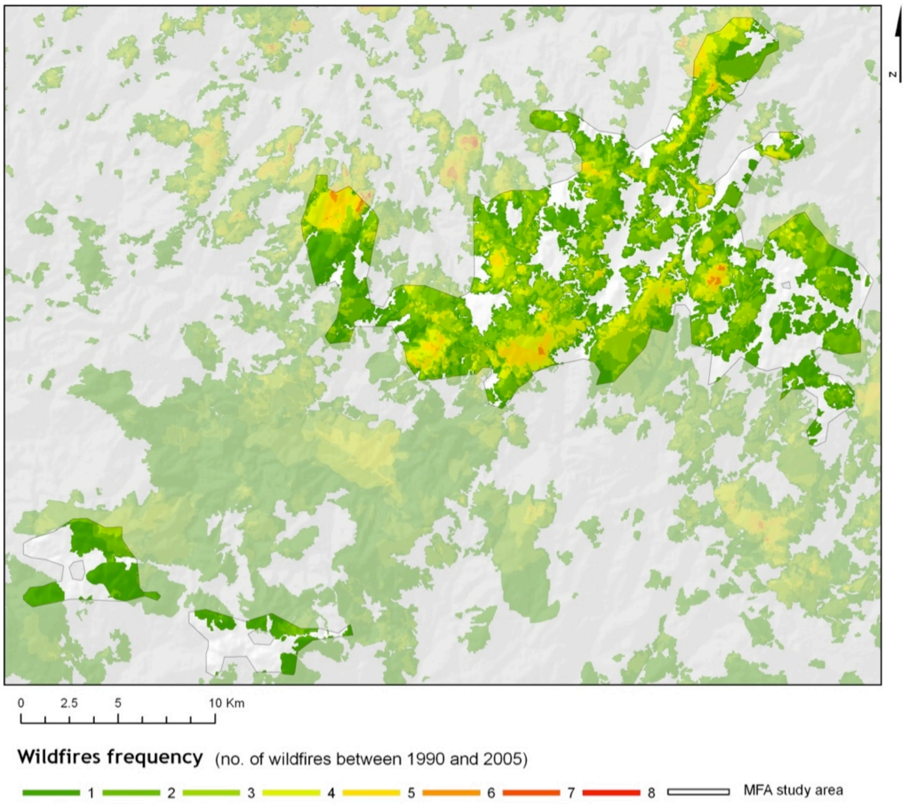

Figure 25 – Number of wildfires between 1990 and 2005 in the MFA mountain range (Direção Geral dos Recursos Florestais - DGRF).

11.5 Natural vegetation communities of the MFA area with landscape scale expression

As specified in subchapter 11.1, the Montemuro-Freita-Arada (MFA) study area is constrained to the potential distribution area of the *Holcus mollis-Quercetum pyrenaicae* series, as modelled by Monteiro-Henriques (2010).

Hereafter, I give a brief description, adapted from Monteiro-Henriques (2010), of the vegetation communities included in this series and generally occurring in the area, with landscape scale expression, focusing on forests, shrublands and perennial grasslands.

11.5.1 Forest communities

11.5.1.1 *Holcus mollis-Quercetum pyrenaicae*

The *Holcus mollis-Quercetum pyrenaicae* is the climactic vegetation community of the series. It occurs in the supra-temperate (sub-Mediterranean), punctually supramediterranean, humid to hyper-humid, semi-hyper-oceanic to eu-oceanic bioclimatic area, on oligotrophic, acid, deep soils. This community is a deciduous-marcescent forest, dominated by *Quercus pyrenaica*, accompanied by *Holcus mollis* subsp. *mollis, Teucrium scorodonia* subsp. *scorodonia*, *and Stellaria holostea*, among others. Although frequent within the study area, above all in the Montemuro range, these forest communities are fragmented and degraded, due to the recurrence of wildfires. Therefore, different subserial communities, according to local conditions, occupy its potential distribution area.

11.5.2 Tall shrub communities

11.5.2.1 *Cytiso striati-Genistetum polygaliphyllae cytisetosum multiflori*

This microphanerophytic community is dominated by *Genista florida* subsp. *polygaliphylla*, accompanied by *Cytisus grandiflorus* subsp. *grandiflorus*, *C. striatus* subsp. *striatus* and *Cytisus multiflorus*. It frequently occupies anthrosols, i.e. deep soils of abandoned fields. Traditionally a managed form of these communities (“tapadas”, which are characterized by a reduction of the shrub layer in order to enhance the herb layer) is used to complete the livestock grazing cycle, when meadows are set aside during spring.

11.5.2.2 *Lavandulo sampaioanae-Cytisetum multiflori*

Very common in the area, this nanophanerophytic community is characterized by *Cytisus multiflorus*, *C. striatus*, *Pteridium aquilinum* subsp. *aquilinum* and *Lavandula pedunculata* subsp. *sampaiana*, although the last species is normally absent. It occurs on deep granitic soils and marginally on schists.

11.5.3 Perennial grasslands

11.5.3.1 *Arrhenathero bulbosi-Armerietum beiranae*

This hemicryptophytic perennial grassland is dominated by *Armeria beirana* and *Arrhenatherum elatius* subsp. *bulbosum*, with co-occurrence of *Agrostis castellana* and *Avenula sulcata* subsp. *sulcata*. It is frequent in the granitic area of the Montemuro range, and its expansion is related to the abandonment of rural activities – which lead to a considerable reduction of the cultivated areas, as well as of the Molinio-Arrhenatheretea and Nardetea communities – and to the high frequency of fires (Monteiro-Henriques et al., *submitted*).

11.5.4 Heliophilous shrublands

11.5.4.1 *Halimio alyssoidis-Pterospartetum cantabrici*

This nanophanerophytic scrubland, characterized by *Pterospartum tridentatum* subsp. *cantabricum*, *Erica umbellata*, *E. australis*, *E. cinerea*, *Halimium lasianthum* subsp. *alyssoides* and *Ulex minor* among other species, is very frequent in the area, extensively favoured by wildfires. It occurs on different soils, appearing with an *E. australis* dominated facies on schists.

Other frequent communities of the study area are the *Polytricho-Agrostietum truncatulae* (hemicryptophytic grassland) and the annual grassland communities of the *Hispidello hispanicae-Tuberarietum guttatae* and the *Airo praecocis-Sedetum arenarii*.

11.6 Target vegetation type: semi-natural hay meadows

The MFA landscape is characterized, likewise other mountainous areas of central and Northern Portugal, by the presence of the traditional system of pasture and hay-meadows (“lameiros”). These synanthropic communities, on which the present section focuses, are floristically similar to those occurring in the study area of the Natural Park of Montesinho. Hereafter a brief description of the main phytosociological associations is given.

11.6.1.1 *Peucedano lancifolii-Juncetum acutiflori*

This synanthropic rush community is subserial of hygrophilous forests (as alder and birch forests). It is characterized by *Juncus acutiflorus* subsp. *acutiflorus*, *Peucedanum lancifolium* and *Potentilla erecta* among other species. It generally occupies the most humid part of meadows.

11.6.1.2 *Agrostio castellanae-Arrhenatheretum bulbosi*

This meadow community, which characteristic composition comprises *Arrhenatherum elatius* subsp. *bulbosum*, *Agrostis castellana*, *Chamaemelum nobile*, *Dactylis glomerata* subsp. *lusitanica*, *Anthoxanthum amarum*, among other species, corresponds to the less humid, or deficit irrigated hay meadows. As elsewhere explained (see subchapter 6.1), the major threat for these meadows is land abandonment, since they are strictly related to traditional management. This community occupies the same ecological position of the *Agrostis x fouilladei* e *Arrhenatherum elatius* subsp. *bulbosum* occurring in the NPM area.

11.6.1.3 *Anthemido nobilis-Cynosuretum cristati*

This perennial hemicryptophytic grassland corresponds to the great part of the irrigated meadows of the study area. As a rule, it is grazed during autumn, winter and beginning of spring, then set-aside to be harvested during summer. The characteristic composition includes *Cynosurus cristatus*, *Chamaemelum nobile*, *Dactylorhiza maculata* subsp. *caramulensis*, *Centaurea nigra* subsp. *rivularis*, among other species.

11.6.1.4 *Genisto anglicae-Nardetum strictae*

This community occurs at higher elevations in the Montemuro range, occupying humid depressions. Its persistence is strictly linked to grazing, particularly of sheep herds, so the progressive decline of this activity is threating it. The remaining communities are currently impoverished due to wildfire recurrence and local overgrazing. It is generally found in a vegetation mosaic, with association of the *Holco mollis-Querco pyrenaicae* S. series occupying drier zones, and bogs more humid ones.

12. Predictive habitat use models for roe deer use of semi-natural meadows in the Montemuro-Freita-Arada mountain range

12.1 Introduction: reintroduction of wildlife ungulate species and predictive habitat use models

Until the nineties Montemuro massif was the final destination of the traditional transhumance of sheep flocks coming from the Beira's lowlands (Sousa et al. 2005). Together with the local farming in the MFA area, this seasonal presence of concentrated livestock (up to 25000 animals in the fifties, and only around a thousand in 1998) acted as an indirect source of food for the wolf populations occurring in the area. Considering the end of transhumance and the regression tendency of the extensive farming activity in this mountainous region, and considering as well that the stock of big wild preys for wolves is currently restricted to wild boar, the reintroduction of deer as a wild prey is being considered for the improvement of the habitat suitability for this endangered wolf sub-population (Alexandre, Cândido, & Petrucci-Fonseca 2000).

Wildlife reintroduction programmes must have clear objectives and be aware of potential ecological constraints of species reintroductions, which depend on the target species and on the characteristics of the reintroduction area. For example, Wallach et al. (2007) alerted for the importance of considering the presence of permanent open water sources when planning roe deer reintroduction within the drier Mediterranean areas, to allow deer survival during the summer. Local water availability and water point distribution depend on patterns and amount of local rainfall, lithology and soil characteristics (which influence the local hydrological balance) and vegetation cover, which mediates the water fluxes between the soil and the atmosphere. Reintroduction programmes should be preceded by accurate research on the suitability of the specific area for the reintroduced species.

Various studies on ungulates habitat suitability have been carried on in Portugal, and the information gathered by these studies is valuable for future reintroduction projects.

Oliveira & Carmo (2000) for example, analysed the distribution and habitat suitability of roe deer, the main wild preys of the Iberian wolf, and the related habitat suitability, north of the Douro River, excluding the three protected areas of Montesinho Natural Park, Peneda-Gerês National Park and Alvão Natural Park. Data on occurrence of roe deer was related to habitat suitability index values assigned to the vegetation types or land uses at 5x5 km grid cells. To assess habitat suitability the authors attributed a value to the level of cover for shelter, food availability and human disturbance (settlements and rural activities). The sum of the three partial values gave the final index of habitat suitability for the specific cell (see Oliveira & Carmo 2000 for details). According to this study, roe deer distribution was positively correlated to landscape mosaics characterized by forest patches, meadows and improved pastures, which provide both shelter and foraging areas.

Lopes et al. (2007) assessed habitat suitability in the Freita-Arada massif (partly coincident with the study area of the present section of the thesis) for red and roe deer (absent in the area) and wild boar (frequent in the area), showing that this area offers suitable foraging resources conditions for both deer species and a high tranquillity index as human population density is low and concentrated in small villages, and car traffic is also low. According to Lopes et al. (2007) the main constraint in the area was the lack of cover for shelter as the dominant cover is low to very low shrubland (< 1m). The more frequent shrub community is the *Halimio alyssoidis-Pterospartetum cantabrici*, frequently dominated by *Erica* spp. The prevalence of this vegetation type is strictly related to the highly recurrent wildfires, typical of the Portuguese mountain ranges, which are in turn related to decrease of rural population and land abandonment, and also to mismanagement of pine and eucalyptus plantations (Aguiar et al. 2009). Grazing pressure by sheep and goats, still present in the area, was considered a second constraint for the re-introduction of red and roe deer, because of competition for foraging resources and for the disturbance associated to human and livestock presence. According to Lopes et al. (2007) the areas with better habitat suitability for deer had low grazing pressure and a fair presence of tall shrubland and broadleaved forest patches.

A project for the reintroduction of roe deer in the Montemuro mountain range was promoted by the Association for the preservation of the Iberian wolf habitat (ACHLI), and is being realized by the University of Aveiro (Fonseca & Torres 2011). Considering the fragmentation of suitable habitats and the scattered presence of human settlements and infrastructures, the Montemuro area is considered more suitable for the reintroduction of roe than red deer, in particular because roe deer has a comparably small average home range and potentially reduced interactions with human rural activities, when compared to red deer (Carlos Fonseca, pers. comm.).

Besides fulfilling the major objective (improving wolf habitat), and, eventually, generate income for local human populations through hunting, the reintroduction of wild ungulates in the area will also have consequences on vegetation communities. Effects of deer on vegetation, in particular forest regeneration and ecosystem ecology have been investigated for a range of environments (Gill & Beardall 2001; Bugalho et al. 2011). The potential contribution of large mammalian herbivores, for landscape and vegetation management, and maintenance of natural and semi-natural meadows have also been addressed (van Wieren 1995; Tschöpe et al. 2011)

To assess potential interactions between re-introduced deer populations and vegetation it is crucial to assess potential habitat use. This can be done through modelling approaches, using habitat suitability indexes or existing information about the ecological requirement of the target species (Leaper et al. 1999; Hirzel et al. 2004).

I modelled the probability of roe deer use of the meadows occurring in the MFA study area using the information gathered in the analysis of deer use of meadows in Montesinho Natural Park, and on the existing information on land use cover of MFA. The methodology and results of this modelling exercise is detailed in the following chapter.

12.2 Methods

I used the ESRI ArcMap^{TM} 9.2 SP4 geographical information system software, aerial photographs and field knowledge, to adapt the map of landscape scale vegetation mosaic from the COS ’90 map of land uses cover, realized in the nineties by the Portuguese Geographical Institute (Carta de Ocupação do Solo – COS ’90 - IGP), as shown in Figure 26.

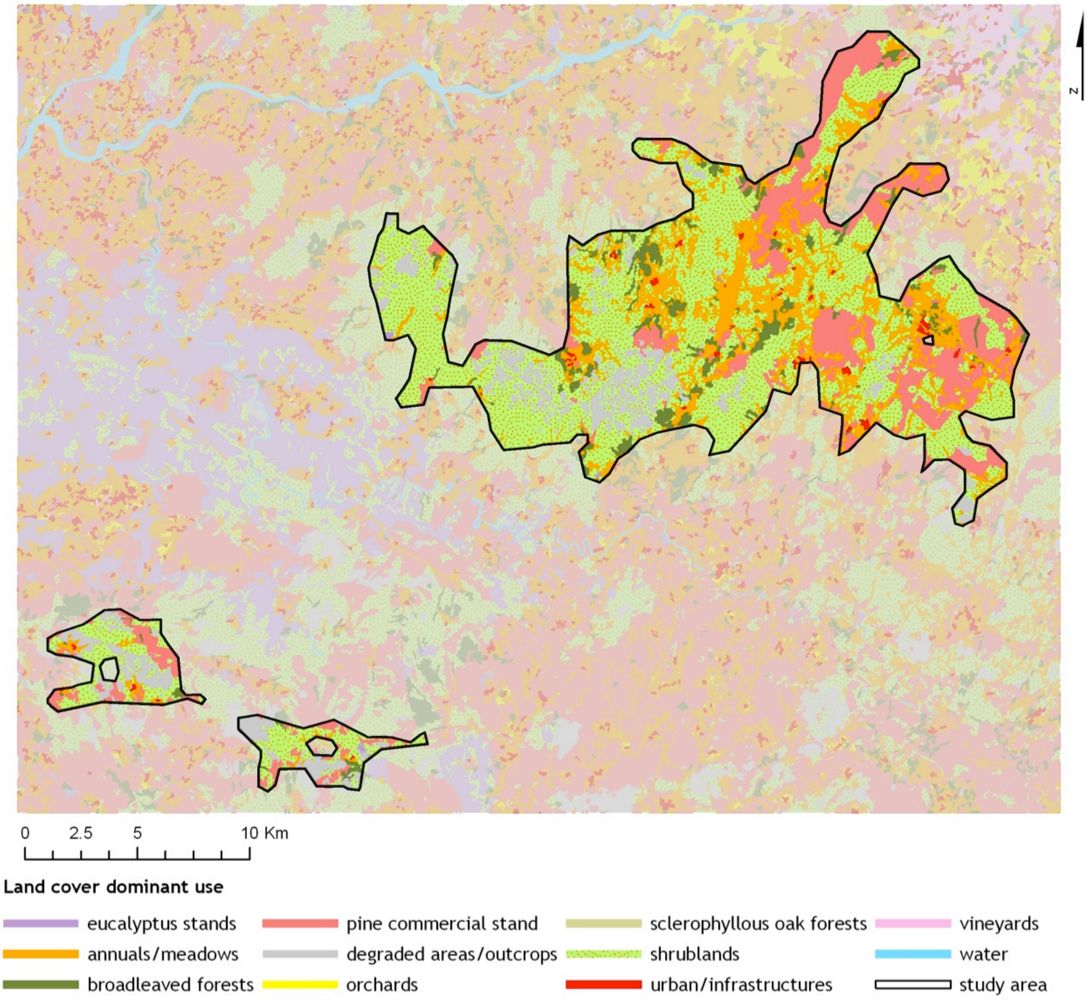

Figure 26 - Land use cover classes in the Montemuro-Freita-Arada mountain range. The map was based on COS’90 map (IGP) and related legend with adjustments derived from field surveys.

Within the range of potential distribution of the *pyrenaica* oak series, I selected, from the COS ’90 map, all the area occupied by meadows. In the referred map, semi-natural meadows) are joined together with crops in the category “Arable land/annual crop”. To separate the two broad classes, I cut off a 500 m buffer around urban centres, as normally, in higher mountain ranges, agriculture is currently confined in the proximities of villages (Aguiar et al. 2009). To improve the meadows map I reshaped misclassified and/or presently out-dated polygons (old abandoned meadows already completely covered by woody vegetation), over aerial photographs from the national coverage (November 2004-September 2006) obtained from the Instituto Geográfico Português. I also decided to exclude from the analysis all meadows occurring in a 200 m buffer area along the A24 highway that crosses the Montemuro portion of the MFA mountain range (see final result in Figure 27).

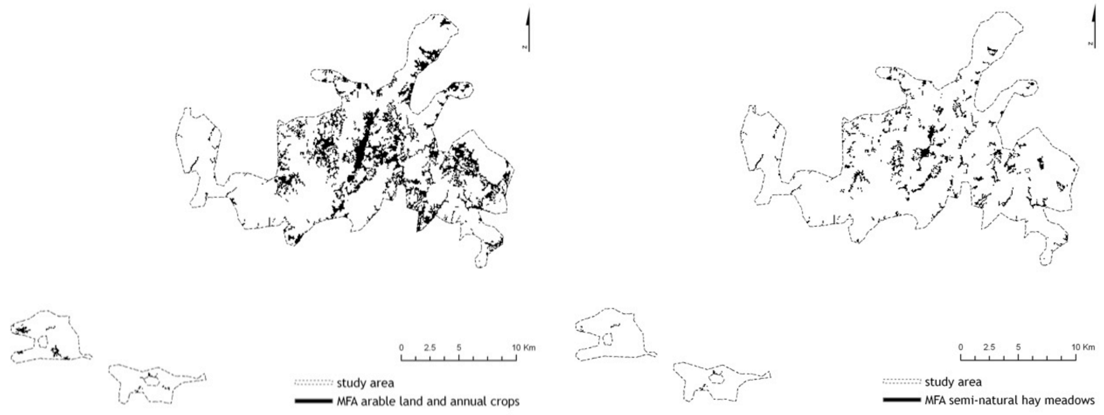

Figure 27 – Extraction of the semi-natural hay meadows of the MFA study area from the COS ’90 map category “Arable land and annual crops”.

Considering the much bigger extent of the MFA study area (280 km^2 ca. *vs.* 48 km^2) and the adaptation from the COS ’90 map, the scale of the MFA meadows map is slightly coarser than that of NPM, where each meadow unit was digitalized manually over the aerial photographs. The greater scale means that landscape mosaic details are averaged out. Specifically, neighbouring meadow units, which are separated by patches of different vegetation on the ground (shrubland and/or forest fragments), are clustered together in the map. Instead of considering each meadow polygon, I used raster cells of 80 x 80 m as elementary units, that corresponds to the cell dimension of the SRTM digital terrain model (CGIAR-CSI 2008) used to compute topographic indexes, and is similar to the smallest cartographic unit of the COS ’90 map (IGP).

12.2.1 Environmental variables used in the modelling exercise

Considering the variables employed in the modelling of deer use of meadows in the area of Natural Park of Montesinho (see chapter 9, for more details), the subset available for the model extrapolation to the MFA range included:

- OAK cover type: percentage cover of broadleaved forests (this category includes mainly *Holco mollis-Quercetum pyrenaica* forests, but also chestnut stands and riparian forests ascribed to the *Galio broteriani-Alnetum glutinosae* and the *Carici reuterianae-Betuletum celtibericae* associations);
- COM cover type: percentage cover of commercial stands (mainly *Pinus pinaster*, but also other coniferous species);
- MEA cover type: percentage cover of meadows
- SHR cover type: percentage cover of shrublands;
- urb_dist: distance to urban centres;
- road_dist: distance to paved roads
- mean_slope: mean slope of the surrounding area;
- Δ_elev: elevation index (meadow raster cell elevation − buffer mean elevation).

As for the NPM analysis, I considered cover percentage of the vegetation types in a buffer around MFA's meadows of 500 m maximum (Figure 28).

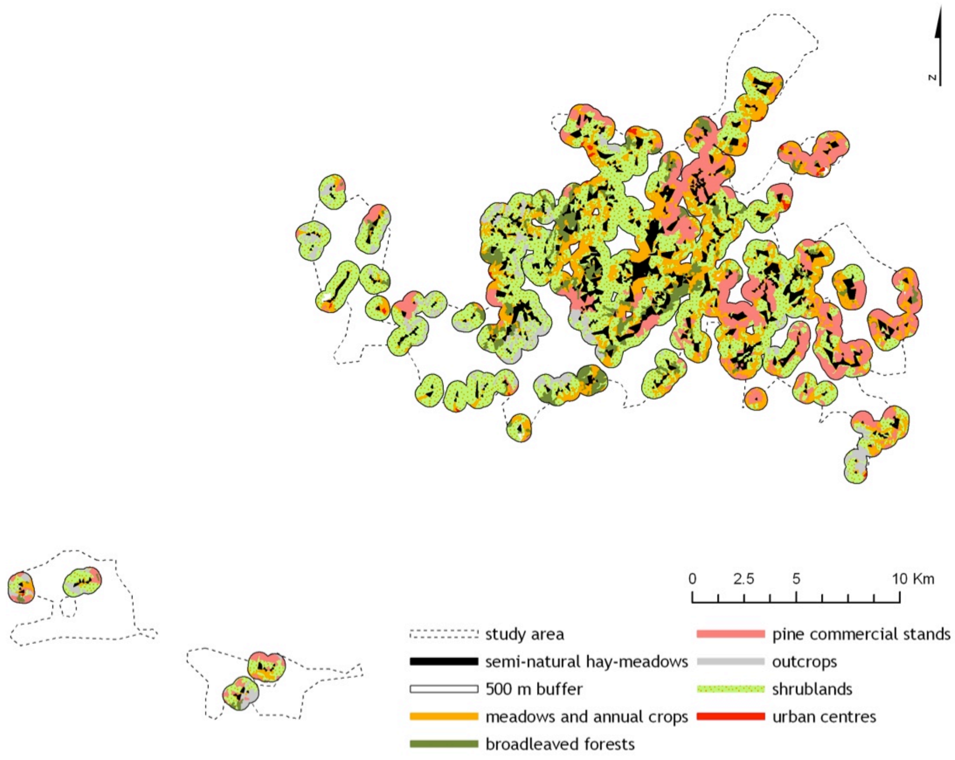

Figure 28 – Dominant cover classes within a 500 m neighbourhood around MFA semi-natural meadows.

12.2.2 Modelling procedure

The predictive modelling of deer use of MFA semi-natural meadows was based on the results obtained modelling roe deer use of meadows in the NPM (Natural Park of Montesinho) area (chapter 9).

I focused on roe deer predictive use as this species is currently being considered in a reintroduction programme in the area (Fonseca & Torres 2011), as previously explained. Moreover, the environmental variables included in the best models for red deer use of meadows in the NPM area were not available or partly missing in the COS '90 map information.

To obtain a predictive use model for roe deer I first re-run the generalized linear model (GLM) with NPM roe deer data (logistic regression, logit link-function) with *glmulti* package (Calcagno 2011), using a subset of the variables included in the first analysis (see above subchapter). Of the variables available for the MFA area, I only considered those included in the selected models related to the 250 and 500 m buffers: OAK (250 and 500), MEA (250 and 500), SHR (250), Δ_elev (250 and 500), mean_slope (250), and urb_dist. I excluded variables related to the 100 m buffer in the predictive modelling, although those models had yielded lower AIC_c in the analysis of roe deer use of meadows, because the use of 80 x 80 m raster cells for vegetation cover mapping that is, a coarser resolution compared to vegetation cover map of the NPM area, would lead to greater degree of uncertainty and error. As the number was reduced, I allowed the concurrent introduction of variables related with different buffers. I constrained the number of variables to three, following Maroco (2007).

The final selection of models was made among the set of alternative ones, which included the one with lowest AIC_c and any other with Δ AIC_c from the lowest < 2.

12.3 Results and discussion

The set of alternative models is shown in Table 43.

Table 43 – Best and alternative models for roe deer use of meadows.

Best and alternative models	Res.d	Df	GOF	AICc
1 + MEA_250 + Δ_elev_250	30.3696	25	0.2107	37.37
1 + MEA_250	32.9865	26	0.1625	37.45
1 + OAK_500 + Δ_elev_250	30.7645	25	0.1969	37.76
1 + OAK_500 + MEA_250 + Δ_elev_250	28.4829	24	0.2402	38.22
1 + OAK_500 + MEA_500 + Δ_elev_250	28.5567	24	0.2373	38.29
1 + MEA_500 + Δ_elev_250	31.3954	25	0.1762	38.39
1 + MEA_250 + urb_dist	31.4625	25	0.1741	38.46

1 + MEA_500	33.9840	26	0.1354	38.46
1 + OAK_500 + Δ_elev_250+ urb_dist	28.7639	24	0.2291	38.50
1 + MEA_250 + Δ_elev_250+ urb_dist	28.8616	24	0.2254	38.60
1 + Δ_elev_250+ urb_dist	31.6036	25	0.1698	38.60
1 + MEA_250 + SHR_500	32.0134	25	0.1576	39.01
1 + urb_dist	34.6681	26	0.1190	39.15
1 + OAK_500 + MEA_250	32.2200	25	0.1517	39.22
1 + OAK_500 + SHR_500 + Δ_elev_250	29.5911	24	0.1987	39.33

Res.d = residual deviance; Df = degrees of freedom; GOF = goodness of fit test; AICc = modified Akaike information criteria.

As each model includes few variables, using a single model in the prediction of roe deer use of meadows in the MFA area would strongly reflect the effect of such variables only (Figure 29 to 32. As alternative models included different variables that were significant in the Wald test and Likelihood ratio test (see Table 62 in chapter 7 of the Appendix), I built a final ensemble of models (Araújo & New 2007) that included the greater number of significant variables (avoiding repetitions among models), to present a final unweighted average of the models that allows checking for consensual trends of the predicted use of meadows for roe deer. For the ensemble I used the three distinct models shown in Table 44.

Table 44 – Selected models used for the predictive use modelling.

Selected models	Estimate	SE	z value	Pr(>|z|)	Pr(Chi)
1 + MEA_250					
(Intercept)	2.0349	1.0284	1.9787	0.0479*	
MEA_250	-0.2423	0.114	-2.1254	0.0336*	0.0158*
1 + OAK_500 + Δ_elev _250					
(Intercept)	0.5665	0.8608	0.6581	0.5105	
OAK_500	0.2289	0.1213	1.8868	0.0592	0.0195*
Δ_elev_250	0.0964	0.0505	1.907	0.0565	0.0294*
1 + urb_dist					
(Intercept)	-1.6873	0.9816	-1.719	0.0856	
urb_dist	0.0008	0.0004	1.8344	0.0666	0.0417*

SE = standard error; Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: ‘***’ < 0.001; ‘**’ < 0.01; ‘*’ < 0.05

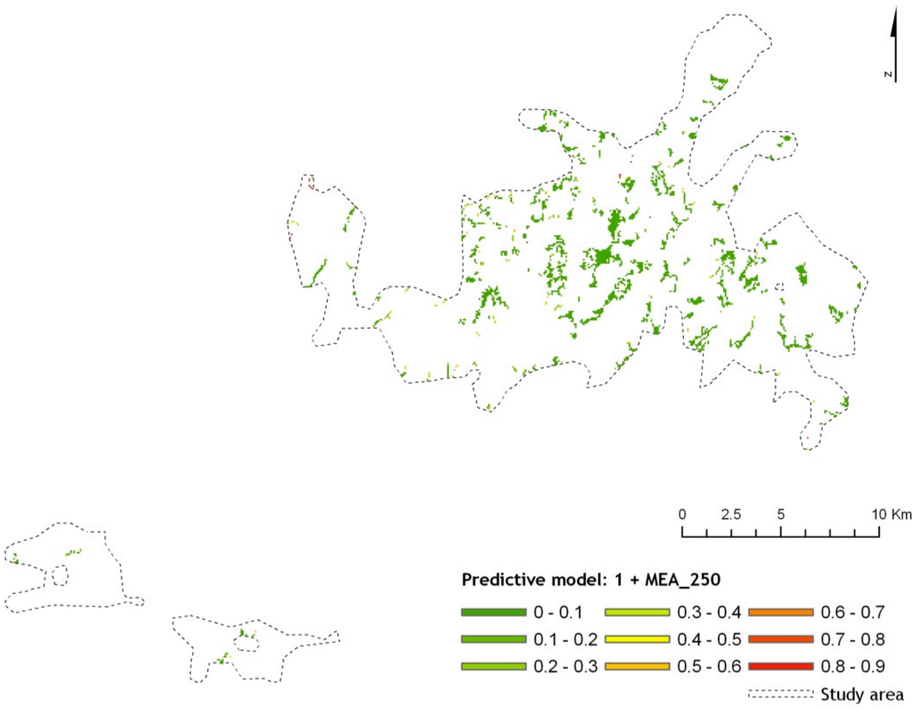

Figure 29- Predictive model for roe deer use of meadows: 1 + MEA_250.

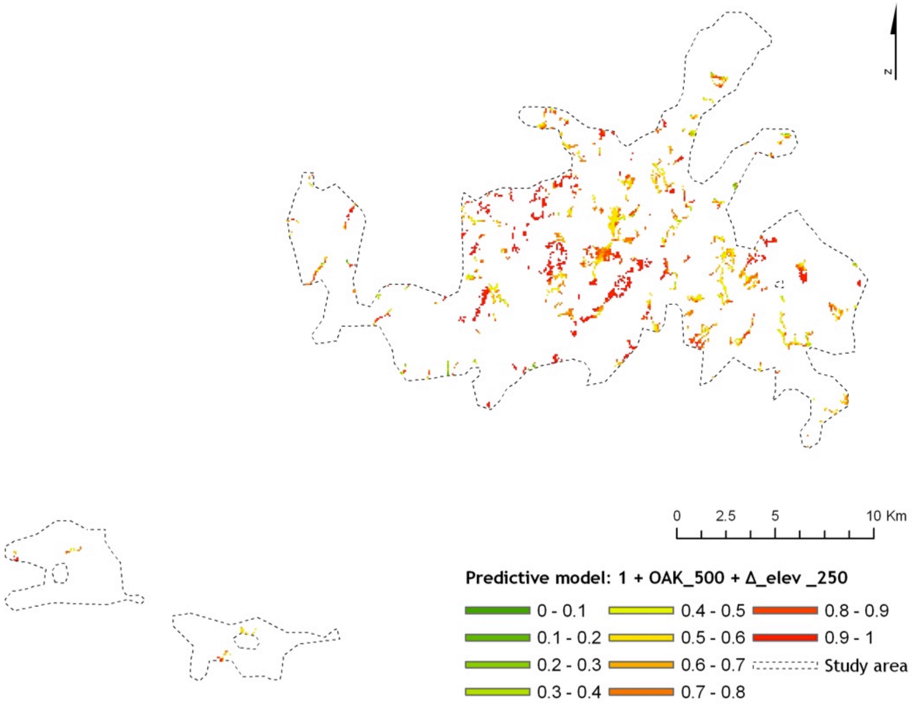

Figure 30- Predictive model for roe deer use of meadows: 1 + OAK_500 + Δ_elev _250.

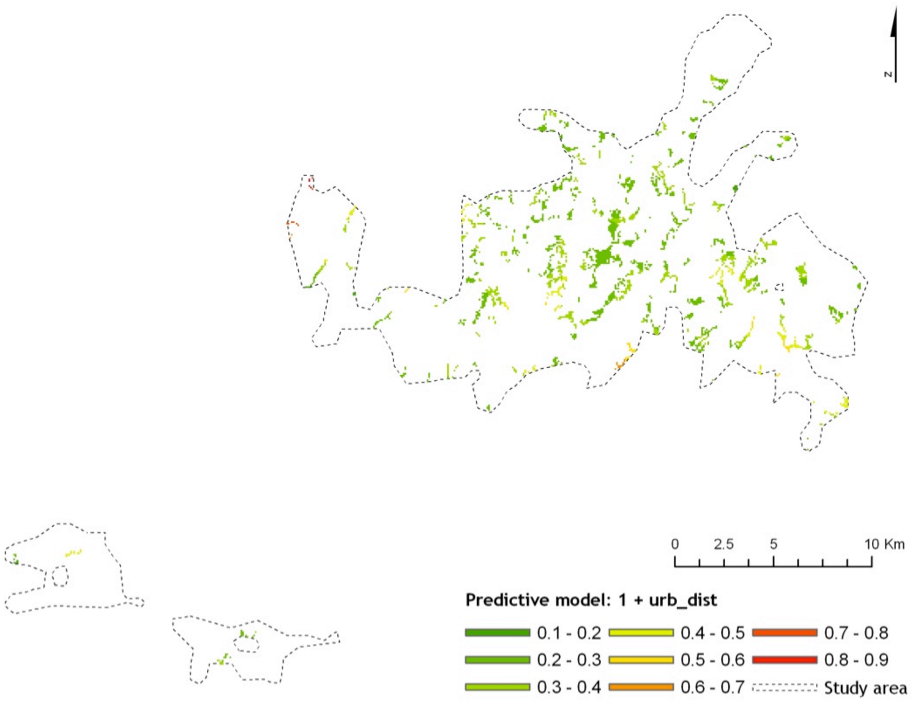

Figure 31- Predictive model for roe deer use of meadows: 1 + urb_dist.

The final ensemble of the three selected models is visualized in Figure 32.

According to this map, roe deer predicted use of MFA meadows is rather low. Roe deer impact on areas with greater presence of meadows, like, for example the Balsemão River valley (see Figure 23 for details) should not be relevant. Although meadows are considered a suitable foraging habitat for roe deer (Oliveira & Carmo 2000), the higher cover of meadows generally implies a lack of concealing habitats, which are important for roe deer shy temperament (Mysterud et al. 1999). The higher trends of roe deer use occur in marginal and isolated meadows, farther from the urban centres and closer to broadleaved forests, or located at higher elevations.

The map presented below, which was built as an ensemble of the three selected models (Figure 32), should be read not as a prediction of the probability of deer use, but as a trend for roe deer use of semi-natural meadows, based only on the variables that were included in those models (Araújo & New 2007). This trend could be calibrated with an evaluation of the regional suitability for roe deer, beyond the 500 m buffer limitation used for this analysis.

A better prediction would also depend on the models on which the estimation is based on. In the specific case of this thesis, the main restriction to deer use model strength has been the sample size in the NPM area (28 meadows values averaged from 112 plots), which limited the maximum number of variables entering each model to three, constraining the possible combinations. Another restriction was the fact that some of the variables that best performed in the NPM analysis were not available for the MFA area. The collection and inclusion of such variables in the models would improve the prediction. Even though, the final map resulted consistent with the ecology of the species taking into account the vegetation landscape of the MFA study area.

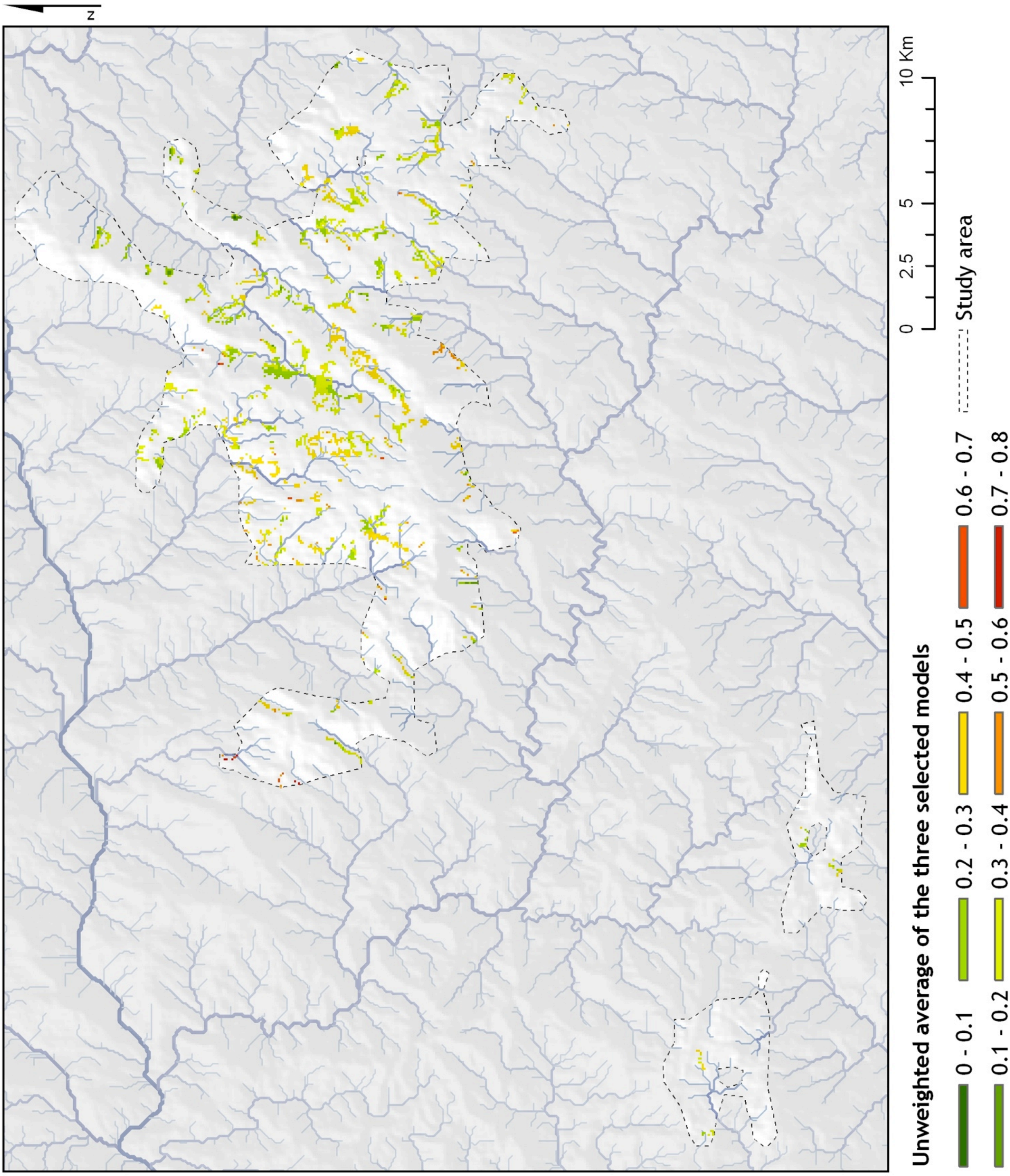

Figure 32 – Ensemble of the three predictive models for roe deer use of MFA meadows.

IV. General conclusion

13. Concluding remarks and directions for future research

The main aim of the present thesis was to assess the usefulness of phytosociology for wildlife management. Phytosociology has been widely used to describe and characterize plant communities all over Europe, including Portugal, and any attempt of application beyond pure vegetation research is appealing. One of the advantages of phytosociology (as a floristic classification) over physiognomic/structural ones is the possibility of accounting for the existing vegetation diversity at a finer scale. This attribute suggests that its application to fine scale studies on wildlife habitat use pattern is at least compelling. Management of wild large mammalian herbivores is frequently based on large-scale studies. However, when the objective is the management of both wildlife and specific vegetation communities, which can be affected (positively or negatively) by herbivores, finer scales analyses are needed (Gordon et al. 2004).

In the present thesis I addressed deer use of two habitat types, semi-natural meadows and forest communities, using faecal pellets counts of free ranging red and roe deer populations occurring in the Natural Park of Montesinho (Section II).

In chapter 8, I investigated red deer spring use of meadow patches, comparing the phytosociological approach to coarser criteria for patch classification. Considering the reduced spatial extent of the study area, semi-natural meadows showed a considerable heterogeneity (6 different types, according to the phytosociological method), related to both local environmental conditions and management status. Phytosociological classification contributed to discriminate red deer use of semi-natural meadows at finer scale. Results also suggested that clustering of plant communities can be made according to proxies such as the cover of dominant species, which is an efficient surrogate when dealing with this type of vegetation, at least if the extent of the research study area is limited, like in this case. Spring corresponds to the growing stage of the herbaceous vegetation, when forage overall nutritive quality is at its best. This might have determined a more evident selection pattern for grazing red deer.

In chapter 9 I examined red and roe deer use of the same meadows at a coarser scale, using a multi-scale modelling approach. The meso-scale analysis assessed deer use of habitat using circular buffers of three different widths. The vegetation mosaic affected patterns of habitat use by red and roe deer, differently. While red deer preferred meadows surrounded by open and low vegetation types, avoiding those with high cover of riparian forest in the vicinity, roe deer preferred using isolated meadows, not far from the concealing cover of oak forest patches. The effect of these variables was stronger at smaller and medium buffer widths. The introduction of macro-scale variables related with human disturbance (i.e. the distance to both settlements and paved roads) did not enhance much the explicative power of the models. On the other hand, the consideration of micro-scale variables, related to features of the sampled meadows, improved the models. Management status of meadows (i.e. abandoned, recently abandoned or currently managed) contributed significantly to explain selection of meadow by red and roe deer. Both deer species preferred to use long abandoned over currently managed meadows, even considering the low pressure and non-continuous character of human activity that characterizes meadows in the study area of NPM. The dominant phytosociological association (or community) of the sampled meadow units contributed to explain red deer use of meadows in spring, in line with the results of the patch-scale analysis (chapter 8), but was not relevant for the other seasons. Red deer selective ability might decline with the reduction of meadows' forage nutritional quality (Owen-Smith & Novellie 1982) after spring.

In chapter 10 I compared red and roe deer use of the three most representative forest types of the NPM study area: pine plantations and autochthonous deciduous and evergreen oak forests ascribed to the mesic *Genisto falcatae-Quercetum pyrenaicae* association and to the edaphoxerophilous *Genisto hystrix-Quercetum rotundifoliae* association, respectively. Results showed that red and roe deer used oak forests more than pine plantations. During winter and spring red deer preferred holm oak patches, while roe deer preferred deciduous oak forests, though marginally. The two species showed a significant overlap of habitat use, with no segregation of roe deer, generally the weaker competitor, in disagreement with other studies (e.g.: Torres 2011). The low population density of red and roe deer in the study area (respectively 3 to 4 and 1 to 2 individuals/km^2 according to Paiva 2004) may have implied a low degree of competition between the two deer species.

In Section III, chapter 12, I extended modelling results of chapter 9 to Montemuro-Freita-Arada mountain range. Results suggest that potential use of MFA semi-natural meadows by roe deer would be low except for more isolated areas closer to broadleaved forest patches. The produced map of potential use of meadows by roe deer may contribute to evaluate re-introduction programs of that species in MFA.

The present thesis raised questions relevant for future research. For example, the system of semi-natural meadows is undergoing a process of progressive declining and abandonment. How will this affect the landscape mosaic and consequently influence patterns of habitat use by red and roe deer? How will changes in the species composition of plant communities, associated with lack of management, affect patterns of selection at finer scales? How will lack of management of meadows and effects of deer on vegetation interact and shape the landscape mosaic? May grazing by deer contribute to maintain open meadows? Or will these be colonised by woody vegetation? Considering the consequences on the landscape vegetation mosaic, evaluating the possible role of free-ranging deer in the succession dynamic is challenging. The results of the present thesis showed that both red and roe deer prefer abandoned over those meadows currently managed for livestock grazing and hay harvesting. It would be therefore interesting to assess the effects that deer grazing may have on plant diversity and ecological succession considering the different phytosociological associations found in meadow communities.

The framework used to analyse deer use of meadows, based on phytosociological classification and assessment of the influence of meso-scale variables, can be used in other areas and vegetation communities where free-ranging populations of deer occur, to assess patterns of habitat selection by deer at finer scales. This information could be used to develop fine scale habitat suitability maps such as was done here (see chapter 12).

In conclusion phytosociology can be considered a useful tool for understanding fine-scale herbivore-habitat relationships and for managing the effects of herbivores on vegetation communities, such as semi-natural meadows. Extending phytosociology beyond the scope of vegetation classification, namely to wildlife management, may contribute to understand patterns of wildlife use of habitat at different scales and serve nature conservation purposes.

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VI. Appendix

1. Raw data and supplementary material (chapter 8)

Table 45 - Resuming table: red deer spring pellet groups counts.

Plot	red deer FAR	Plot	red deer FAR	Plot	red deer FAR
01a	0	**14d**	0	**30c**	1
01b	0	**16a**	0	**30d**	2
01c	0	**16b**	0	**31a**	0
01d	0	**16c**	0	**31b**	1
02a	0	**16d**	0	**31c**	5
02b	0	**17a**	1	**31d**	2
02c	0	**17b**	0	**32a**	1
02d	0	**17c**	2	**32b**	2
03a	1	**17d**	0	**32c**	0
03b	0	**18a**	1	**32d**	1
03c	0	**18b**	0	**33a**	1
03d	3	**18c**	0	**33b**	0
04a	2	**18d**	0	**33c**	2
04b	3	**19a**	0	**33d**	1
04c	1	**19b**	0	**34a**	0
04d	2	**19c**	0	**34b**	0
05a	0	**19d**	0	**34c**	0
05b	1	**21a**	1	**34d**	0
05c	0	**21b**	1	**35a**	0
05d	0	**21c**	0	**35b**	0
07a	0	**21d**	2	**35c**	0
07b	0	**22a**	1	**35d**	0
07c	1	**22b**	0	**39a**	0
07d	0	**22c**	0	**39b**	0
08a	0	**22d**	0	**39c**	0
08b	0	**23a**	1	**39d**	0
08c	0	**23b**	0		
08d	3	**23c**	0		
09a	0	**23d**	0		
09b	1	**24a**	0		
09c	0	**24b**	0		
09d	1	**24c**	0		
11a	0	**24d**	0		
11b	0	**25a**	1		
11c	0	**25b**	1		
11d	0	**25c**	0		
12a	0	**25d**	1		
12b	0	**29a**	0		
12c	0	**29b**	0		
12d	0	**29c**	3		
14a	0	**29d**	2		
14b	0	**30a**	3		
14c	0	**30b**	0		

Table 46 – Meadow patch clusters according to the five criteria considered (related to Chapter 7). CYN = *Agrostio castellanae-Cynosuretum cristati*; JUNC = *Hyperico undulati-Juncetum acutiflori*; BRACHY = Community of *Brachypodium rupestre*; AVESU = Community of *Avenula sulcata*; NARD = Community of *Festuca rothmaleri* and *Nardus stricta*; ARRH = Community of *Agrostis* x *fouilladei* and *Arrhenatherum elatius* subsp. *bulbosum*.

Relevé n°	Phytosociological unit	Total species K-mean clusters	Dominants K-mean clusters	Graminoids/forbs ratio	legumes cover
1	CYN	group 4	group 4	group 2	group 2
2	CYN	group 4	group 4	group 1	group 5
3	JUNC	group 5	group 5	group 3	group 4
4	NARD	group 6	group 6	group 2	group 2
5	AVESU	group 1	group 1	group 3	group 2
6	OTHER	group 7	group 7	group 1	group 1
7	JUNC	group 5	group 5	group 1	group 4
8	CYN	group 4	group 4	group 5	group 2
9	OTHER	group 7	group 7	group 3	group 3
10	AVESU	group 1	group 1	group 5	group 3
11	NARD	group 6	group 6	group 5	group 1
12	AVESU	group 1	group 1	group 4	group 3
13	CYN	group 4	group 4	group 5	group 1
14	AVESU	group 1	group 1	group 2	group 2
15	OTHER	group 7	group 7	group 4	group 1
16	BRACHY	group 3	group 3	group 3	group 1
17	BRACHY	group 3	group 3	group 2	group 2
18	AVESU	group 1	group 1	group 2	group 3
19	BRACHY	group 3	group 3	group 5	group 1
20	CYN	group 4	group 4	group 2	group 5
21	NARD	group 6	group 6	group 5	group 2
22	CYN	group 4	group 4	group 1	group 2
23	AVESU	group 1	group 1	group 5	group 1
24	BRACHY	group 3	group 3	group 4	group 2
25	CYN	group 4	group 4	group 5	group 2
26	CYN	group 4	group 4	group 3	group 4
27	AVESU	group 1	group 1	group 2	group 5
28	CYN	group 4	group 4	group 3	group 5
29	AVESU	group 1	group 1	group 2	group 4
30	CYN	group 4	group 4	group 4	group 3
31	CYN	group 4	group 4	group 3	group 2
32	AVESU	group 1	group 1	group 3	group 3
33	BRACHY	group 3	group 3	group 3	group 2
34	AVESU	group 1	group 1	group 1	group 2
35	AVESU	group 1	group 1	group 3	group 3
36	JUNC	group 5	group 5	group 4	group 2
37	ARRH	group 2	group 2	group 2	group 3
38	ARRH	group 2	group 2	group 1	group 5
39	ARRH	group 2	group 2	group 2	group 4
40	ARRH	group 2	group 2	group 1	group 5
41	ARRH	group 2	group 2	group 2	group 5
42	CYN	group 4	group 4	group 4	group 2
43	AVESU	group 1	group 1	group 2	group 3
44	NARD	group 6	group 6	group 5	group 2
45	AVESU	group 1	group 1	group 3	group 2
46	AVESU	group 1	group 1	group 1	group 1
47	BRACHY	group 3	group 3	group 5	group 1
48	CYN	group 4	group 4	group 3	group 3
49	AVESU	group 1	group 1	group 3	group 3
50	BRACHY	group 3	group 3	group 3	group 2

2. Red deer use of meadows (chapter 9): raw count data and explorative plots

Table 47 – Resuming table of red deer count data for the three field seasons.

sampled meadow	spring	summer	autumn-winter
1	0	0	1
2	0	2	0
3	4	2	3
4	8	4	3
5	1	2	2
7	1	0	2
8	3	3	2
9	2	2	0
11	0	0	1
12	0	1	1
14	0	0	1
16	0	0	0
17	3	4	3
18	1	4	2
19	0	1	0
21	4	2	0
22	1	4	0
23	1	3	0
24	0	3	2
25	3	4	4
29	5	5	3
30	6	4	6
31	8	4	7
32	4	2	4
33	4	0	0
34	0	2	0
35	0	1	1
39	0	5	10

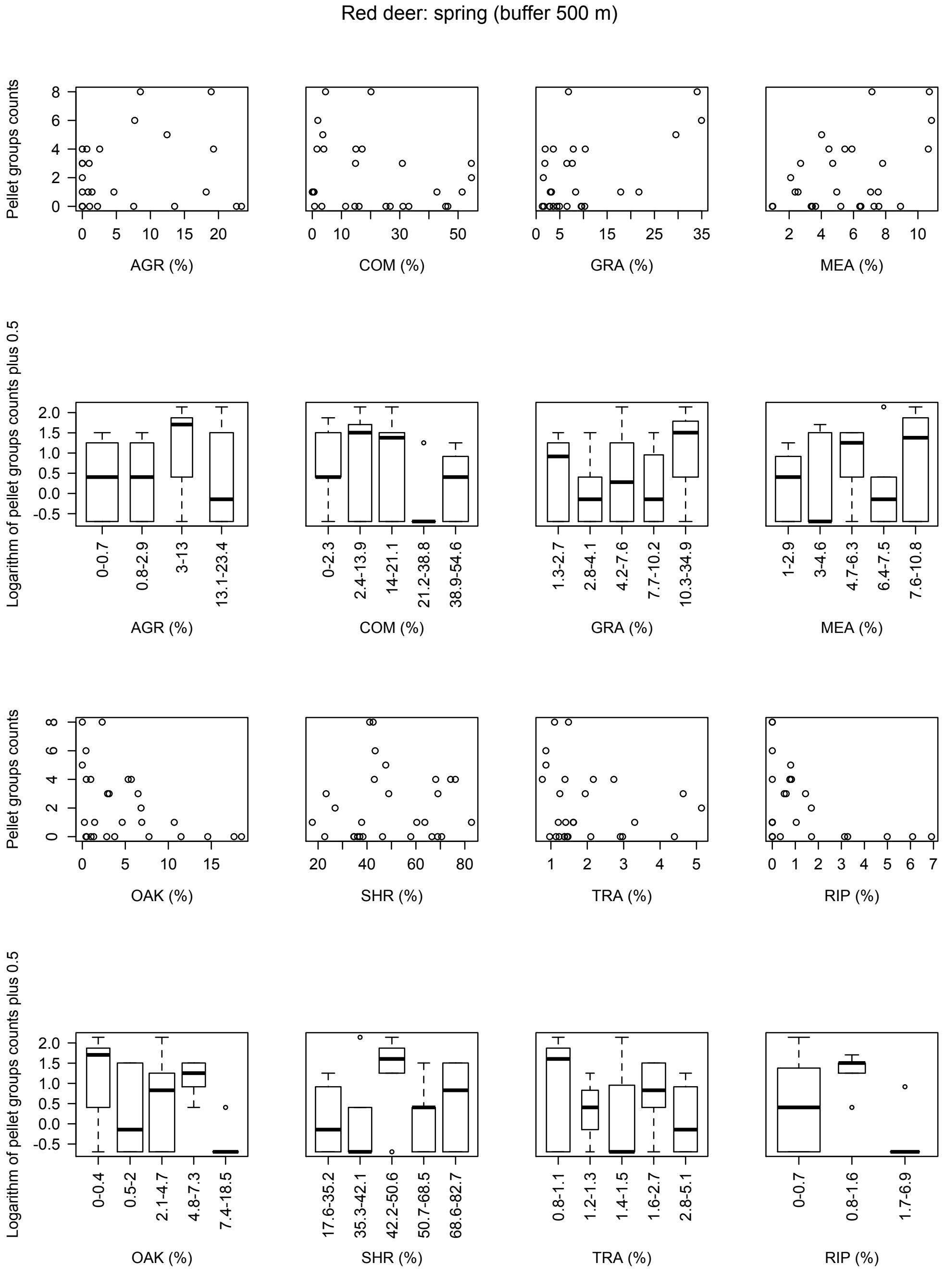


Figure 33- Explorative plots for spring red deer FAR against cover types (%), corresponding to the 500 m buffers.

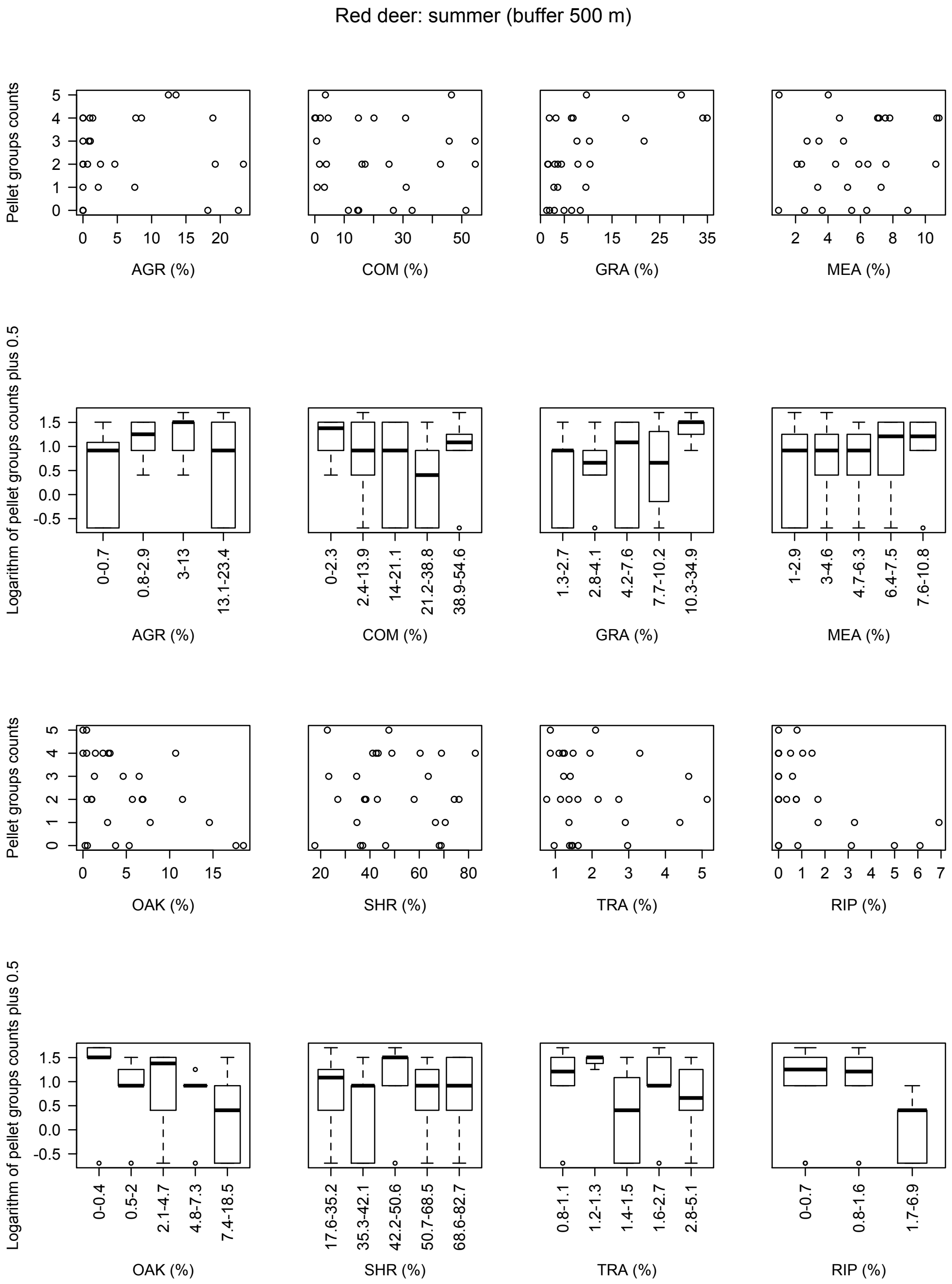


Figure 34 - Explorative plots for summer red deer FAR against cover types (%), corresponding to the 500 m buffers.

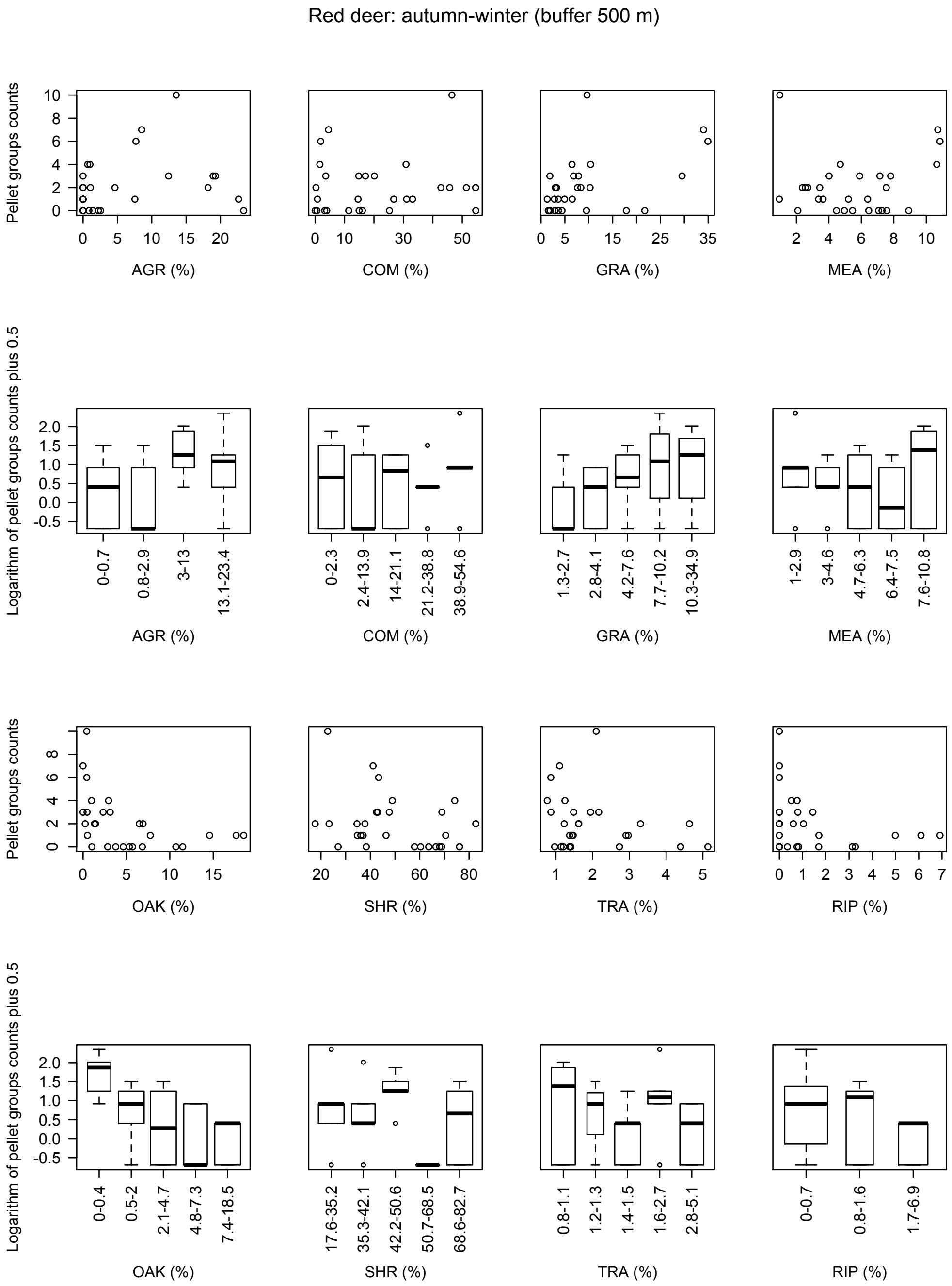


Figure 35 - Explorative plots for autumn-winter red deer FAR against cover types (%), corresponding to the 500 m buffers.

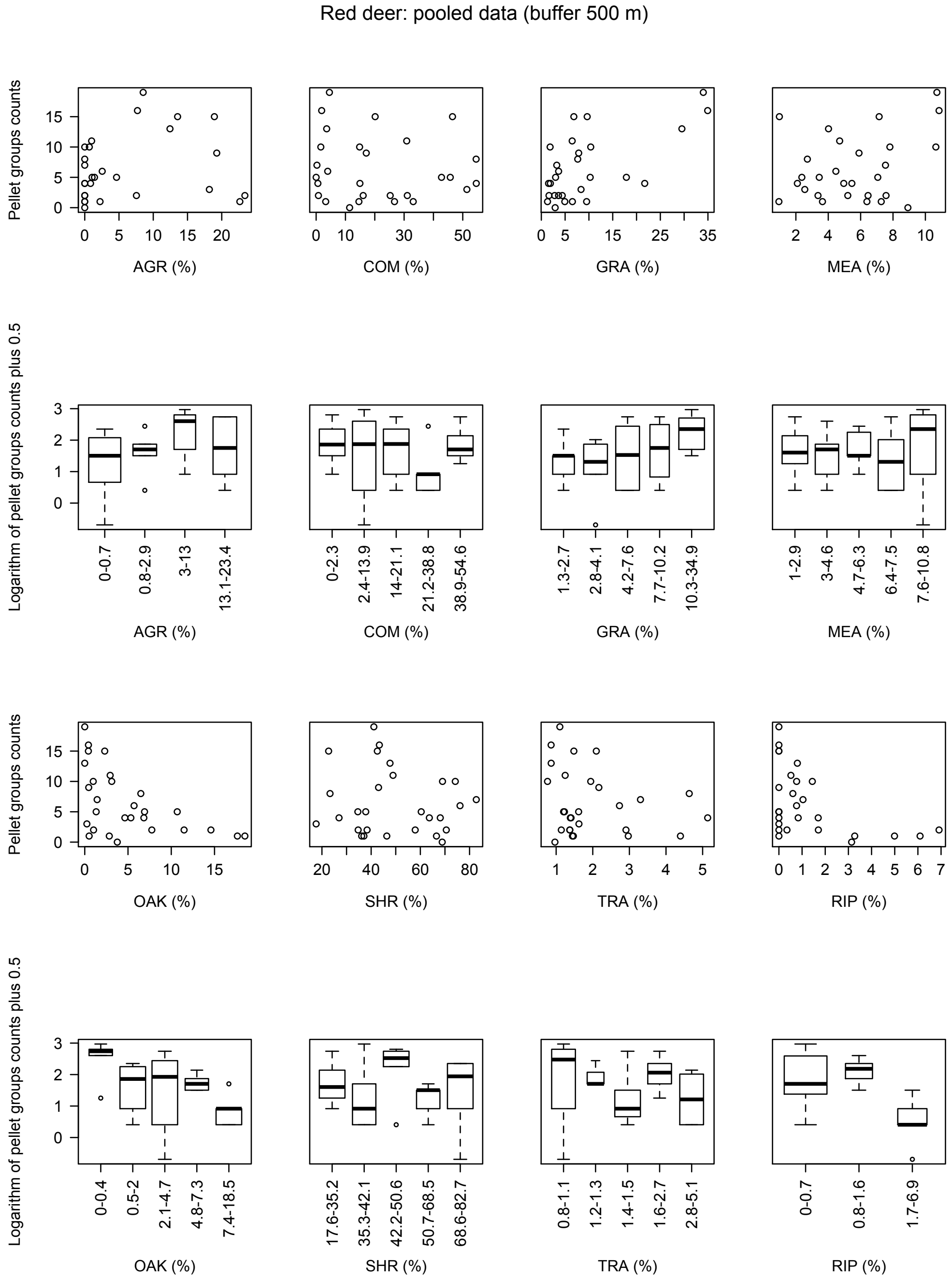


Figure 36 - Explorative plots for pooled annual red deer FAR against cover types (%), corresponding to the 500 m buffers.

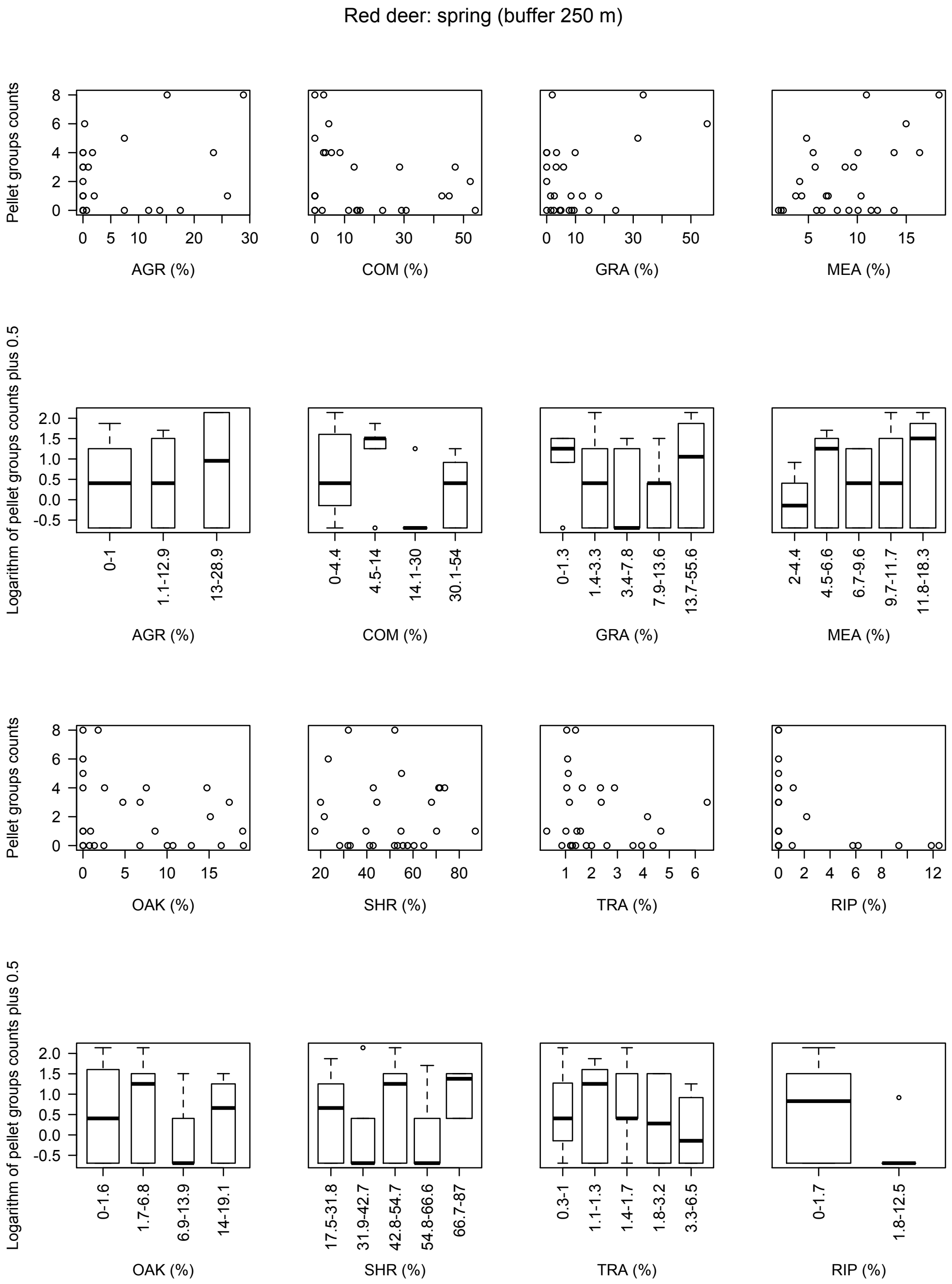


Figure 37 - Explorative plots for spring red deer FAR against cover types (%), corresponding to the 250 m buffers.

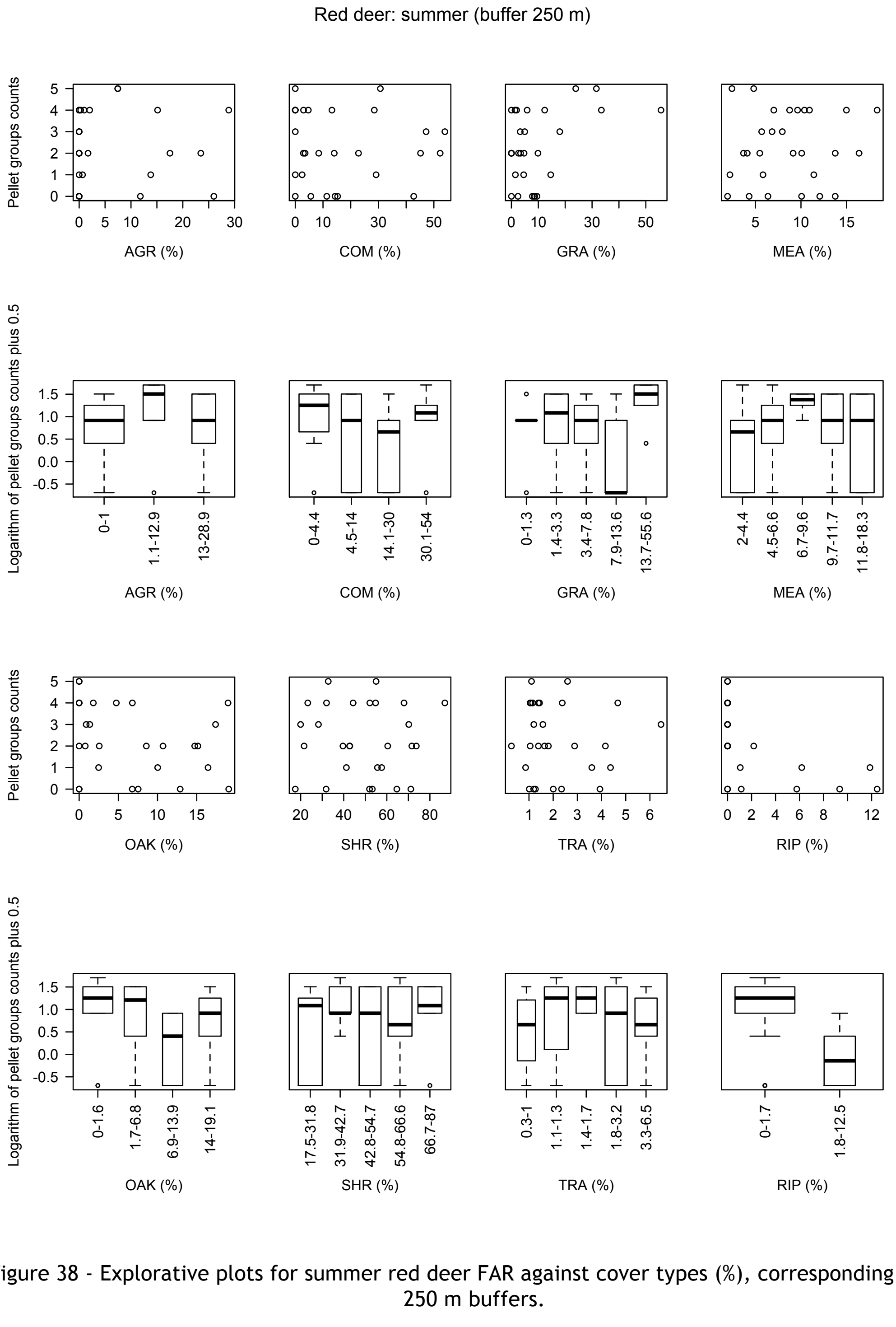


Figure 38 - Explorative plots for summer red deer FAR against cover types (%), corresponding to the 250 m buffers.

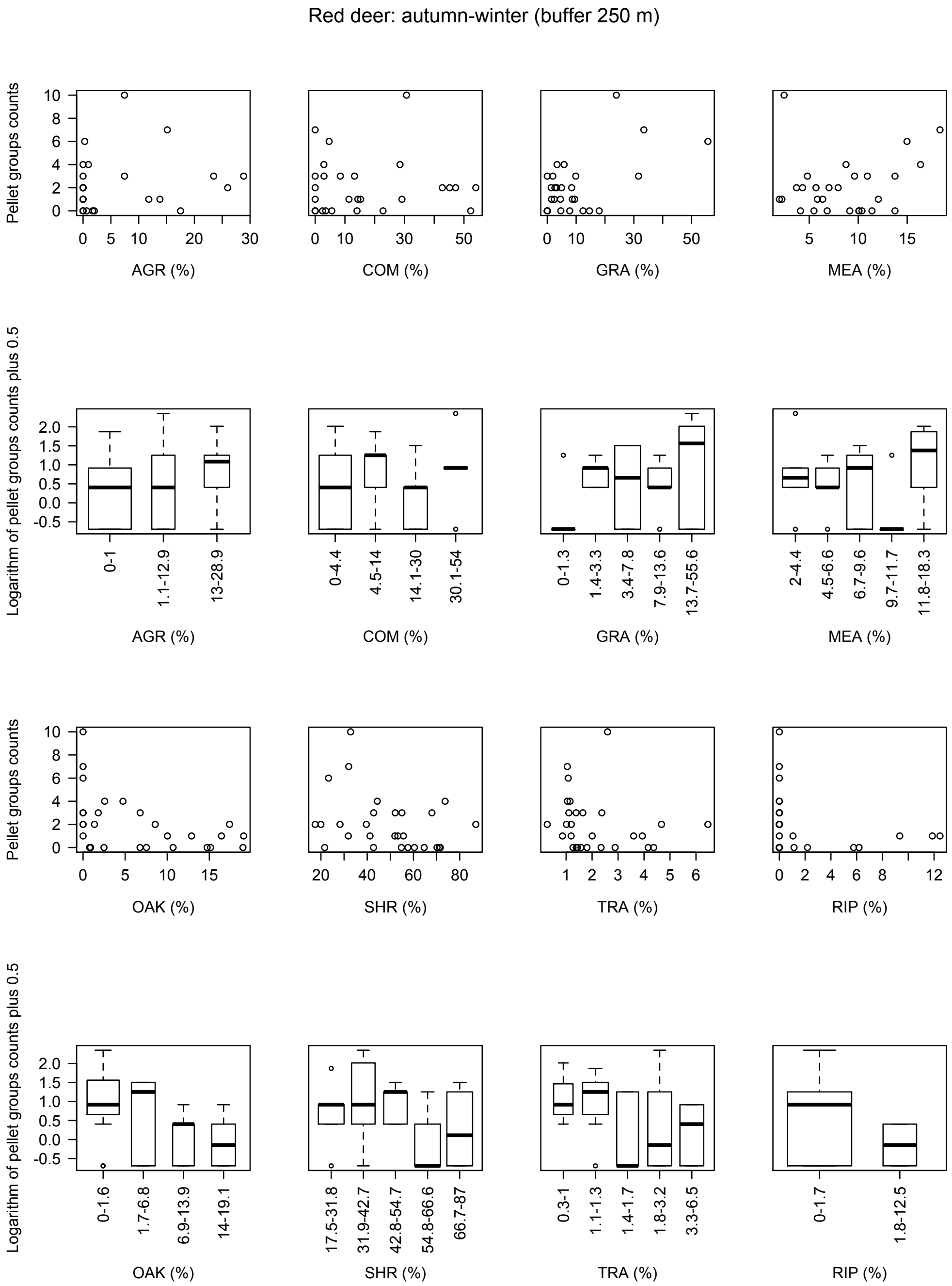


Figure 39 - Explorative plots for summer autumn-winter red deer FAR against cover types (%), corresponding to the 250 m buffers.

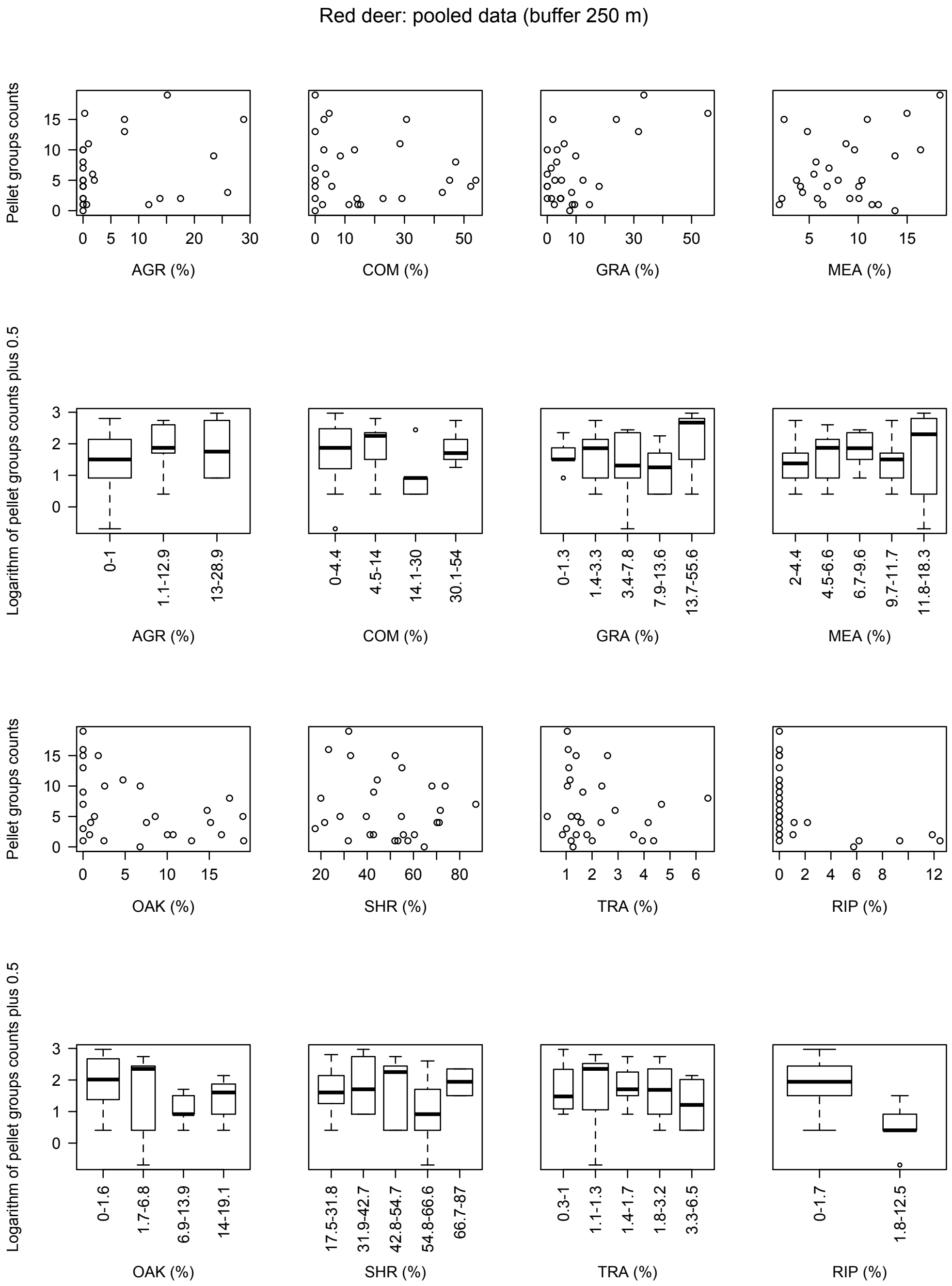


Figure 40 - Explorative plots for pooled annual red deer FAR against cover types (%), corresponding to the 250 m buffers.

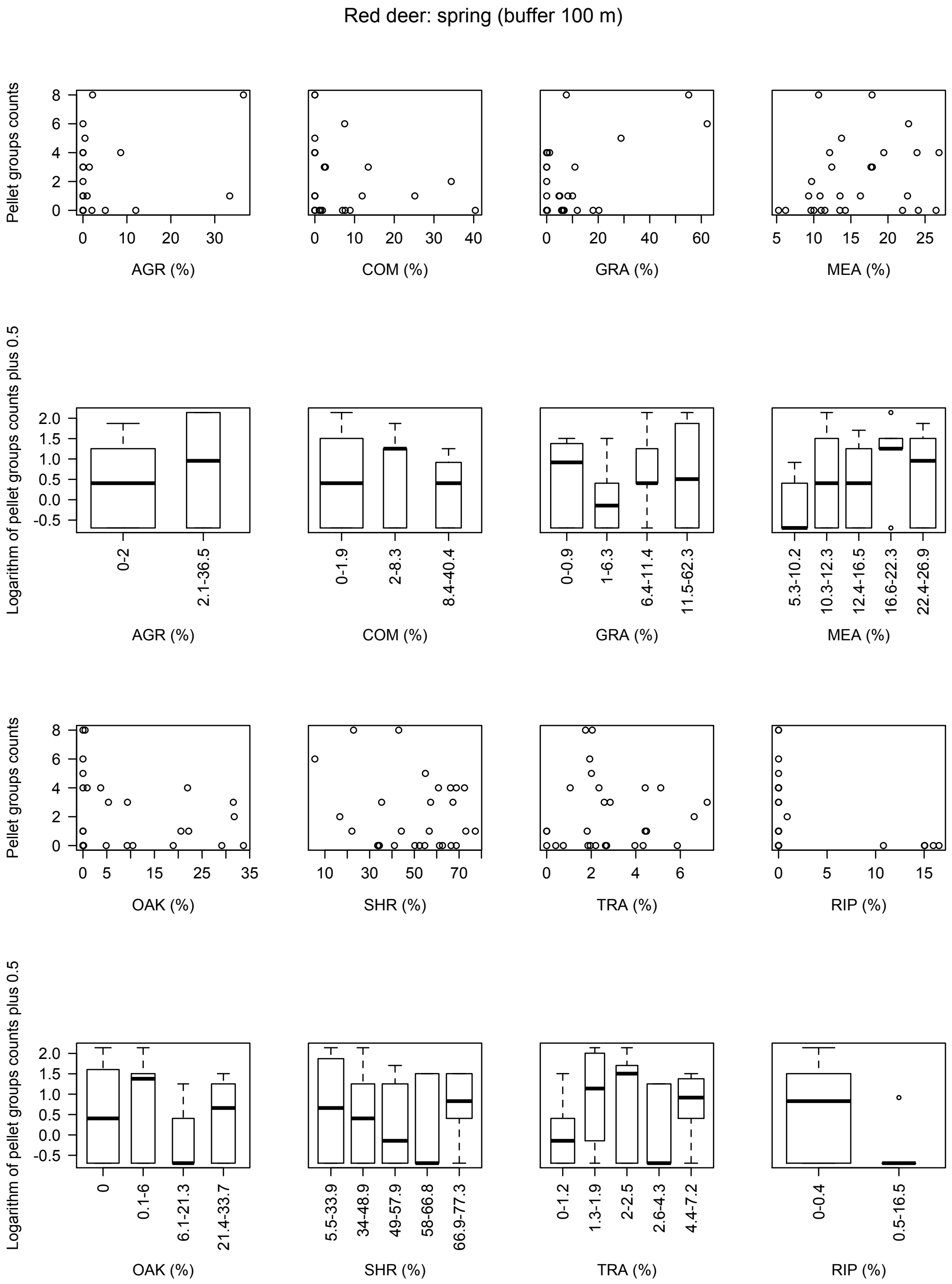


Figure 41 - Explorative plots for spring red deer FAR against cover types (%), corresponding to the 100 m buffers.

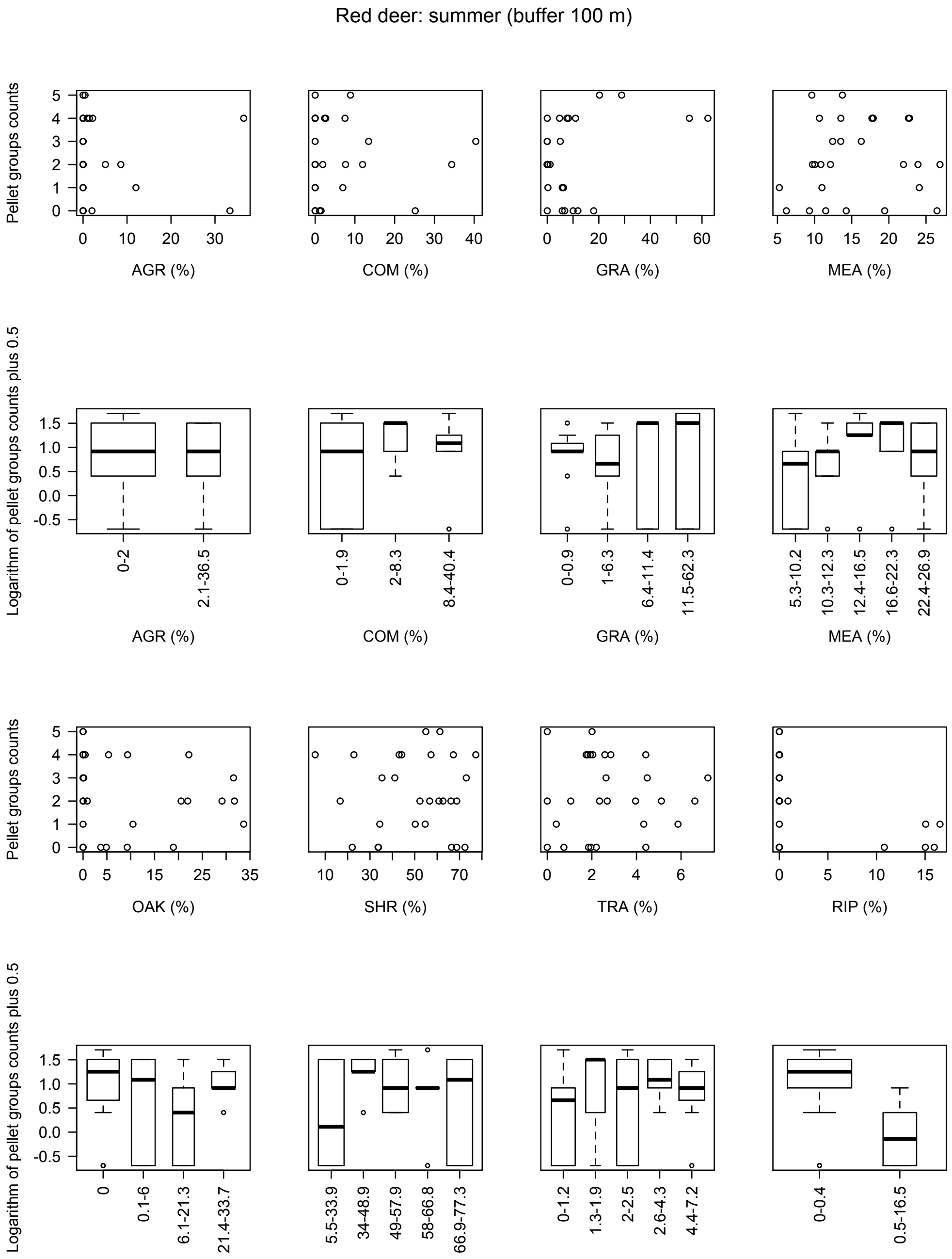


Figure 42 - Explorative plots for summer red deer FAR against cover types (%), corresponding to the 100 m buffers.

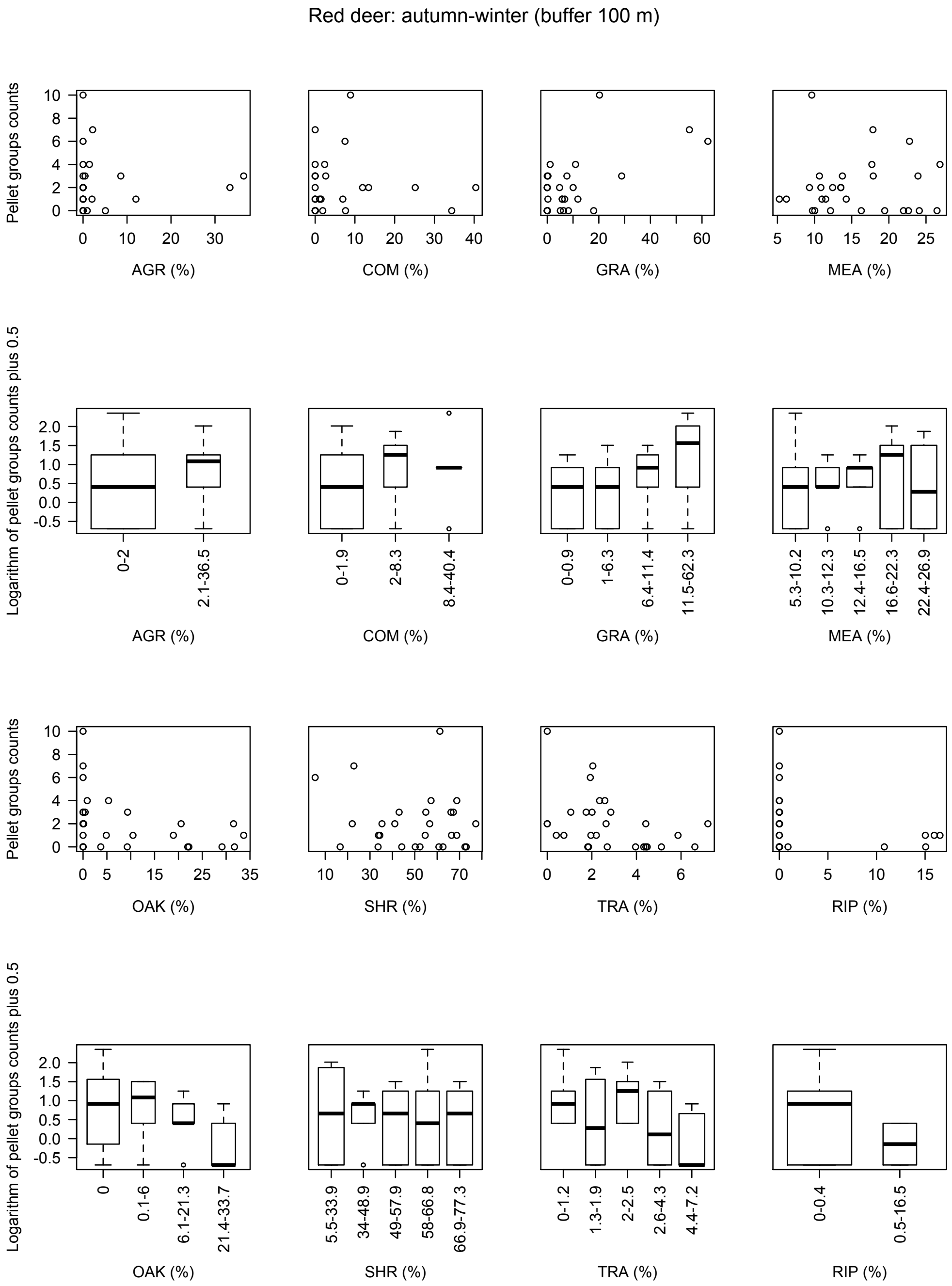


Figure 43 - Explorative plots for autumn-winter red deer FAR against cover types (%), corresponding to the 100 m buffers.

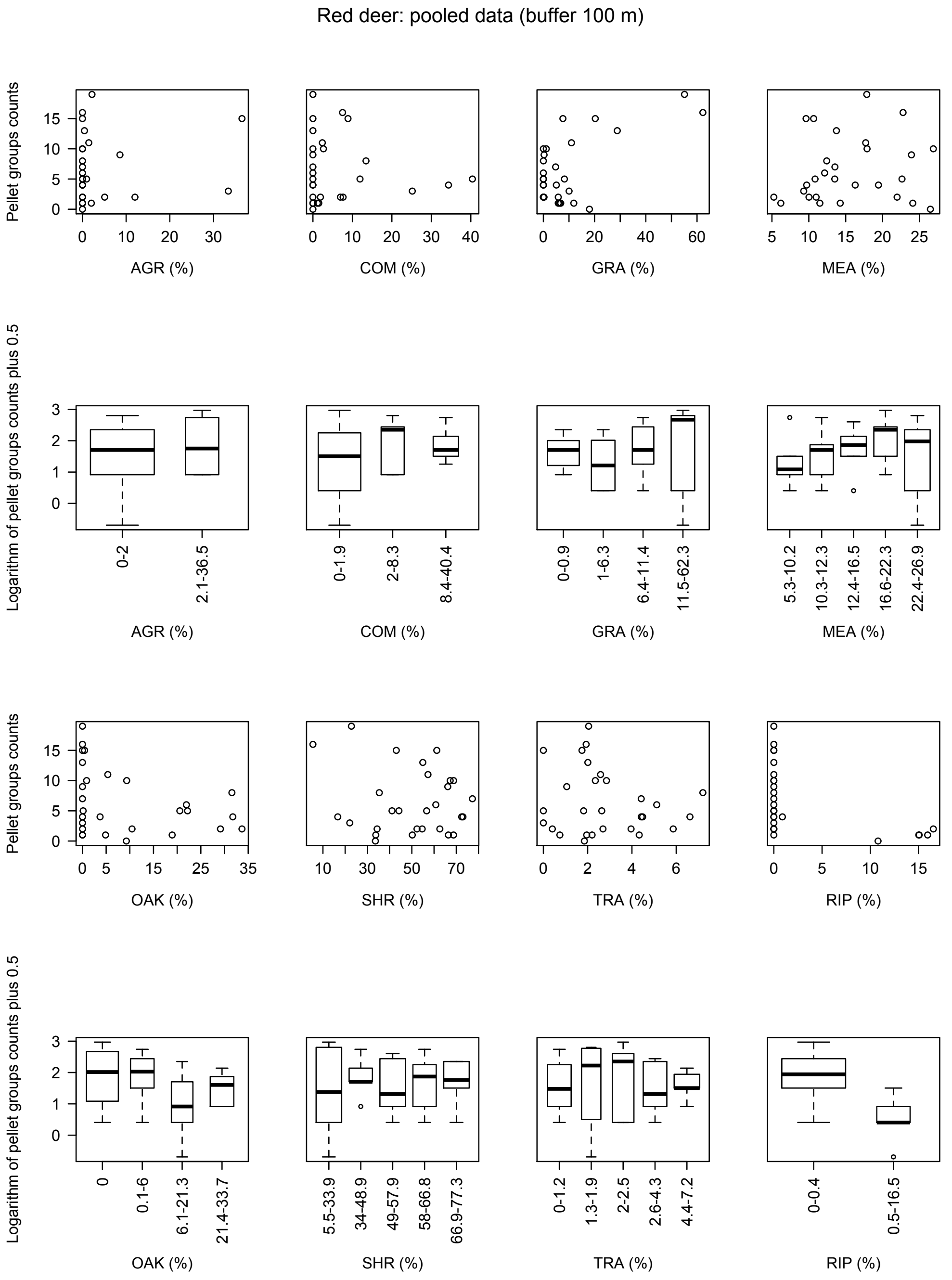
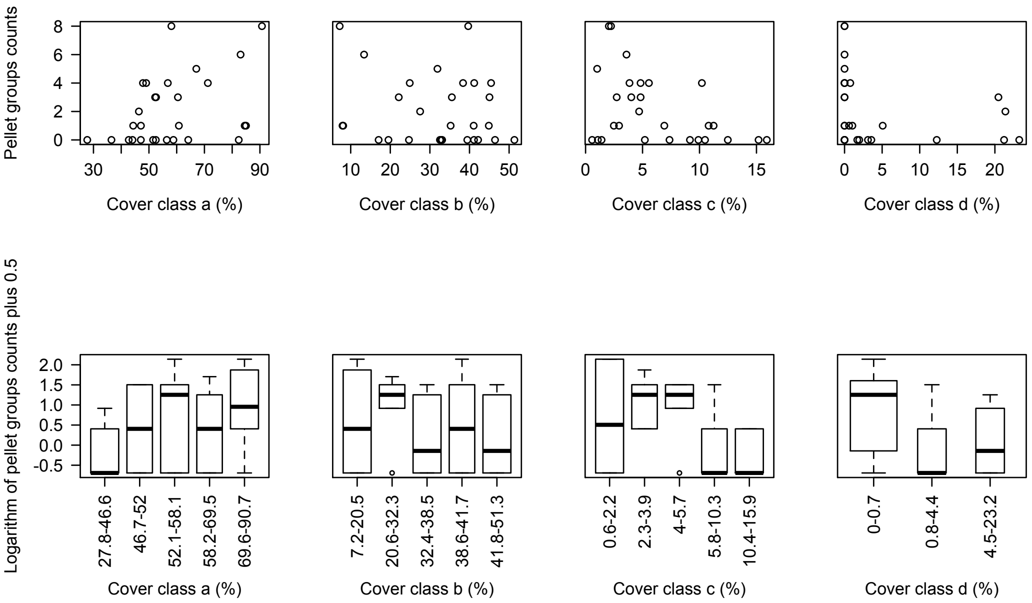


Figure 44 - Explorative plots for pooled annual red deer FAR against cover types (%), corresponding to the 100 m buffers.

Red deer: spring (buffer 500 m)



Red deer: summer (buffer 500 m)

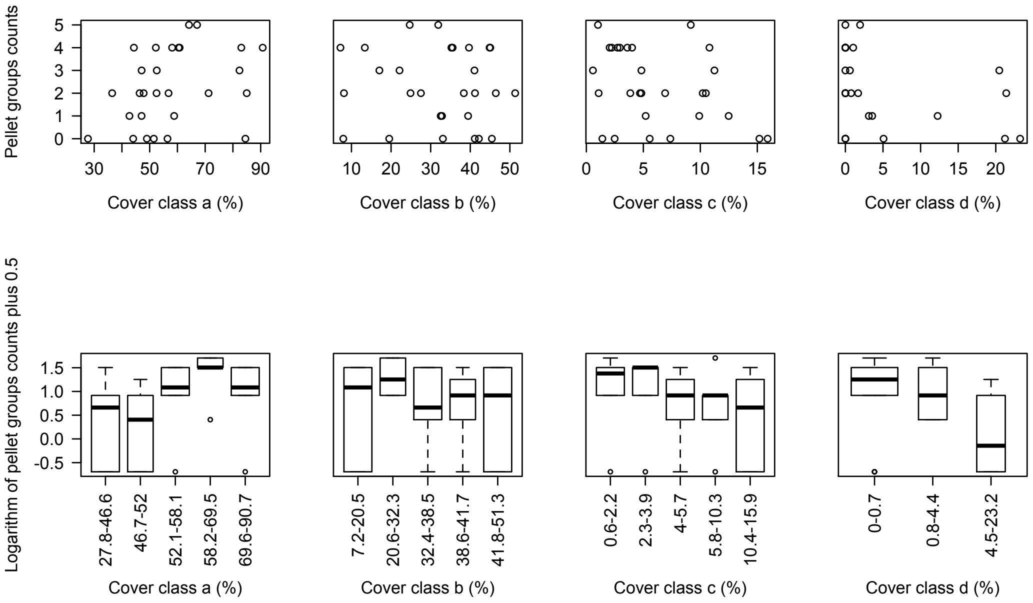


Figure 45 - Explorative plots for spring and summer red deer FAR against cover classes (%), corresponding to the 500 m buffers.

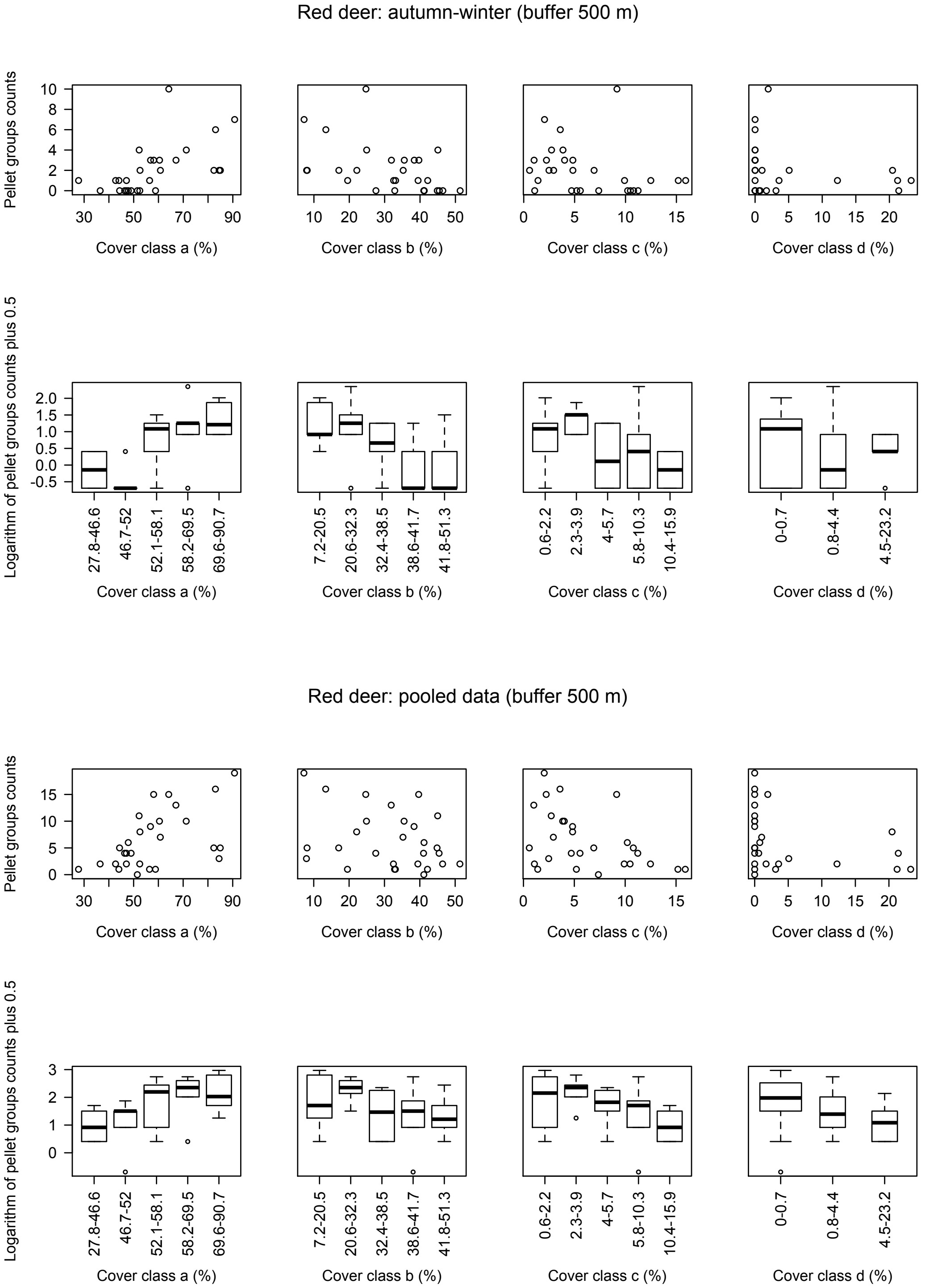
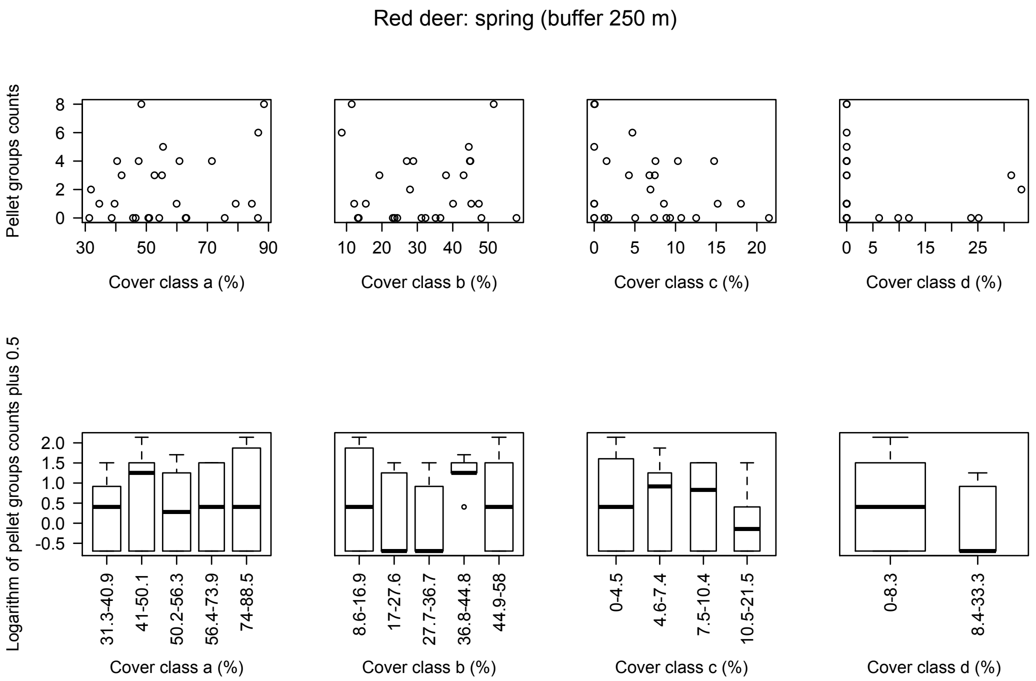
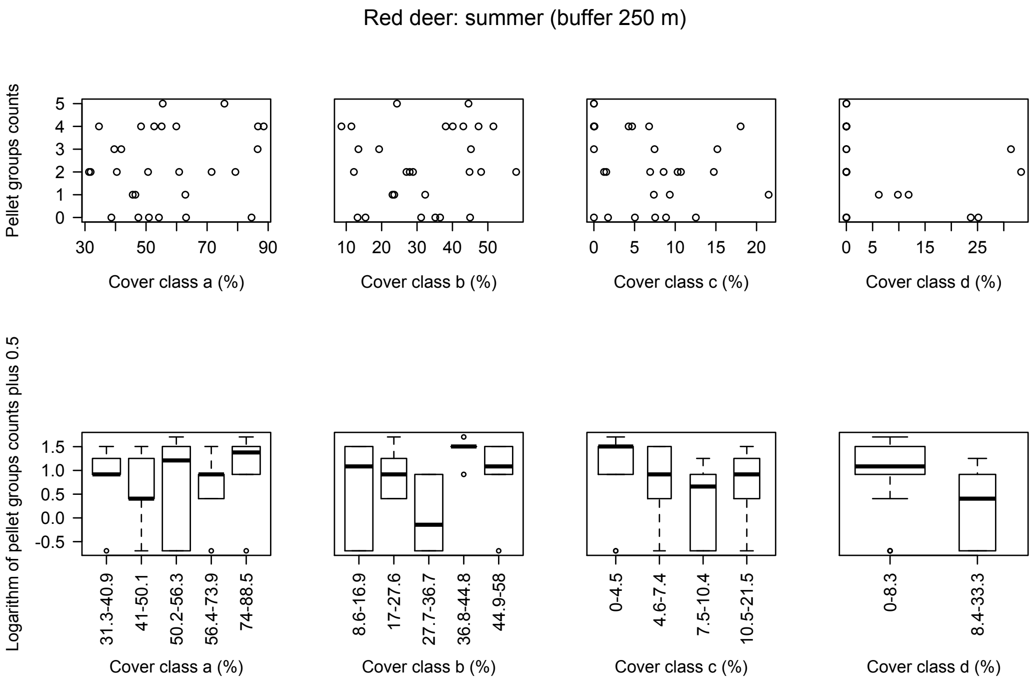


Figure 46 - Explorative plots for autumn-winter and pooled annual red deer FAR against cover classes (%), corresponding to the 500 m buffers.



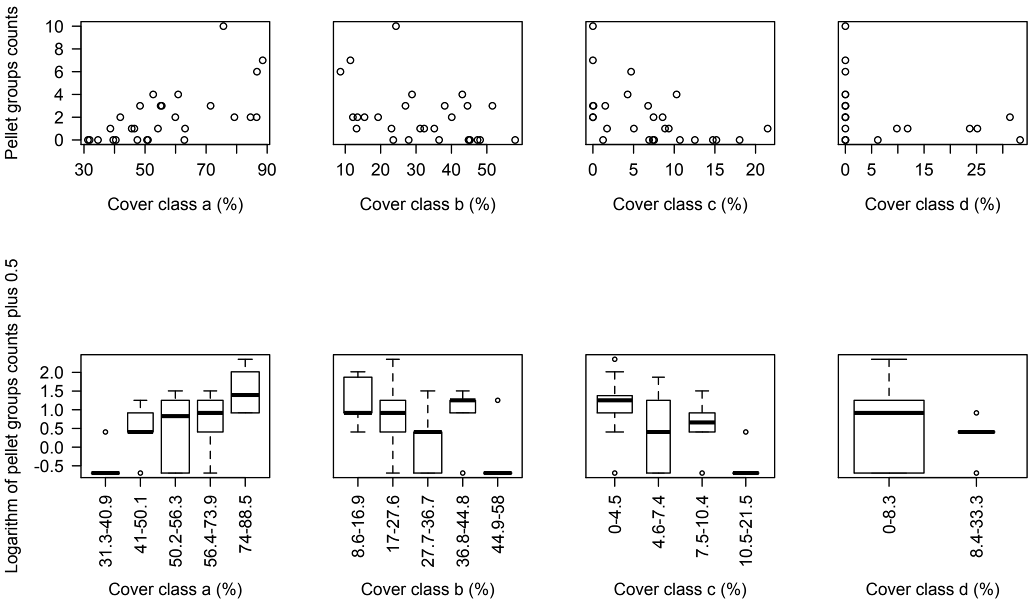
Red deer: spring (buffer 250 m)



Red deer: summer (buffer 250 m)

Figure 47 - Explorative plots for spring and summer red deer FAR against cover classes (%), corresponding to the 250 m buffers.

Red deer: autumn-winter (buffer 250 m)



Red deer: pooled data (buffer 250 m)

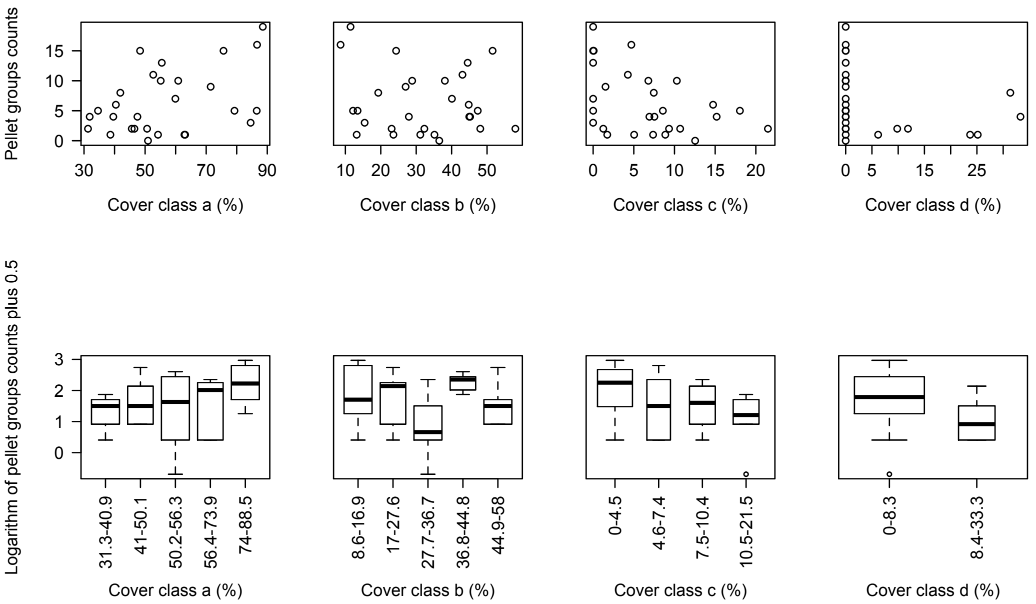
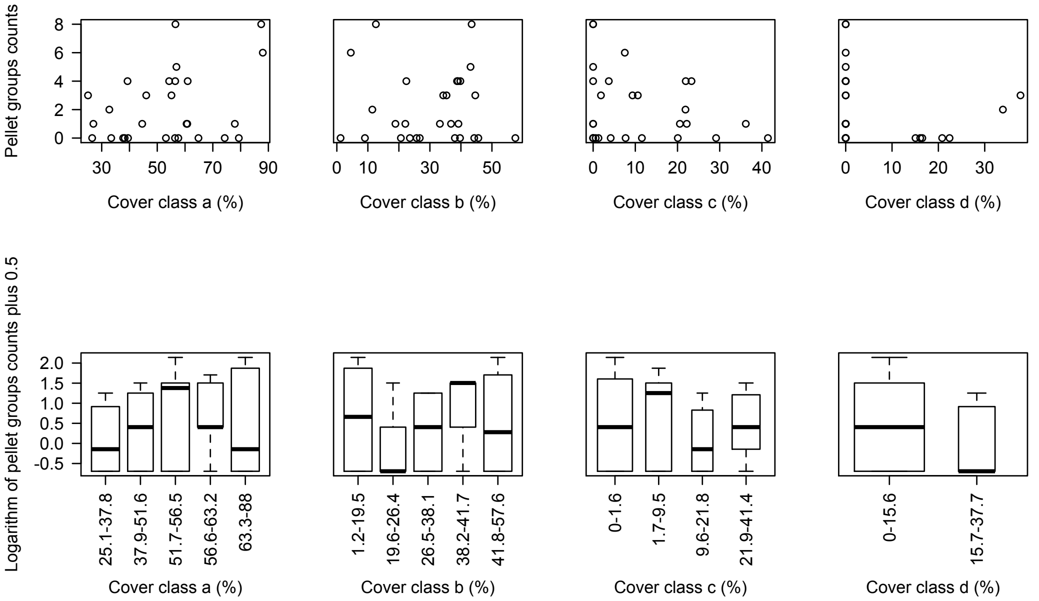


Figure 48 - Explorative plots for autumn-winter and pooled annual red deer FAR against cover classes (%), corresponding to the 250 m buffers.

Red deer: spring (buffer 100 m)



Red deer: summer (buffer 100 m)

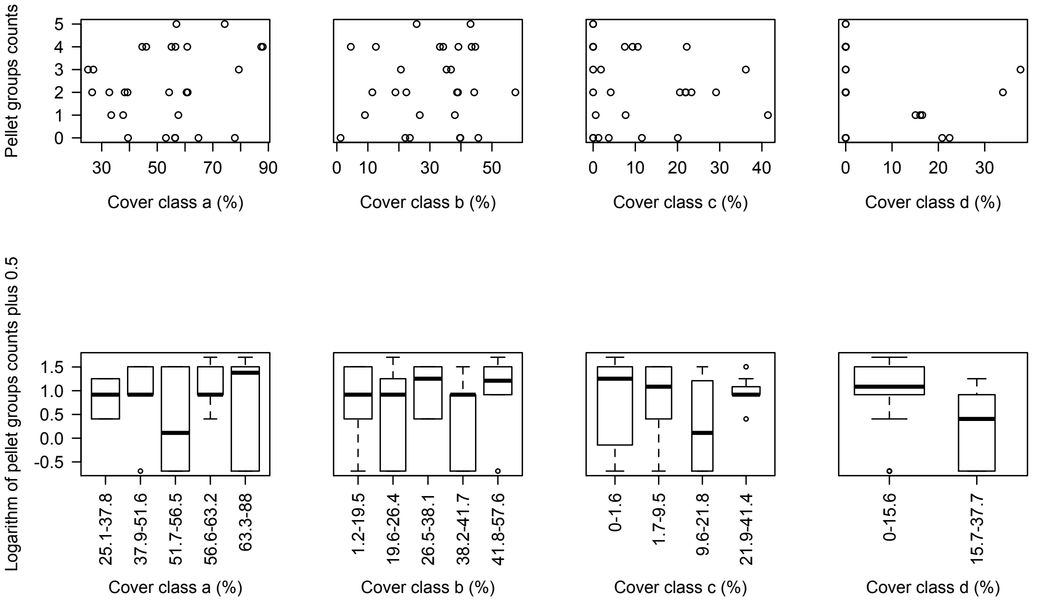
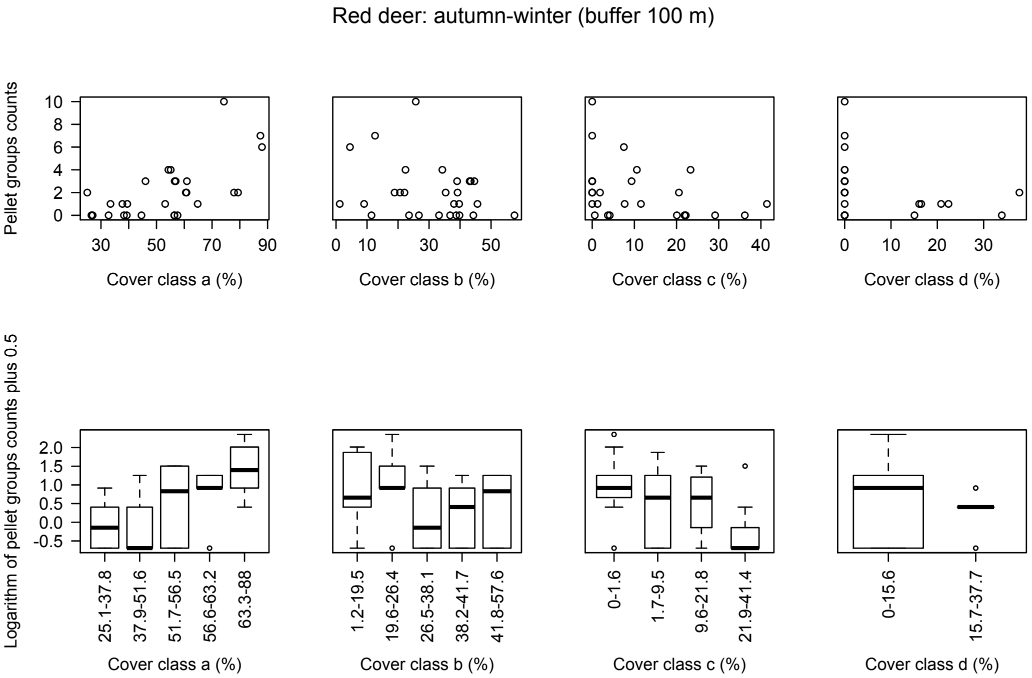


Figure 49 - Explorative plots for spring and summer red deer FAR against cover classes (%), corresponding to the 100 m buffers.


Red deer: autumn-winter (buffer 100 m)

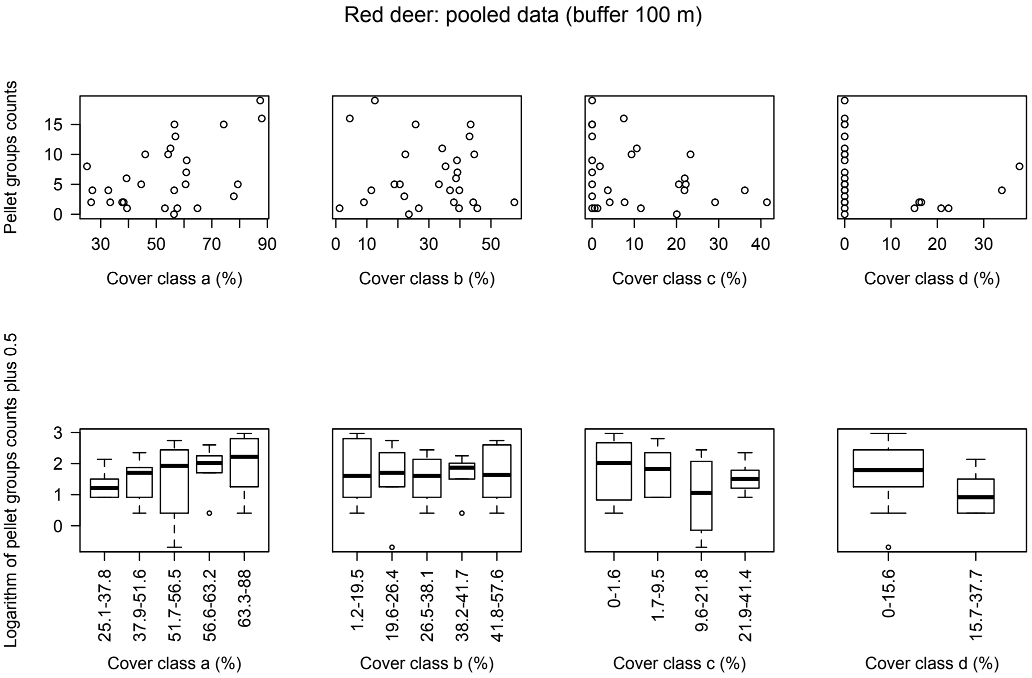

Red deer: pooled data (buffer 100 m)

Figure 50 - Explorative plots for autumn-winter and pooled annual red deer FAR against cover classes (%), corresponding to the 100 m buffers.

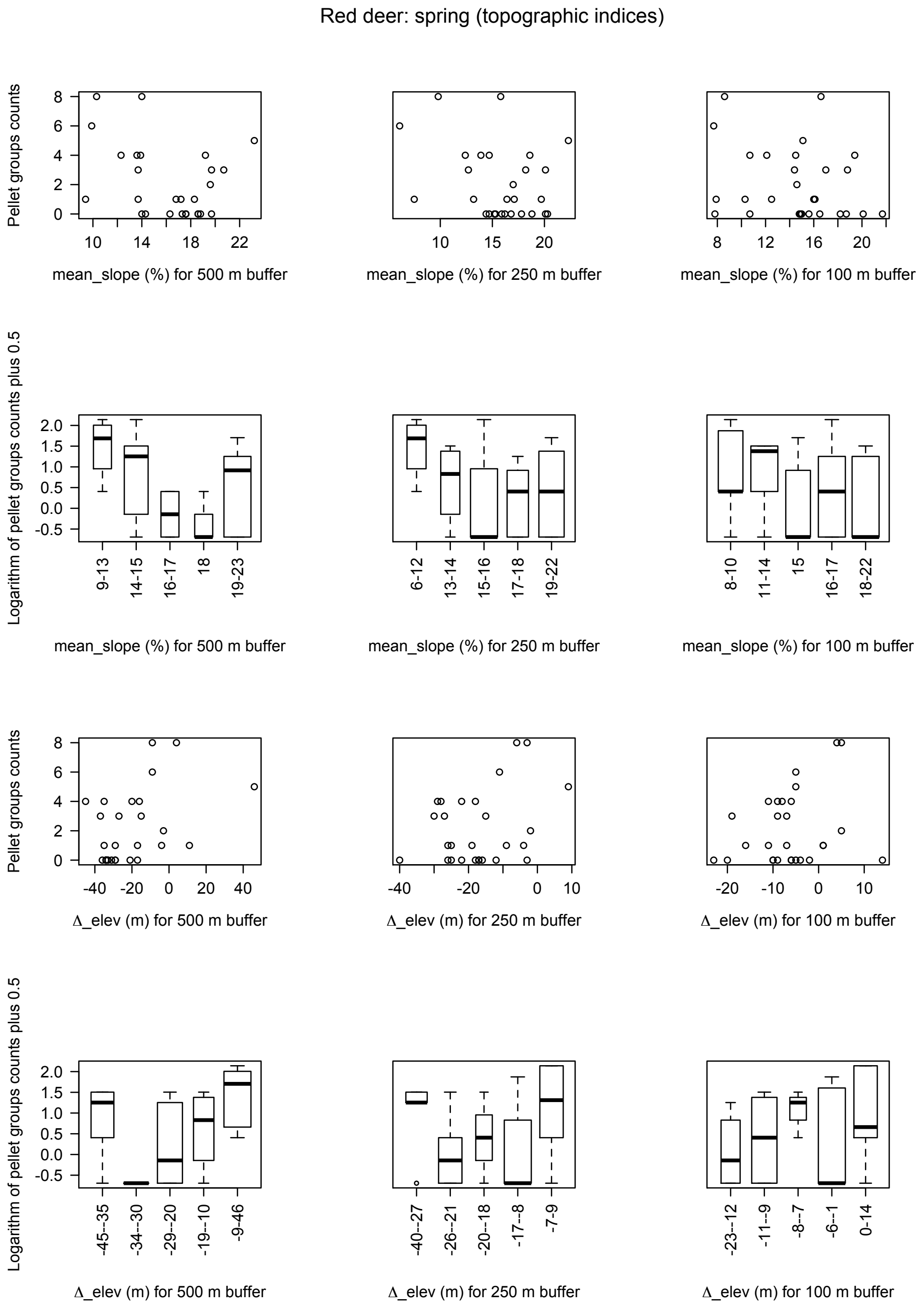


Figure 51 - Explorative plots for spring red deer FAR against topographic indexes corresponding to the three buffers.

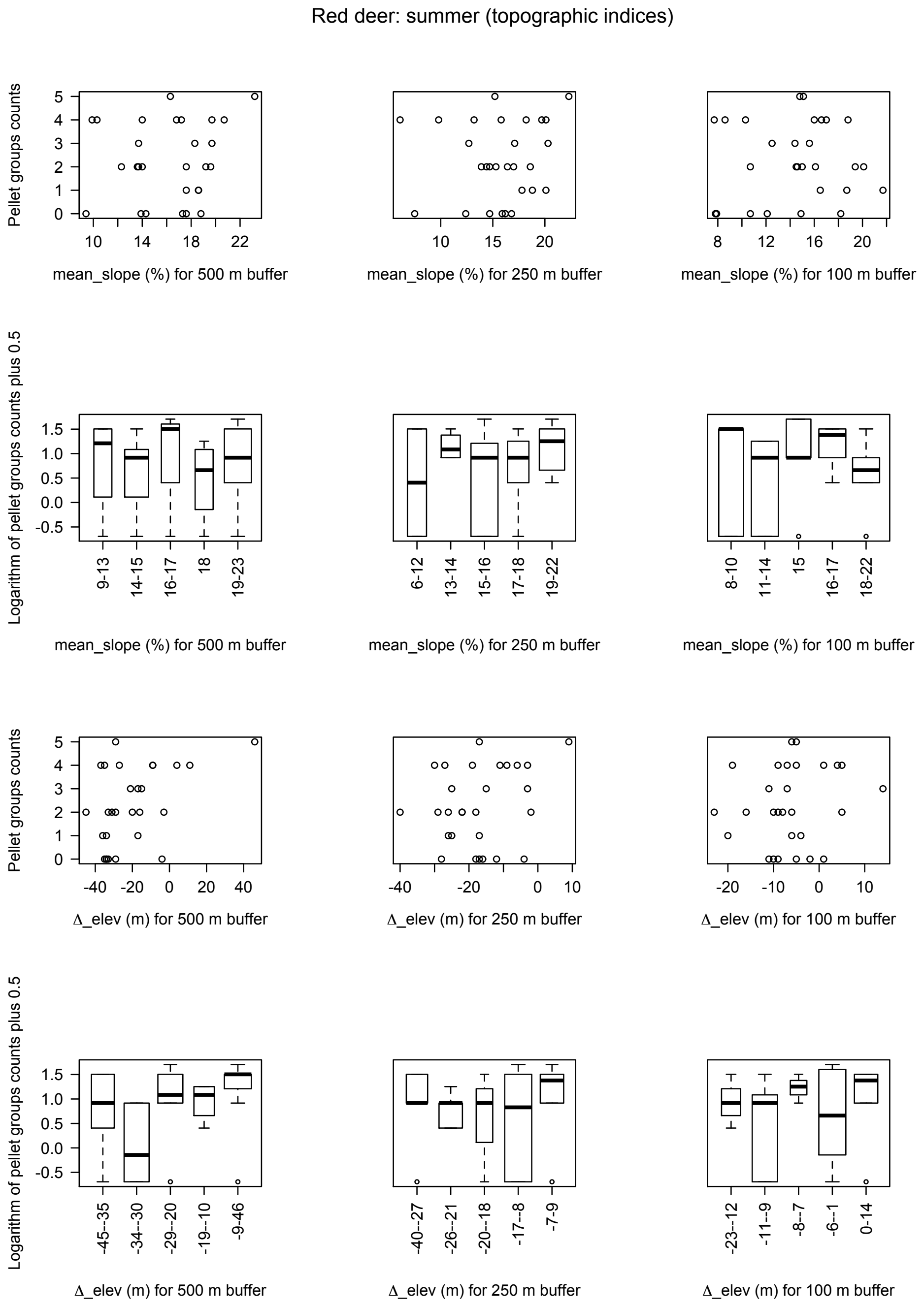


Figure 52 - Explorative plots for summer red deer FAR against topographic indexes corresponding to the three buffers.

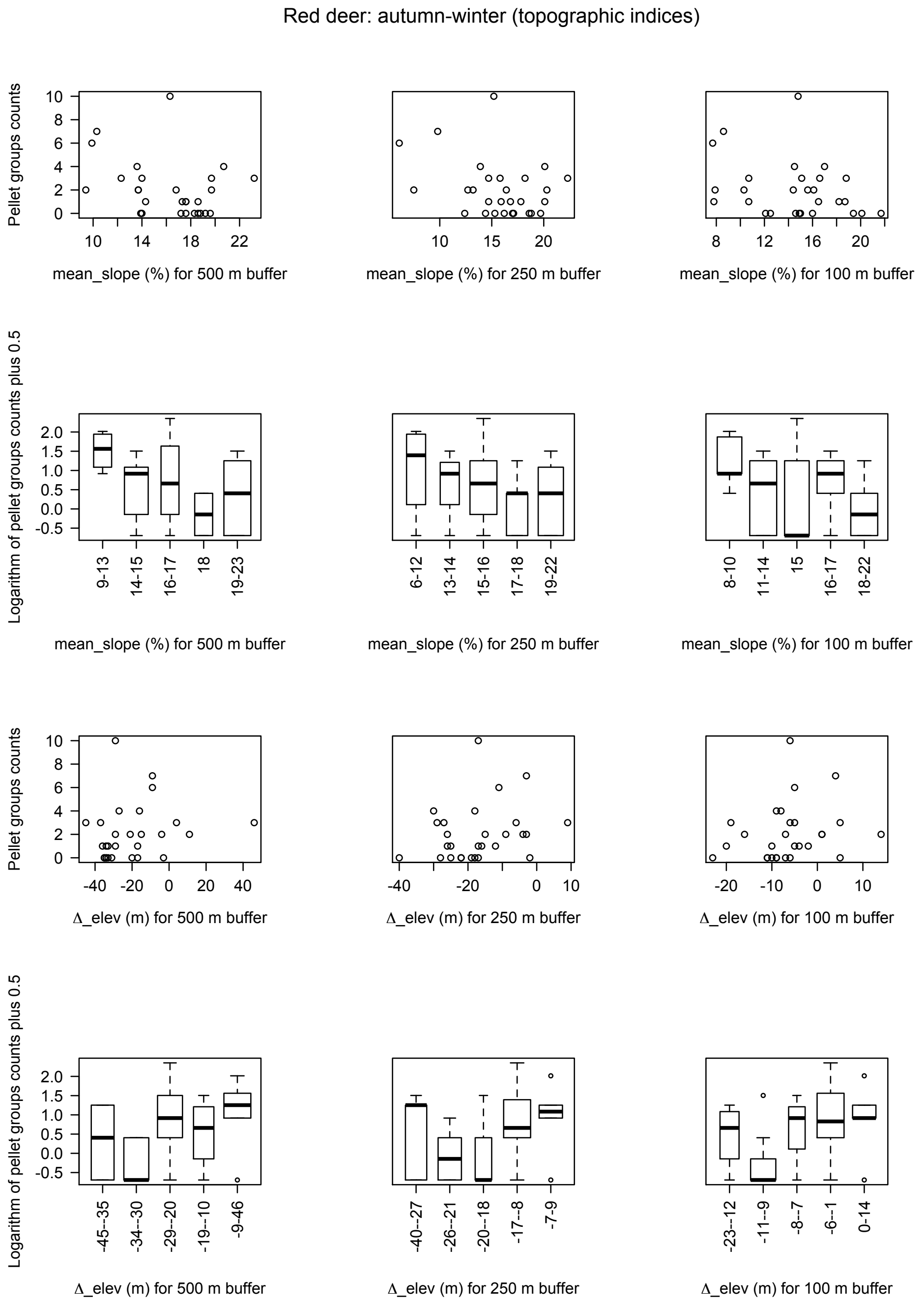


Figure 53 - Explorative plots for autumn-winter red deer FAR against topographic indexes corresponding to the three buffers.

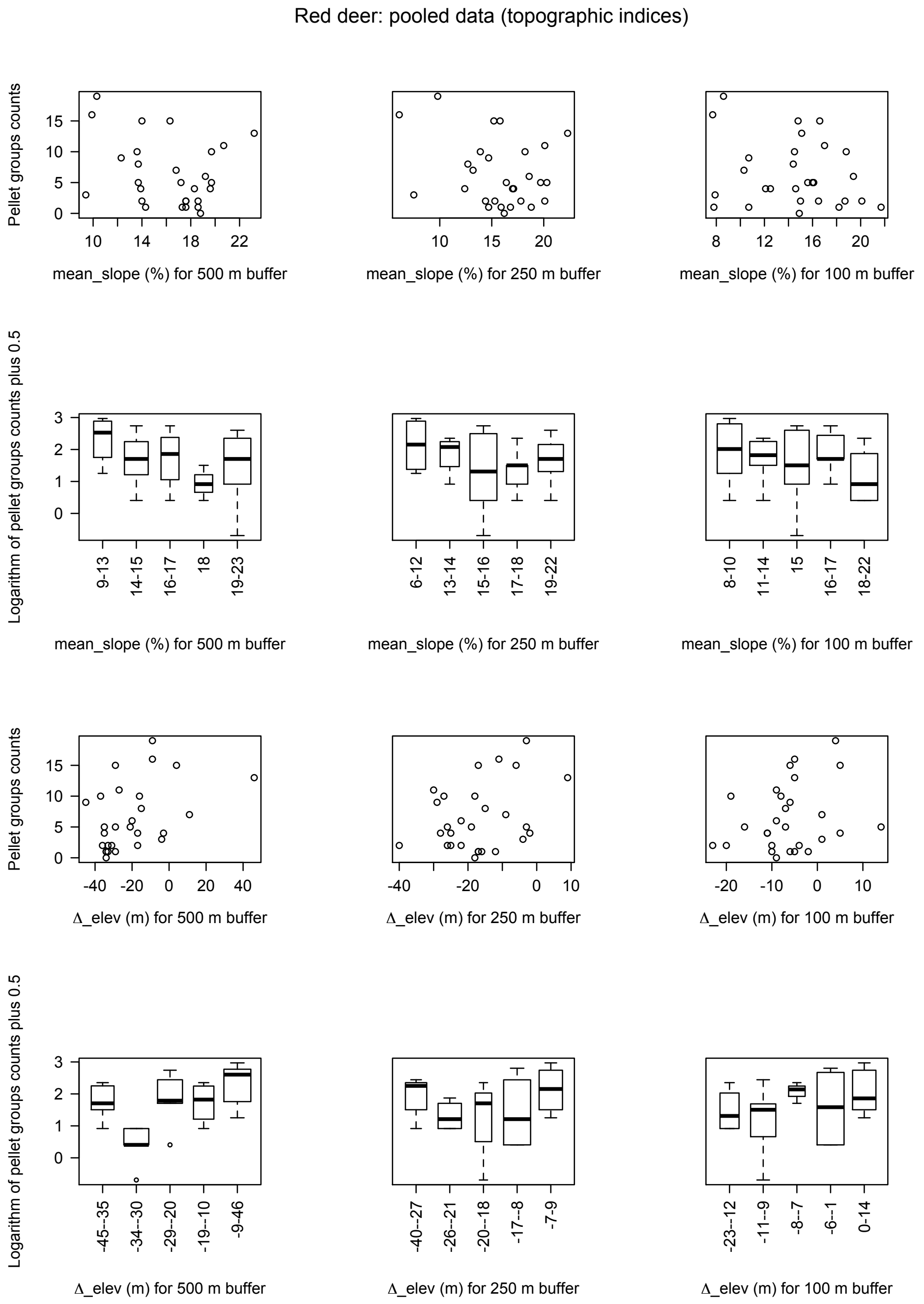


Figure 54 - Explorative plots for pooled annual red deer FAR against topographic indexes corresponding to the three buffers.

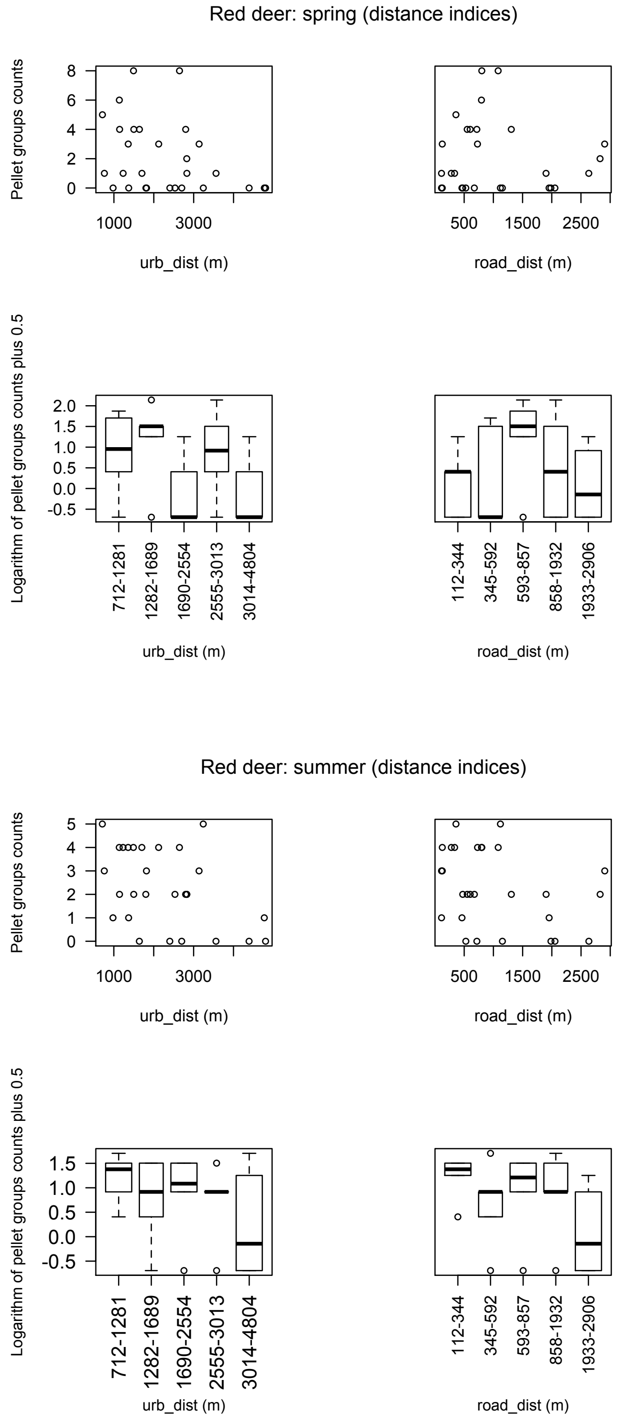
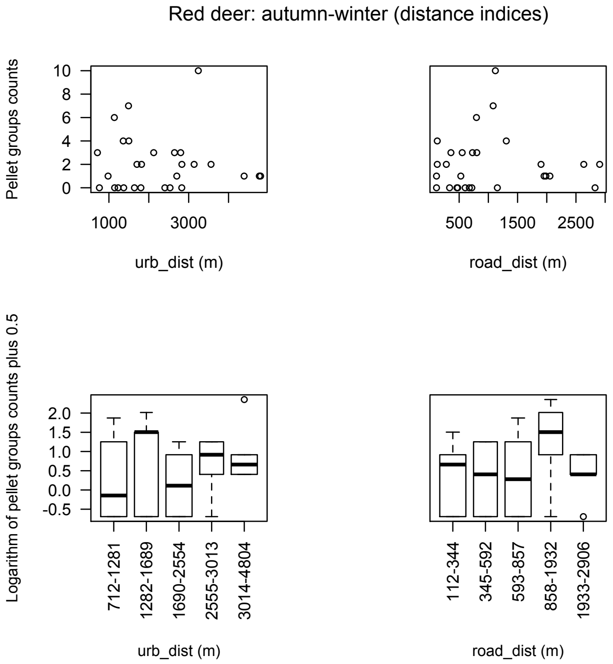


Figure 55 - Explorative plots for spring and summer red deer FAR against distance indexes.



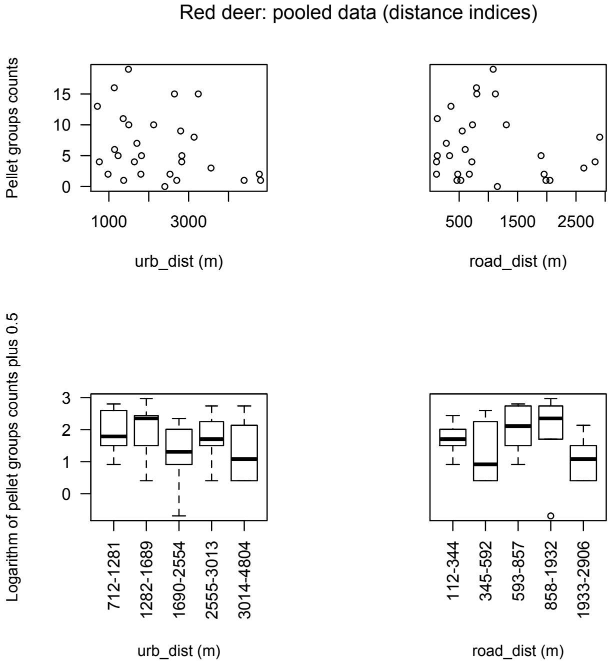


Figure 56 - Explorative plots for autumn-winter and pooled annual red deer FAR against distance indexes.

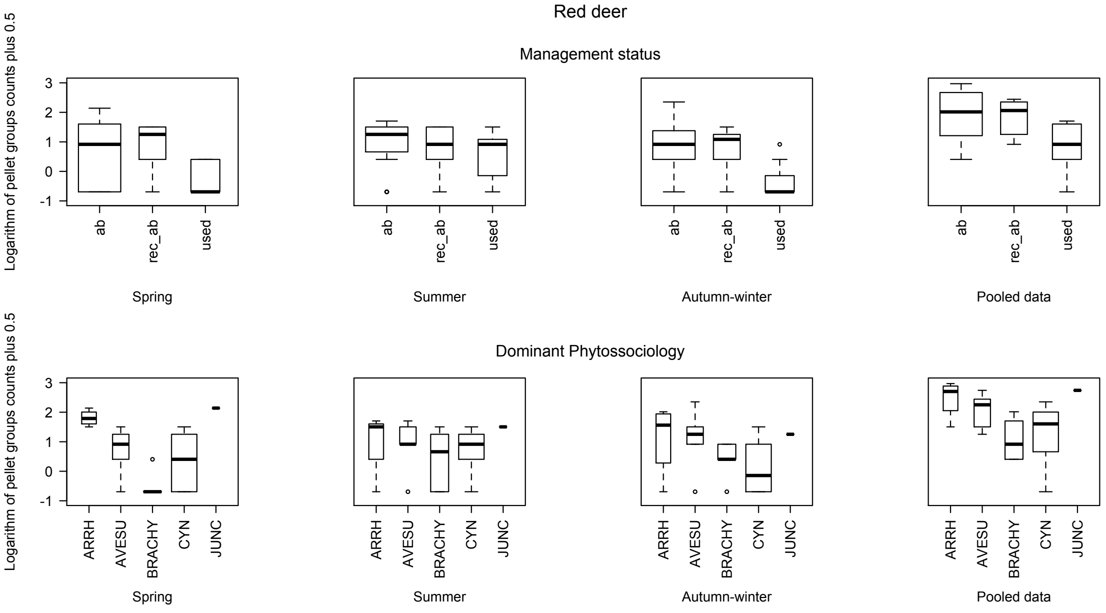


Figure 57 - Box plots for seasonal and pooled annual red deer FAR against management status and dominant Phytosociology.

3. Summary of the best models for red deer use of meadows (chapter 9)

Table 48 – Best models for red deer spring use of meadows, considering cover types percentage and topographic indexes in the three buffer widths as predictors.

Models formula (spring - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest	
1 + RIP_100 + COM_100 + Δ_elev_100	29.6241	24	0.1975	101.24	0.1196	
1 + RIP_100 + COM_100 + SHR_100	27.9975	24	0.2601	102.13	0.043	
1 + GRA_100 + RIP_100	27.8907	25	0.3129	103.17	0.0115	
Models formula (spring – 250 m buffers)						
1 + RIP_250 + MEA_250	29.0757	25	0.2608	104.16	0.0135	
1 + RIP_250 + MEA_250 + Δ_elev_250	30.4173	24	0.1713	104.22	0.0793	
1 + RIP_250	27.0719	26	0.4056	105.05	0.0002	
1 + COM_250 + RIP_250	28.7047	25	0.2764	105.44	0.0037	
1 + RIP_250 + Δ_elev_250	27.5762	25	0.3277	105.72	0.0013	
Models formula (spring – 500 m buffers)						
1 + MEA_500 + RIP_500 + Δ_elev_500	32.0868	24	0.1249	106.67	0.0922	
1 + RIP_500 + Δ_elev_500	28.7622	25	0.2740	107.18	0.0018	
1 + RIP_500	27.7131	26	0.3727	107.51	< 0.0001	
1 + MEA_500 + RIP_500	29.4766	25	0.2445	108.04	0.0033	
1 + RIP_500 + OAK_500	28.0091	25	0.3074	108.42	0.0002	*
1 + OAK_500	29.1317	26	0.3051	108.5	0.0001	
1 + GRA_500 + RIP_500	29.0503	25	0.2618	108.54	0.0017	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, inclusion of the null model, bad fit or numerical problems.

Table 49 - Best models for red deer summer use of meadows, considering cover types percentage and topographic indexes in the three buffer widths as predictors.

Models formula (summer - 100 m buffers)	Res.d	Df	GOF test	AICc	DPqpoisson
1 + GRA_100 + RIP_100	27.7428	25	0.3198	97.83	0.0214
1 + RIP_100	30.3098	26	0.255	97.88	0.86
1 + GRA_100 + RIP_100 + mean_slope_100	26.2208	24	0.3420	99.05	0.7879
1 + RIP_100 + Δ_elev_100	29.1372	25	0.2582	99.23	0.8599
1 + AGR_100 + RIP_100	29.3778	25	0.2484	99.47	0.90555
1 + RIP_100 + OAK_100	29.5839	25	0.2402	99.68	0.8377
1 + GRA_100 + RIP_100 + SHR_100	26.9108	24	0.3086	99.74	0.7901
Models formula (summer – 250 m buffers)					
1 + GRA_250 + RIP_250 + mean_slope_250	22.2575	24	0.5639	95.09	0.7408
1 + GRA_250 + RIP_250	25.6281	25	0.4277	95.72	0.7989
1 + RIP_250	28.2679	26	0.3454	95.84	0.8559
1 + RIP_250 + Δ_elev_250	26.7919	25	0.3664	96.88	0.8449
1 + GRA_250 + RIP_250 + TRA_250	24.1752	24	0.4516	97.01	0.7978
1 + RIP_250 + mean_slope_250	26,9187	25	0.3599	97.01	0.8735
Models formula (summer – 500 m buffers)					
1 + GRA_500 + RIP_500 + mean_slope_500	24.5155	24	0.4325	97.35	0.8141

1 + RIP_500 + mean_slope_500	28.0128	25	0.3073	98.11	0.9069
1 + RIP_500 + Δ_elev_500	28.0615	25	0.305	98.15	0.8389
1 + AGR_500 + RIP_500 + Δ_elev_500	25.6712	24	0.3701	98.5	0.856
1 + RIP_500 + mean_slope_500 + Δ_elev_500	25.7075	24	0.3682	98.54	0.8346
1 + GRA_500 + RIP_500	29.1038	25	0.2596	99.2	0.8916

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; DPqpoisson = dispersion parameter fitting a quasipoisson; * = model is excluded because of either multicollinearity, inclusion of the null model, bad fit or numerical problems.

Table 50 - Best models for red deer autumn-winter use of meadows, considering cover types percentage and topographic indexes in the three buffer widths as predictors.

Models formula (autumn-winter - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest	
1 + GRA_100 + RIP_100 + TRA_100	34.6813	24	0.0733	105.12	0.2408	
1 + GRA_100 + TRA_100 + SHR_100	38.9113	24	0.0279	105.35	0.4760	
1 + GRA_100 + TRA_100	34.2704	25	0.1022	105.53	0.1112	
1 + GRA_100 + OAK_100 + TRA_100	35.9291	24	0.0558	105.73	0.285	
1 + GRA_100 + RIP_100 + OAK_100	33.1677	24	0.1006	106.80	0.1056	
Models formula (autumn-winter – 250 m buffers)						
1 + OAK_250 + SHR_250	31.2927	25	0.1795	105.41	0.029	
1 + GRA_250 + OAK_250	32.5428	25	0.1429	106.49	0.0388	
1 + OAK_250	31.411	26	0.2133	106.83	0.0049	
1 + GRA_250 + COM_250 + OAK_250	32.8018	24	0.1083	107.3	0.0871	
1 + GRA_250 + OAK_250 + SHR_250	32.6148	24	0.1125	107.39	0.0799	
Models formula (autumn-winter – 500 m buffers)						
1 + OAK_500 + SHR_500	32.0399	25	0.1569	105.75	0.0359	
1 + COM_500 + GRA_500 + OAK_500	33.6312	24	0.0914	106.56	0.1329	
1 + GRA_500 + OAK_500 + SHR_500	33.373	24	0.0964	106.91	0.1158	
1 + OAK_500	32.9684	26	0.163	107.1	0.0132	
1 + AGR_500 + OAK_500 + SHR_500	33.0939	24	0.1021	107.23	0.0946	*
1 + OAK_500 + TRA_500 + SHR_500	31.4325	24	0.1417	107.53	0.0379	
1 + OAK_500 + MEA_500 + SHR_500	32.0339	24	0.1261	107.66	0.0521	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, inclusion of the null model, bad fit or numerical problems.

Table 51 - Best models for red deer pooled annual use of meadows, considering cover types percentage and topographic indexes in the three buffer widths as predictors.

Models formula (pooled annual - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest
1 + GRA_100 + RIP_100	29.6906	25	0.2361	149.01	0.0062
1 + GRA_100 + RIP_100 + Δ_elev_100	29.7176	24	0.1943	150.15	0.0157
1 + GRA_100+ RIP_100 + OAK_100	29.8121	24	0.1910	150.21	0.0150
1 + GRA_100+ RIP_100 + SHR_100	29.8021	24	0.1913	150.64	0.0139
Models formula (pooled annual – 250 m buffers)					
1 + GRA_250 + RIP_250	30.2496	25	0.2151	151.62	0.0017

1 + GRA_250 + RIP_250 + Δ_elev_250	30.5824	24	0.1662	153.59	0.0041	
Models formula (pooled annual – 500 m buffers)						
1 + GRA_500 + RIP_500	29.7087	25	0.2354	154.75	0.0002	
1 + GRA_500 + OAK_500	30.025	25	0.2234	155.07	0.0004	
1 + RIP_500 + Δ_elev_500	28.9512	25	0.266	155.5	<0.0001	
1 + GRA_500 + RIP_500 + OAK_500	30.1878	24	0.1786	155.6	0.0015	*
1 + GRA_500 + RIP_500 + Δ_elev_500	29.5784	24	0.1991	156.01	0.0005	
1 + OAK_500	29.2046	26	0.3019	156.08	<0.0001	
1 + RIP_500 + OAK_500	29.4884	25	0.244	156.3	<0.0001	*
1 + RIP_500 + OAK_500 + Δ_elev_500	29.3186	24	0.2084	156.57	0.0001	*

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, inclusion of the null model, bad fit or numerical problems.

Table 52 – Best models for red deer spring use of meadows, considering cover classes percentage and topographic indexes in the three buffer widths as predictors.

Models formula (spring - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest	
1	30.0001	27	0.3142	113.45	> 0.0001	*
1 + a_100	30.4716	26	0.2485	113.87	> 0.0001	
1 + c_100	30.1278	26	0.2624	114.39	> 0.0001	
1 + Δ_elev_100	30.1439	26	0.2617	114.45	> 0.0001	
1 + mean_slope_100	30.2286	26	0.2583	114.67	> 0.0001	
1 + d_100	30.3058	26	0.2551	114.93	> 0.0001	
Models formula (spring - 250 m buffers)						
1	30.0001	27	0.3142	113.45	> 0.0001	*
1 + c_250	30.2814	26	0.2561	113.90	> 0.0001	
1 + Δ_elev_250	30.463	26	0.2489	114.16	> 0.0001	
1 + mean_slope_250	30.4802	26	0.2482	114.50	> 0.0001	
1 + d_250	30.2347	26	0.258	115.04	> 0.0001	
1 + a_250	30.183	26	0.2601	115.10	> 0.0001	
1 + d_250 + Δ_elev_250	30.8249	25	0.1949	115.42	0.0001	
Models formula (spring - 500 m buffers)						
1 + c_500	29.692	26	0.2806	108.75	0.0001	
1 + c_500 + mean_slope_500	30.288	25	0.2137	110.50	0.0005	
1 + c_500 + Δ_elev_500	30.0956	25	0.2207	110.69	0.0004	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, numerical problems, inclusion of null model, or bad fit.

Table 53 – Best models for red deer summer use of meadows, considering cover classes percentage and topographic indexes in the three buffer width as predictors.

Models formula (summer - 100 m buffers)	Res.d	Df	GOF test	AICc	DPqpoisson	
1 + d_100	40.1037	26	0.0381	107.68	1.1488	
1	43.1895	27	0.025	108.44	1.1944	*
1 + d_100 + Δ_elev _100	38.9793	25	0.037	109.07	1.1597	
1 + a_100	42.0245	26	0.0244	109.6	1.163	

Models formula (summer - 250 m buffers)					
1 + d_250 + Δ_elev_250	37.4062	25	0.0528	107.5	1.0876	
1 + d_250	39.9323	26	0.0396	107.51	1.1524	
1 + a_250 + b_250	38.133	25	0.0449	108.23	1.1166	
1 + c_250	40.7409	26	0.0329	108.31	1.1354	
1	43.1895	27	0.025	108.44	1.1944	*
1 + c_250 + d_250	38.3468	25	0.0428	108.44	1.1127	
1 + Δ_elev_250	41.2856	26	0.029	108.86	1.1516	
1 + a_250 + b_250 + Δ_elev_250	36.5326	24	0.0487	109.36	1.0901	
Models formula (summer - 500 m buffers)						
1 + d_500 + Δ_elev_500	33.1025	25	0.1285	103.2	1.0259	
1 + Δ_elev_500	37.56	26	0.0665	105.13	1.1106	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; Dpqpoisson = dispersion parameter; * = model is excluded because of either multicollinearity, inclusion of null model, numerical problems, or bad fit.

Table 54 – Best models for red deer autumn-winter use of meadows, considering cover classes percentage and topographic indexes in the three buffer width as predictors.

Models formula (autumn-winter - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest	
1 + a_100	32.3089	26	0.1831	101.35	0.0754	
1 + a_100 + c_100	31.823	25	0.1632	103.23	0.0838	*
Models formula (autumn-winter - 250 m buffers)						
1 + a_250 + c_250	29.4047	25	0.2474	100.94	0.0596	*
1 + a_250	30.3088	26	0.255	101.16	0.0318	
1 + b_250 + c_250	29.8288	25	0.2308	102.89	0.0376	
Models formula (autumn-winter - 500 m buffers)						
1 + a_500	30.6446	26	0.2418	104.5	0.009	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, numerical problems, inclusion of null model, or bad fit.

Table 55 – Best models for red deer pooled annual use of meadows, considering cover classes percentage and topographic indexes in the three buffer width as predictors.

Models formula (annual - 100 m buffers)	Res.d	Df	GOF test	AICc	odTest	
1 + a_100	30.5355	26	0.246	162.6	< 0.0001	
1 + a_100 + b_100	30.6851	25	0.1997	164.26	< 0.0001	
Models formula (annual - 250 m buffers)						
1 + c_250	30.3271	26	0.2543	162.95	< 0.0001	
1 + c_250 + d_250	30.3465	25	0.2116	163.8	< 0.0001	
1 + a_250	30.329	26	0.2542	163.98	< 0.0001	
1 + a_250 + b_250	30.5874	25	0.203	164.35	< 0.0001	*

1 + a_250 + c_250	30.4027	25	0.2096	164.38	< 0.0001	*
Models formula (annual - 500 m buffers)						
1 + a_500	29.7147	26	0.2796	159.39	< 0.0001	
1 + a_500 + Δ_elev_500	29.9357	25	0.2267	160.04	< 0.0001	
1 + a_500 + b_500	29.5978	25	0.2397	160.44	< 0.0001	*
1 + a_500 + c_500	29.4658	25	0.2449	160.65	< 0.0001	*
1 + a_500 + d_500	29.742	25	0.2341	161.26	< 0.0001	
1 + a_500 + b_500 + Δ_elev_500	29.6896	24	0.1953	161.38	< 0.0001	*

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; odTest = over-dispersion test; * = model is excluded because of either multicollinearity, inclusion of null model, numerical problems, or bad fit.

4. Roe deer use of meadows (chapter 9): raw count data and explorative plots

Table 56 - Resuming table of roe deer count data for the three field seasons.

sampled meadow	spring	summer	autumn-winter
1	0	0	0
2	0	0	0
3	0	2	0
4	1	2	1
5	0	0	0
7	0	0	2
8	3	0	2
9	0	0	0
11	0	0	1
12	0	1	2
14	1	1	0
16	0	0	0
17	0	0	0
18	1	0	0
19	0	0	0
21	0	0	0
22	0	3	0
23	0	0	0
24	0	0	1
25	0	0	0
29	0	1	0
30	0	0	0
31	0	0	0
32	0	0	0
33	0	0	0
34	1	0	0
35	0	0	2
39	1	1	3

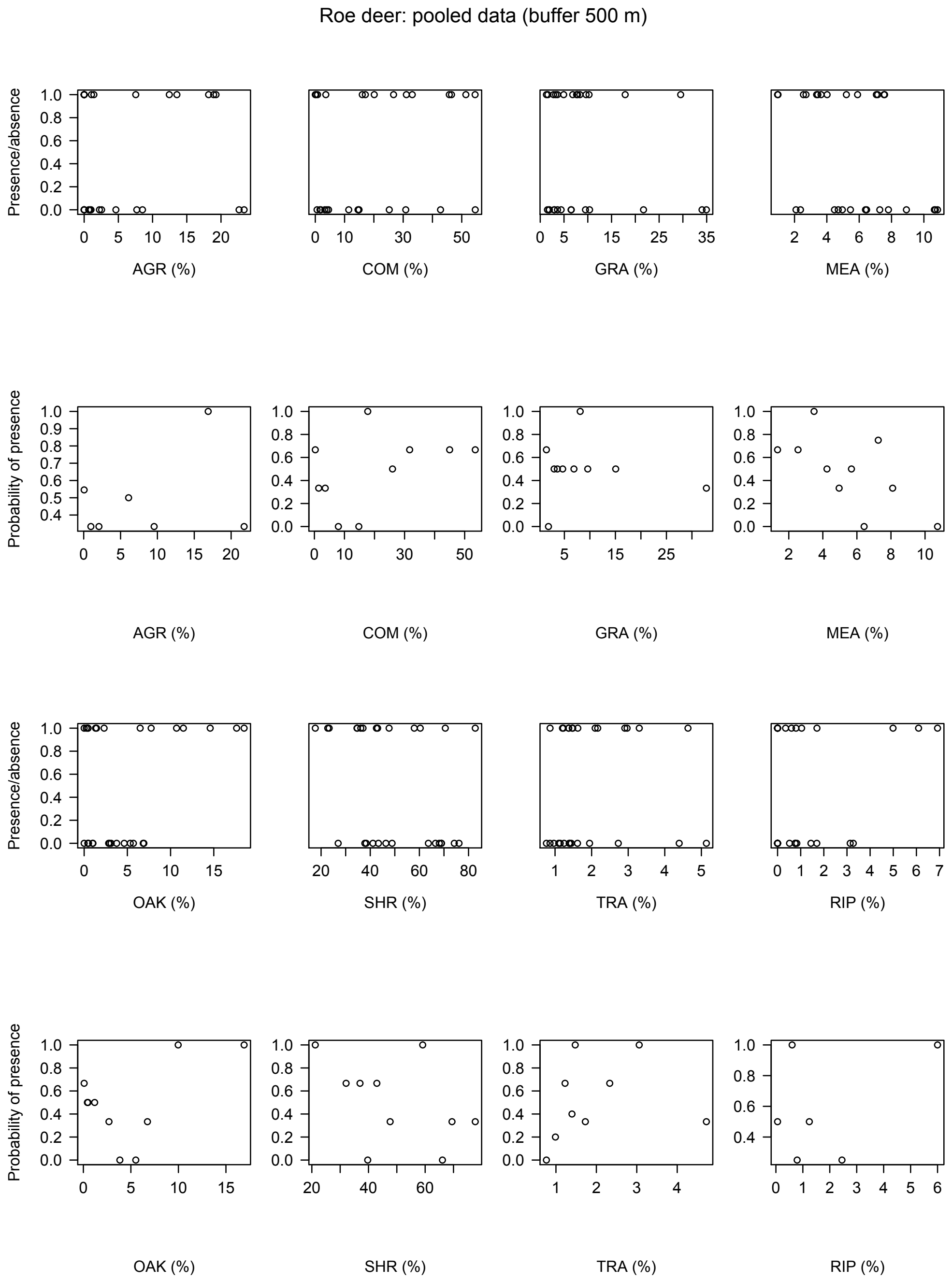


Figure 58 - Explorative plots for pooled annual roe deer presence/absence against cover types (%), corresponding to the 500 m buffers.

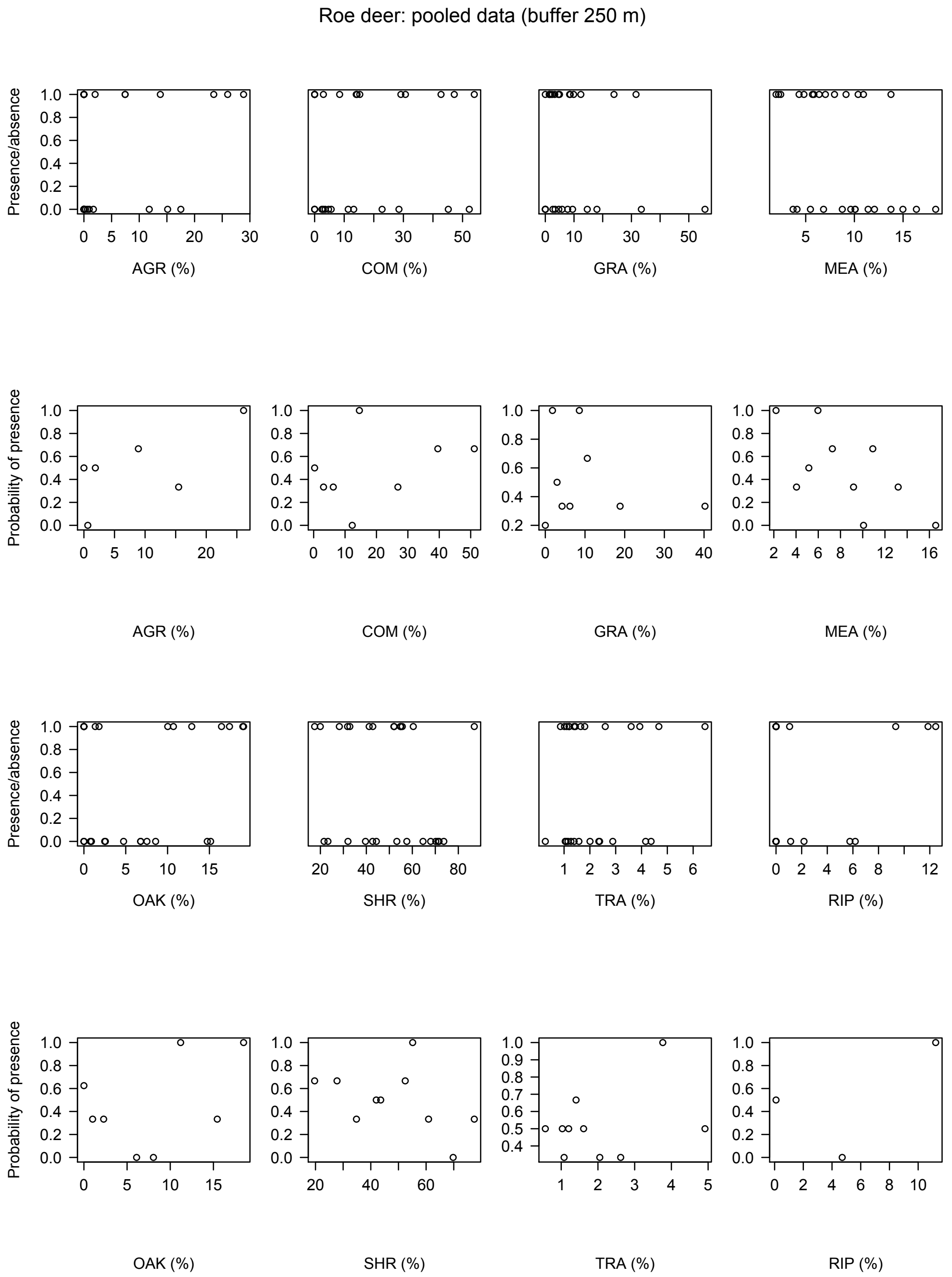


Figure 59 - Explorative plots for pooled annual roe deer presence/absence against cover types (%), corresponding to the 250 m buffers.

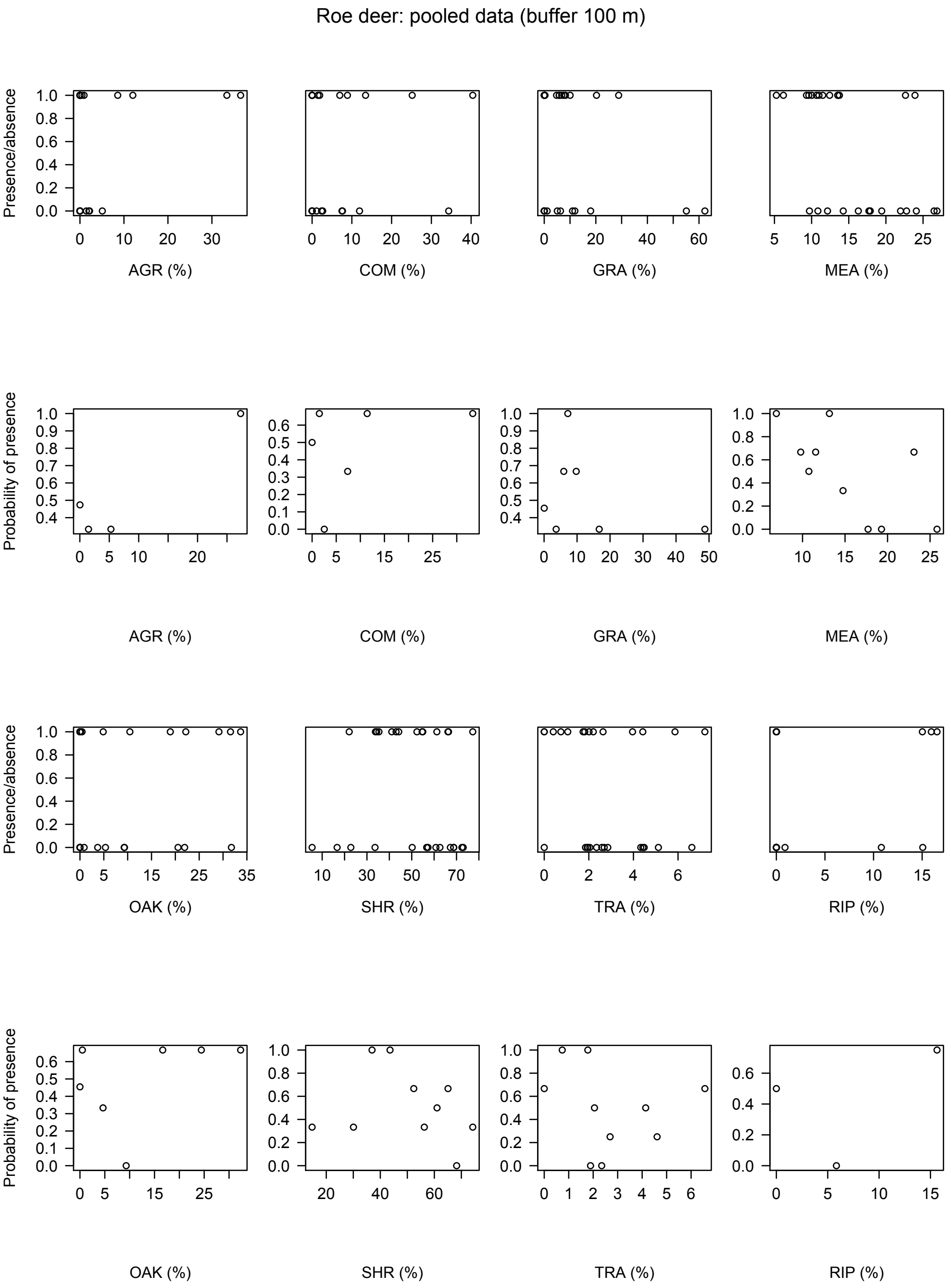


Figure 60 - Explorative plots for pooled annual roe deer presence/absence against cover types (%), corresponding to the 100 m buffers.

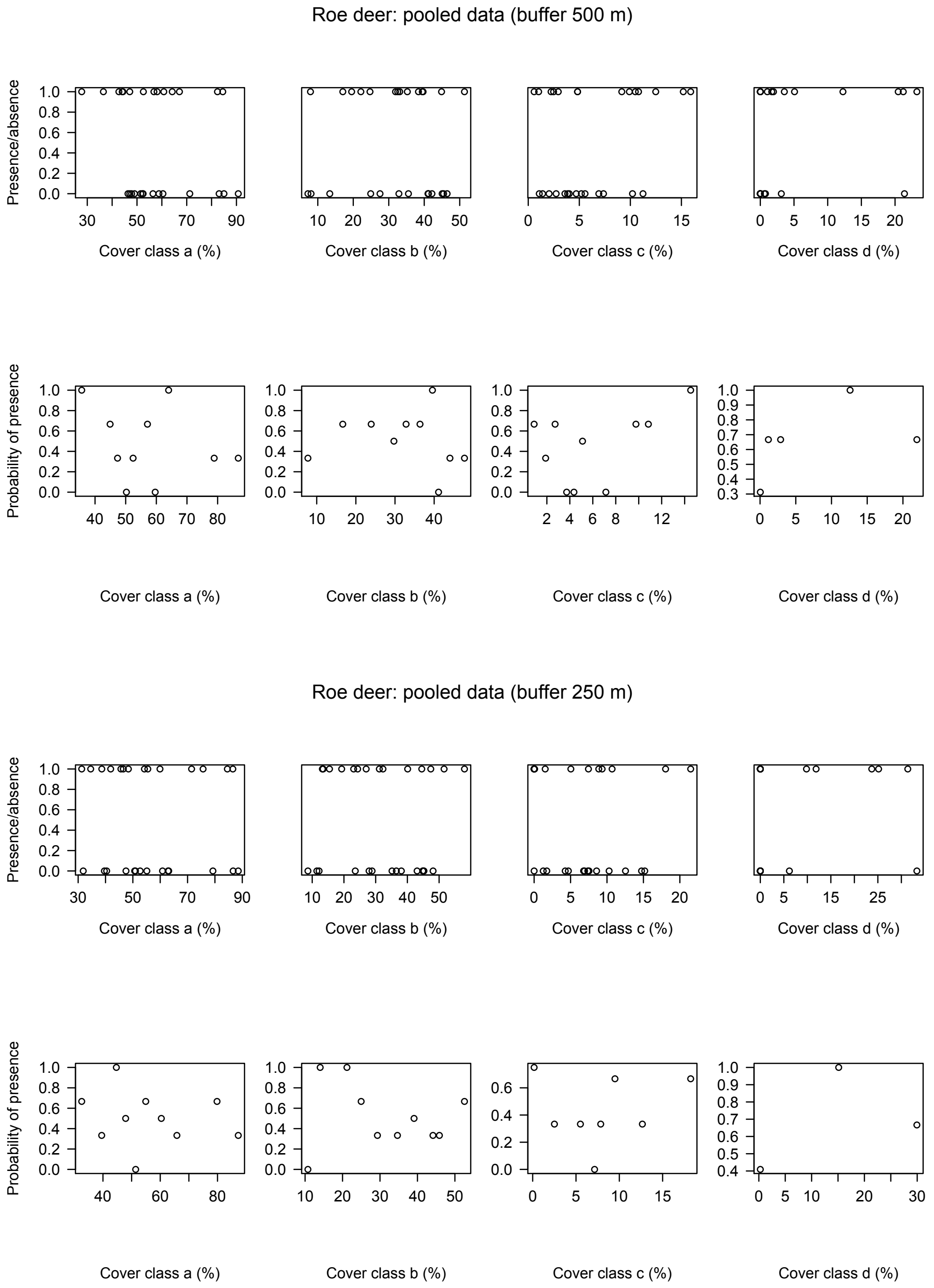


Figure 61 - Explorative plots for pooled annual roe deer presence/absence against cover classes (%), corresponding to the 500 and 250 m buffers.

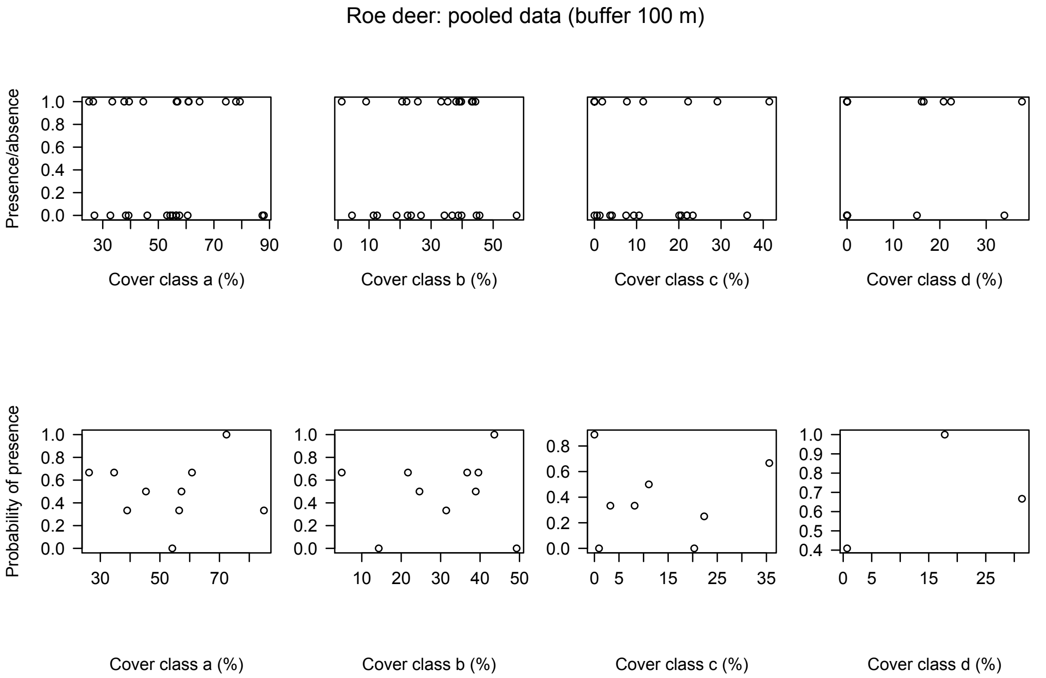


Figure 62 - Explorative plots for pooled annual roe deer presence/absence against cover classes (%), corresponding to the 100 m buffers.

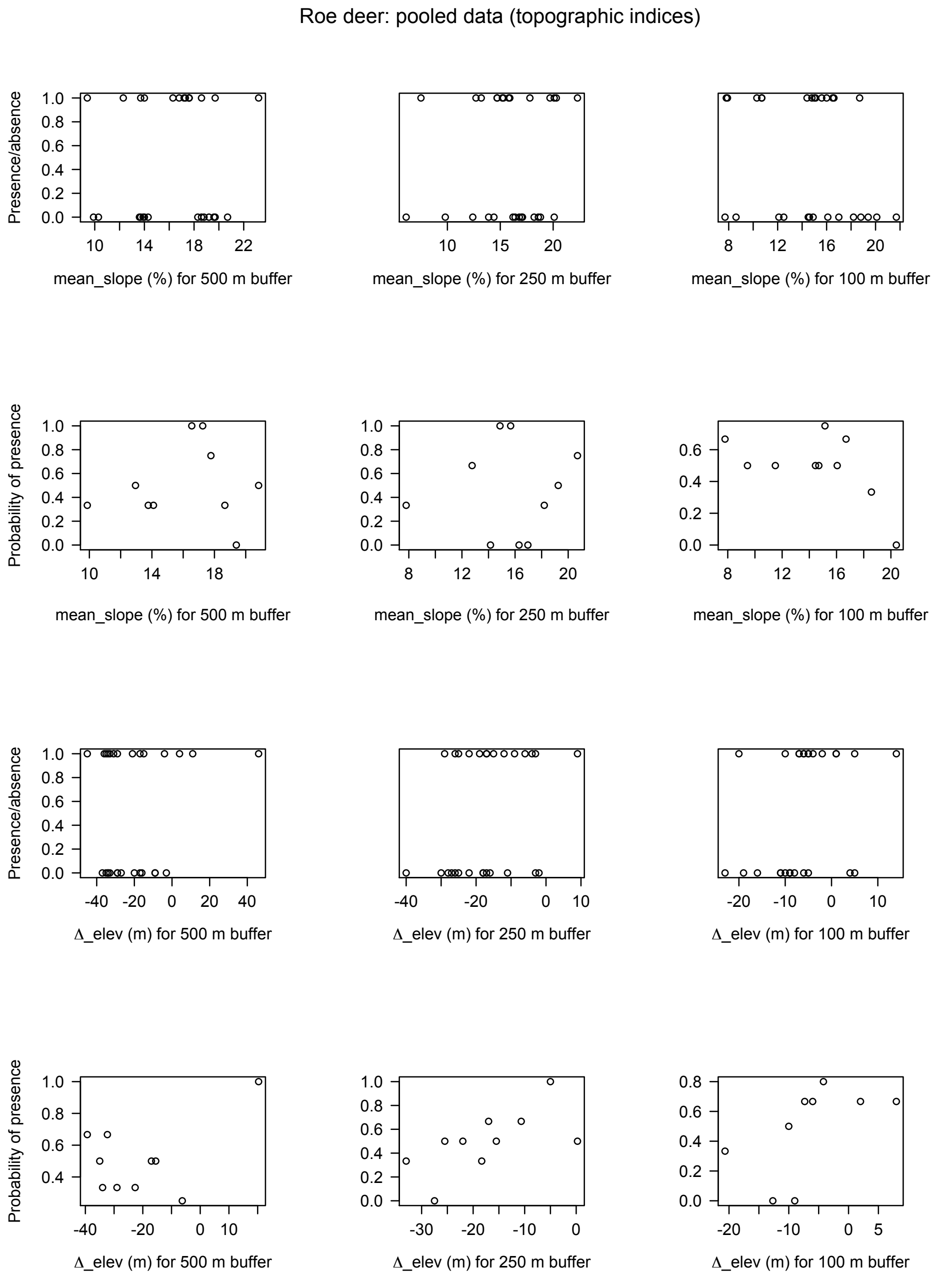


Figure 63 - Explorative plots for pooled annual roe deer presence/absence against topographic indexes corresponding to the three buffers.

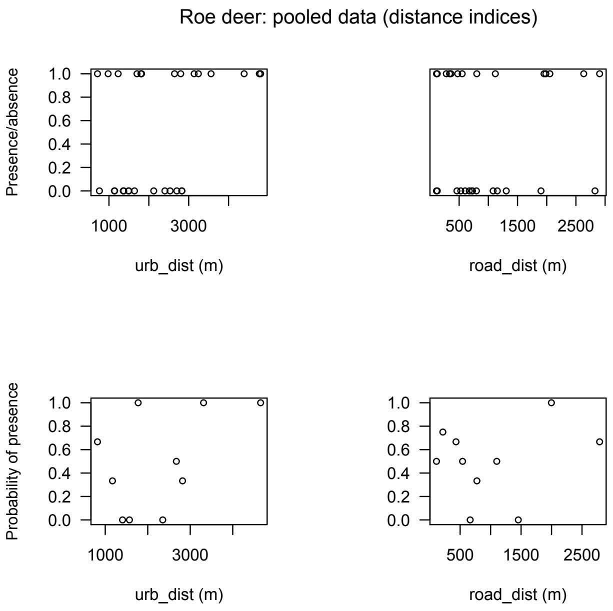


Figure 64 - Explorative plots for pooled annual roe deer presence/absence against distance indexes.

Table 57 - Roe deer presence-absence annual data, in relation to the management status of the sampled meadows.

Management status	Roe deer pooled data	
	presence	absence
used	1	6
rec_ab	3	3
ab	10	5

Table 58 – Roe deer presence-absence annual data, in relation to the dominant phytosociological unit of the sampled meadows.

Dominant Phytosociology	Roe deer pooled data	
	presence	absence
ARRH	1	3
AVESU	4	1
BRACHY	6	0
JUN	0	1
CYN	3	9

5. Summary of the best models for roe deer use of meadows (chapter 9)

Table 59 – Best models for roe deer pooled annual use of meadows, considering cover types percentage and topographic indexes in the three buffer widths as predictors.

Models formula (100 m buffers)	Res.d	Df	GOF test	AICc	
1 + AGR_100 + MEA_100	27.0038	25	0.3557	34	
1 + AGR_100 + MEA_100 + Δ_elev_100	24.5845	24	0.4286	34.32	
1 + AGR_100 + MEA_100 + mean_slope_100	25.0212	24	0.4046	34.76	
1 + MEA_100	30.9370	26	0.2306	35.42	
Models formula (250 m buffers)					
1 + AGR_250 + MEA_250 + Δ_elev_250	25.9436	24	0.3560	35.68	
1 + AGR_250 + MEA_250	28.7842	25	0.2730	35.78	
1 + MEA_250 + Δ_elev_250	30.3696	25	0.2107	37.37	
1 + MEA_250	32.9865	26	0.1629	37.47	
1 + AGR_250 + OAK_250 + MEA_250	27.8243	24	0.2675	37.56	
Models formula (500 m buffers)					
1 + MEA_500	33.984	26	0.1355	38.46	
1 + AGR_500 + OAK_500 + Δ_elev_500	29.0768	24	0.2172	38.81	*
1 + SHR_500 + OAK_500	32.5984	25	0.1414	39.6	
1 + MEA_500 + OAK_500	32.6215	25	0.1408	39.62	
1 + AGR_500 + OAK_500	32.6229	25	0.14077	39.62	*
1 + OAK_500 + Δ_elev_500	32.6638	25	0.1397	39.66	
1 + OAK_500	35.5075	26	0.1011	39.99	
1 + MEA_500 + Δ_elev_500	33.0408	25	0.13	40.04	
1 + SHR_500 + OAK_500 + Δ_elev_500	30.3481	24	0.1735	40.09	
1 + MEA_500 + OAK_500 + Δ_elev_500	30.4455	24	0.1704	40.18	
1 + AGR_500 + MEA_500 + OAK_500	30.5469	24	0.1673	40.22	*
1 + SHR_500	35.8728	26	0.094	40.35	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; * = model is excluded because of either multicollinearity, inclusion of null model or bad fit.

Table 60 – Best models for roe deer pooled annual use of meadows, considering cover classes percentage and topographic indexes in the three buffer widths as predictors.

Models formula (100 m buffer)	Res.d	Df	GOF test	AICc	
1 + Δ_elev_100	35.2103	26	0.1072	39.69	
1 + a_100 + Δ_elev_100	33.9034	25	0.11	40.9	
1	38.8162	27	0.0658	40.97	*
1 + d_100 + Δ_elev_100	34.3474	25	0.1007	41.35	
1 + b_100 + Δ_elev_100	34.4877	25	0.0979	41.49	
1 + mean_slope_100	37.0914	26	0.0733	41.57	
Models formula (250 m buffer)					
1 + Δ_elev_250	36.2212	26	0.0877	40.7	
1	38.8162	27	0.0658	40.97	*
1 + d_250	37.3878	26	0.0689	41.87	
1 + d_250 + Δ_elev_250	35.2845	25	0.0832	42.28	

1 + a_250 + Δ_elev_250	35.3363	25	0.0823	42.34	
1 + Δ_elev_250 + mean_slope_250	35.6366	25	0.0773	42.64	
Models formula (500 m buffer)					
1 + d_500	35.9725	26	0.0922	40.45	
1 + c_500 + Δ_elev_500	33.5497	25	0.1179	40.55	
1	38.8162	27	0.0658	40.97	*
1 + c_500	36.6729	26	0.08	41.15	
1 + d_500 + Δ_elev_500	34.9723	25	0.0887	41.97	
1 + a_500	37.7647	26	0.0637	42.24	
1 + a_500 + b_500	35.3281	25	0.0824	42.33	
1 + c_500 + d_500	35.3286	25	0.0824	42.33	
1 + Δ_elev_500	37.8919	26	0.062	42.37	

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria; * = model is excluded because of either multicollinearity, inclusion of null model, or bad fit.

6. Red and roe deer use of forest types: raw data (chapter 10)

Table 61 – Raw data corresponding to deer use of forest types.

		Summer-autumn		Winter-spring	
	Sample	red deer	roe deer	red deer	roe deer
Pine	1a	0	0	0	0
	1b	0	0	1	1
	1c	0	0	0	0
	2a	1	0	0	0
	2b	0	0	0	0
	2c	2	1	0	1
	3a	0	0	0	0
	3b	0	0	2	0
	3c	1	0	1	0
	4a	0	0	0	0
	4b	0	0	0	0
	4c	1	0	0	0
Deciduous oak stands	1a	0	1	1	0
	1b	3	7	0	2
	1c	1	4	1	0
	2a	1	2	1	2
	2b	1	7	2	3
	2c	1	0	1	2
	3a	0	0	0	0
	3b	0	0	0	0
	3c	3	1	1	2
	4a	0	1	0	3
	4b	0	6	0	1
	4c	2	0	1	3
Sclerophyllous oak stands	1a	1	2	1	1
	1b	1	3	1	0
	1c	3	3	3	2
	2a	0	0	1	0
	2b	0	0	0	0
	2c	0	0	1	1
	3a	3	1	2	2
	3b	0	0	3	0
	3c	3	0	1	1
	4a	1	3	2	1
	4b	2	0	3	0
	4c	3	0	2	1

7. Predictive modeling for roe deer use of MFA meadows

Table 62 – Best and alternative models for roe deer use of meadows.

Best and alternative models	**Res.d**	**Df**	**GOF**	**AICc**	
1 + MEA_250 + Δ_elev_250	30.3696	25	0.2107	37.37	
1 + MEA_250	32.9865	26	0.1625	37.47	
1 + OAK_500 + Δ_elev_250	30.7645	25	0.1969	37.76	
1 + OAK_500 + MEA_250 + Δ_elev_250	28.4829	24	0.2402	38.22	
1 + OAK_500 + MEA_500 + Δ_elev_250	28.5567	24	0.2373	38.3	
1 + MEA_500 + Δ_elev_250	31.3954	25	0.1763	38.4	
1 + MEA_250 + urb_dist	31.4625	25	0.1742	38.46	
1 + MEA_500	33.984	26	0.1354	38.46	
1 + OAK_500 + Δ_elev_250 + urb_dist	28.7639	24	0.2291	38.5	
1 + MEA_250 + Δ_elev_250 + urb_dist	28.8617	24	0.2254	38.6	
1 + Δ_elev_250 + urb_dist	31.6036	25	0.1698	38.6	
1 + MEA_250 + SHR_500	32.0135	25	0.1576	39.01	
1 + urb_dist	34.6682	26	0.119	39.15	
1 + OAK_500 + MEA_250	32.2201	25	0.1517	39.22	
1 + OAK_500 + SHR_500 + Δ_elev_250	29.5911	24	0.1987	39.33	
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Pr(Chi)**
1 + MEA_250 + Δ_elev_250					
(Intercept)	3.3198	1.4616	2.2713	0.0231*	
MEA_250	-0.2407	0.1109	-2.1709	0.0299*	0.0156*
Δ_elev_250	0.0728	0.0495	1.47	0.1416	0.1057
1 + MEA_250					
(Intercept)	2.0349	1.0284	1.9787	0.0479*	
MEA_250	-0.2423	0.114	-2.1254	0.0336*	0.0158*
1 + OAK_500 + Δ_elev_250					
(Intercept)	0.5665	0.8608	0.6581	0.5105	
OAK_500	0.2289	0.1213	1.8868	0.0592	0.0195*
Δ_elev_250	0.0964	0.0505	1.907	0.0565	0.0294*
1 + OAK_500 + MEA_250 + Δ_elev_250					
(Intercept)	2.3105	1.5561	1.4848	0.1376	
OAK_500	0.1595	0.1281	1.2456	0.2129	0.1696
MEA_250	-0.1723	0.1197	-1.4395	0.15	0.1309
Δ_elev_250	0.0934	0.0551	1.6954	0.09	0.0532
1 + OAK_500 + MEA_500 + Δ_elev_250					
(Intercept)	2.1809	1.5027	1.4514	0.1467	
OAK_500	0.1893	0.1268	1.4933	0.1354	0.092
MEA_500	-0.252	0.1778	-1.4174	0.1564	0.1373
Δ_elev_250	0.0956	0.0546	1.7516	0.0798	0.0438*
1 + MEA_500 + Δ_elev_250					
(Intercept)	3.1112	1.4551	2.1381	0.0325*	
MEA_500	-0.339	0.1702	-1.9924	0.0463*	0.028*
Δ_elev_250	0.0691	0.0469	1.4715	0.1412	0.1076
1 + MEA_250 + urb_dist					
(Intercept)	0.5586	1.5802	0.3535	0.7237	
MEA_250	-0.2018	0.1216	-1.6602	0.0969	0.0734
urb_dist	0.0005	0.0005	1.1726	0.241	0.217
1 + MEA_500					
(Intercept)	1.8433	1.0082	1.8283	0.0675	
MEA_500	-0.335	0.1691	-1.9814	0.0475*	0.0279*
1 + OAK_500 + Δ_elev_250 + urb_dist					
(Intercept)	-0.7965	1.314	-0.6062	0.5444	

OAK_500	0.2092	0.1399	1.495	0.1349	0.092
Δ_elev_250	0.0962	0.0504	1.9101	0.0561	0.0315*
urb_dist	0.0007	0.0005	1.3182	0.1874	0.1572
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Pr(Chi)**
1 + MEA_250 + Δ_elev_250 + urb_dist					
(Intercept)	1.5431	1.9211	0.8033	0.4218	
MEA_250	-0.186	0.1193	-1.5584	0.1191	0.0977
Δ_elev_250	0.0686	0.046	1.4898	0.1363	0.1068
urb_dist	0.0006	0.0005	1.1616	0.2454	0.2195
1 + Δ_elev_250 + urb_dist					
(Intercept)	-0.7015	1.1569	-0.6063	0.5443	
Δ_elev_250	0.0689	0.0416	1.6582	0.0973	0.08
urb_dist	0.0008	0.0004	1.9004	0.0574	0.0316*
1 + MEA_250 + SHR_500					
(Intercept)	3.0272	1.525	1.9851	0.0471*	
MEA_250	-0.2096	0.1172	-1.7885	0.0737	0.0495*
SHR_500	-0.025	0.0257	-0.9714	0.3314	0.3239
1 + urb_dist					
(Intercept)	-1.6873	0.9816	-1.719	0.0856	
urb_dist	0.0008	0.0004	1.8344	0.0666	0.0417*
1 + OAK_500 + MEA_250					
(Intercept)	1.3262	1.2868	1.0306	0.3027	
OAK_500	0.084	0.0995	0.8441	0.3986	0.3813
MEA_250	-0.2051	0.1218	-1.6831	0.0924	0.0698
1 + OAK_500 + SHR_500 + Δ_elev_250					
(Intercept)	1.7108	1.3944	1.2269	0.2198	
OAK_500	0.2253	0.1257	1.792	0.0731	0.0278
SHR_500	-0.0278	0.0264	-1.0546	0.2916	0.2787
Δ_elev_250	0.0787	0.0505	1.5589	0.119	0.0829

Res.d = residual deviance; Df = degrees of freedom; GOF test = goodness of fit test; AICc = modified Akaike information criteria
SE = standard error Pr(>|z|) = Wald test P-value; Pr(Chi) = likelihood-ratio test P-value
Significance code: '***' < 0.001; '**' < 0.01; '*' < 0.05