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Analysis of the relationships between wild ungulates and forest in the Northern Apennines, Italy

PH.D. CANDIDATE: ***Dr. Andrea Marcon*** DIRECTOR OF THE SCHOOL: ***Prof. Marco Curini-Galletti***

SUPERVISOR: ***Prof. Marco Apollonio***

SUMMARY

ABSTRACT

I explored some ecological aspects of the interaction between wild ungulates and forest environment. I reviewed the existent literature on the topic, and I found the relationship to be part of a extended ecological network, that includes several biotic and abiotic factors. The most advocated cause for elevated ungulate impact on forest is ungulate overabundance. Hence, I assessed the precision and applicability of three different census methods (drive census, pellet-group count, camera trapping method – REM) for roe deer in a mountainous forest. I found the R.E.M. method to be the best compromise, with intermediate precision and low demands. Moreover, I analyzed the browsing pressure of roe deer in several areas over a density gradient. I found the impact to be directly related to densities, and that the early-stage effects of browsing pressure will result in long-term differences in volume, between browsed and unbrowsed trees, even several years later the clear-cutting. Finally, to understand the effects of roe deer impact on the forest development, I used a forest development model (LANDIS-II) to simulate 200 years of forest development, considering harvesting and roe deer impact. I found that both disturbances influence species richness, abundance, and forest structure. Roe deer impact does not significantly affect harvesting yield, and the disturbances combined do not seem to represent an hazard for forest functionality.

RIASSUNTO

Ho esplorato alcuni aspetti delle interazioni tra ungulati selvatici e l'ambiente forestale. Analizzando la letteratura esistente sull'argomento, la relazione è risultata essere parte di una più ampia rete ecologica, che include diversi fattori sia biotici che abiotici. Generalmente, un elevato impatto da parte degli ungulati è attribuito alle densità troppo elevate. Ho quindi comparato precisione ed applicabilità di tre differenti metodi di censimento per il capriolo (censimenti in battuta, conteggio dei gruppi fecali, e foto-trappolaggio - R.E.M.) in una foresta dell'Appennino. Il R.E.M. è risultato essere il miglior compromesso, con una precisione intermedia e facilità di applicazione. Ho inoltre analizzato l'impatto del capriolo sui cedui in diverse aree, lungo un gradiente di densità. L'impatto è risultato direttamente proporzionale alle densità, e gli effetti dovuti alla brucatura in giovane età sono risultati evidenti anche svariati anni dopo il taglio di ceduazione. Per valutare gli effetti eco sistemici dell'impatto del capriolo e della gestione forestale, ho utilizzato un modello ecologico (LANDIS-II), per simulare lo sviluppo della foresta. Entrambi i disturbi risultano influenzare la ricchezza ed abbondanza in specie, e la struttura della foresta. L'impatto del capriolo non influenza significativamente la resa delle pratiche forestali, e i due disturbi non sembrano rappresentare un pericolo per la funzionalità della foresta.

THESIS INTRODUCTION

In the last decades, the relationships between wild ungulates and forest received growing attention, followed by a change in the way studies are performed and the problem is addressed. Started as a single-factor issue, i.e. at a higher density would correspond a higher impact, the study of wild ungulate-environment relationships evolved into a more complex and holistic investigation, which helped researchers and managers to recognize and identify the role of wild ungulates in the ecological network. The strong increase in wild ungulates abundance and distribution during the last decades in Europe (Apollonio 2010) was followed by an expansion of the conflict between wild ungulates and forest managers. At first, it seemed that the issue was related to the abundance of herbivores, so there has been a call to increase ungulate harvest, but as investigations advanced, it became clear that it was not a problem that could be solved with a single-factor approach. Several biotic and abiotic factor can influence the presence, abundance, and effect of wild ungulates on the forest, from the composition and structure of the landscape mosaic, to the aspect and light condition on a few square meter wide gap in the forest (Gerhardt *et al.* 2013). The role of forest management in this relationship became rapidly clear, as through management practices humans exert a strong control over some –or many- of those factors. Ungulates can influence forest in several ways, such as changes in species composition and forest structure (Joys, Fuller & Dolman 2004), limiting or preventing regeneration (Ammer 1996), decreased revenue for high plant mortality or decreased timber quality (Welch *et al.* 1992, Gill, Webber & Peace 2000, Ward *et al.* 2004), and up to ecological changes that can affect other wildlife species or groups as birds (Fuller 2001) and invertebrates (Feber *et al.* 2001, Stewart 2001). On the other hand, ungulates can have a positive effect on the ecosystem (Reimoser & Gossow 1996). They can increase biodiversity by regulating plant competition (Kramer, Bruinderink & Prins 2006), can increase seedling presence, maybe because of seed spreading through coat, feces or trampling (Pellerin *et al.* 2010), and even have a positive effect on soil, fertilizing it with droppings and helping gas circulation by trampling or scrape-marking (Persson, Danell & Bergström 2000).

Of course, the ungulates influence on their environment depends on how much the ecological network is altered. In a natural or close-to-nature- situation (e.g. Bialowieza Primeval Forest in Europe or Yellowstone National Park in North America), ungulates are part of the ecosystem and act both as regulator and regulated factor (see Kuijper 2011). On the other hand, when a component of the ecological network is altered or absent, the dynamics that drive the ecosystem change, and this can result in unexpected outcomes, such as major increase or decrease of one or some of its components. That is exactly the case for ungulates in Europe, where human induced modification of the environment unwillingly created a very favorable habitat for herbivores (Kuijper 2011, Gerhardt *et al.* 2013). The absence of predators, the abandonment of rural areas, and forestry practices planned without considering herbivores, created a situation where ungulate populations thrived, and their impact consequently increased. The relationships between all this factor are yet not clear, so I decided to review the existent literature to produce a review (Chapter 1) that would help to look at the interactions between forest and wild ungulates from a new, holistic, perspective. When this network of interactions is not considered, the most often referred to cause for ungulate damage is overabundance, and several authors found positive correlation between ungulate densities and impact (see Gerhardt *et al.* 2013). When looking at the problem from another perspective, ungulate density is only one of the many factors that have a role in the phenomenon of herbivore impact, as several studies show. For example, Bergquist and Örlander (1998) found that, while comparing two different sites in Southern Sweden, the one with the lowest density suffered the highest damage. Other authors (Reimoser 1986, Gill 1992b) stated that, for a given deer density, browsing impact shows substantial variation. This led to the formulation of the idea of a density-threshold, theorized for deer (Vospernik & Reimoser 2008), above which all the action took to mitigate deer impact will be overruled. Despite some attempts to identify the value of this threshold, it remains unknown (see Putman 1996), as the value is strongly site-dependent. A major issue when looking for a density threshold does not lie in the complexity of the forest-ungulate interaction, but is the uncertainty connected with animal abundance estimations. The ideal situation in a case study would be to know exactly the number of animals that live in the study area, and the structure of the population. But as it is often unfeasible to count all the individuals in a populations, especially for wild populations, sampling techniques are used to estimate animal density in a given area (Putman *et al.* 2011). Several methodologies of density estimation have been developed in order to improve our approximations of actual animals numbers, for different species and different habitats. Those methods can be divided into two groups: direct and indirect methods. Direct methods required the operator(s) to see the animals, while indirect methods rely on signs that animals leave in the environment during their activities. While direct methods allow for the collection of additional information on species biology, like behavioral traits, indirect methods are usually less demanding, can be performed independently of animals activity patterns and are not subject to the risk of altering animals behavior as a consequence of operator(s) being detected. Independently from the method of choice, its application on different environments may result in very different performances. As an example, (Andersen 1953) found that observations from vantage points for roe deer (*Capreolus capreolus* L.) in broadleaved woodland in Denmark estimated a density that was one-third of the actual one, and Bongi *et al.* (2009), for the same species and a similar environment in Italy, found that about the 70% of a tagged sample of animals known to be in the drives were actually observed. On these premises, I decided to test three methods, one direct and two indirect, to try and understand which would be the most suited for roe deer in a mountainous environment of the Northern Apennines (Chapter 2). To do so, I assessed and compare the methods' precision, and discuss their applicability in a broadleaved mountainous forest habitat. Not knowing the actual number of individuals in the area, it was impossible for us to test methods' accuracy. I applied the drive census, and use its estimate as a reference value, because it's the method used by Fish and Wildlife Service of Arezzo Province to assess roe deer density in the area, and compile management plans. Then I applied a modified version of the pellet-group count technique, as it should return highly precise results (Fattorini *et al.* 2011), and a fairly new method that uses camera traps, the R.E.M. (Rowcliffe 2008), to test its applicability on our environment. Density data are not enough, though, to infer the impact of those populations on their habitat, and to develop a proper management plan, information on the actual impact of roe deer is needed.

The most direct effect of ungulates on the forest is a change in vegetation regeneration rates, and when this affects economic important tree species, the impact turns into damage (Reimoser, Armstrong & Suchant 1999, Ward *et al.* 2004). In Chapter 3, I analyzed the relationship between animal abundance and browsing impact, in a mountainous region of the Northern Apennines. As mentioned before, this relation is not always linear, and it can vary in direction and magnitude on the basis of the habitat or local situation that is considered (Reimoser 1986, Gill 1992a). To assess that relationship I sampled several areas along a gradient of roe deer densities, and monitored its browsing impact on Turkey oak (*Quercus cerris* L.) coppice on both early and long-term effects. Coppice, as a silvicultural system, is widespread in Italy, especially amongst private owner, and it amounts to about 56% of the total forested area in the country (National Forest Inventory). The Turkey oak represents an economically important species with regard to coppice management, and also a potentially key food for roe deer in the area (Cutini *et al.* 2011). While the effects of deer browsing on coniferous species have been long recognized (Gill 1992a, Motta 1996), those effects on coppice are only recently being addressed in Italy (Cutini *et al.* 2011). Forest stands that are managed as coppice create attractive habitats for roe deer, as they provide both abundant forage and hiding places, due to dense vegetation regrowth. Moreover, coppice practice creates sharp edges between habitats, that are strongly attractive to roe deer (Reimoser & Gossow 1996). Being the relationship between ungulate densities and browsing incidence so complex, I proposed to pair the density estimates with a measure of the browsing impact, and suggested an index as a useful management tool on account of its fast, simple and cost-effective procedures.

Looking at the problem from two points of view could be a start towards the integrated management system, of both wildlife and forestry, that is needed for a proper landscape planning. In fact, one of the major issues in ecological planning lies in the complexity of the relationships between factors, which in turn makes it extremely difficult to predict the outcomes of any strategy, and this makes it very difficult for managers to select the proper actions to fulfill the desired aims. Moreover, to apply a management plan and wait to empirically see its outcomes is not feasible, because of the time span needed by the forest to respond to a modification in the environment. The changes in the forest, caused by the actual management strategies, may be visible in decades, and in the meanwhile other factors may have changed, modifying the situation and making our efforts to understand forest dynamics vain. Moved by those difficulties, in the last decades researchers developed a series of tools to help us understand the outcomes of management actions applied to a complex and ever-changing context: the ecological models. Several types of models have been developed, based on different underlying mechanisms or aimed at answering different questions (Mladenoff & Baker 1999). There are mechanistic models, where the dynamics of the processes are strictly programmed, and stochastic models, where the dynamics are -to some extent- driven by probability functions. Even the extent and the resolution of the analysis influence the type of model to use, from gap models that consider single trees and –for computational limits- small areas, to landscape modeling, where the area is wide and the vegetation is considered as cohorts of species or biomass amount (Mladenoff & Baker 1999). In Chapter 4, I used one of these tools to try and understand the trends and dynamics that will emerge in our study area with the current forest management, and the roe deer impact. The model I decided to use is LANDIS-II (LANDscape DIsturbance and Succession), it is a stochastic, process-based, and spatially explicit model, able to simulate forest development on large temporal and spatial scales (Scheller *et al.* 2007). LANDIS-II model framework simulates the development of forested landscapes taking into account ecological processes, such as succession, seed dispersal, harvesting, and a set of biotic and abiotic disturbances (Scheller *et al.* 2007). It is ideally suited to explore the interaction between forest succession and disturbances – such as forestry and ungulates impact- because it models multiple ecological and anthropogenic processes such that the interactions of these processes are an emergent property of the simulations (Mladenoff 2004). I used LANDIS-II to simulate 4 different scenarios, each with different disturbances: the first scenario has no disturbances, and simulates the development of the forest if the only cause of mortality were senescence; the second scenario considers only forestry, as a simulation of the actual management strategy; the third scenario considers harvesting and roe deer impact, this should simulate the actual situation, and show us the ecological effect of adding ungulate impact over forestry; the last scenario simulates the presence of roe deer impact alone, removing harvesting, to allow for a comparison of the different trends caused by forestry alone and roe deer impact alone.

This thesis deals with some ecological aspects of the interaction between wild ungulates and the forested environment. In the first chapter of the thesis I reviewed the existent literature about the ecological factors that influence the complex relationship between wild ungulates and their habitat. In the second chapter, we dealt with the still unsolved problem of counting animals, comparing three methods and evaluating their precision and their applicability in the Apennine environment. The third chapter explores the relationships between ungulate abundance and impact on coppice managed forest, and propose the use of a browsing index as a complementary tool for census data, to pair ungulate abundances and impacts on different environments. In the fourth chapter I tried and condense that knowledge in a stochastic model, that would return scenarios that enable us to identify interactions and dynamics between wild ungulate and forest. The model I used is a forested landscape simulator (LANDIS-II), which models the development of the forest at large spatial and temporal scale, over which I add the ungulate effect as a disturbance, to see how the latter influences the forest shaping and development in time.

In the appendix I approached the other widely distributed ungulate species of the area, the wild boar (*Sus scrofa*). This species has not been included in the aforementioned studies because its effects on forest ecology is still controversial (Schley & Roper 2003, Gómez & Hódar 2008). While consulting the scientific literature about the species, I realized our lack of knowledge about the interaction of this species with its environment. Though, I decided to analyze some aspect of the species auto-ecology, such as habitat use and anti-predatory behavior, as basis for future studies considering a wider network on interactions.

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Chapter 1

Looking at deer-forest relationship with a wider perspective: a literature review

Manuscript

Looking at deer-forest relationship with a wider perspective: a literature review.

Marcon[1] A., Grignolio[1] S., Apollonio[1] M.

1 Department of Science for Nature and Environmental Resources, University of Sassari, Sassari, Italy

ABSTRACT

The relationship between wild ungulates and forest environment is often approached as a two-factor issue, failing to considering all the actors involved in the ecological network that both surrounds and includes that relationship. Forest development and animal behaviour are both complex phenomena, that affect and are affected by various factors that act at different spatial and temporal scales. Reviewing the current literature, we tried to identify all those factors that may influence the deer-forest relationship and to report the effects they can have on it. Biotic and abiotic factors that act at different spatial and temporal scales have been considered. Several abiotic factors, such as light condition, soil characteristics, terrain roughness, altitude, topography, and climate, have a role in shaping both actors of our relationships. They influence the characteristics of the vegetation that will develop in the area, which will influence the habitat use of deer, but they will also directly affect deer habitat choices at different scales, from which part of a relief to feed on, to home range extent, to seasonal migrations. Biotic factors includes plant species and abundance, forest structure, predators, and humans. The vegetal component of the relationship is not only affected by deer impact, as it's often seen, but can have an important role in shaping both the magnitude and the spatial distribution of the impact. Natural predators have indirect effects on deer impact that are even more important than the direct, lethal, effect of predation, as they influence the spatial and temporal distribution of deer impact through the landscape of fear. Humans affect deer-forest relationship in two ways: forestry and hunting. Through forestry, humans modify the environment altering species abundances and composition, and creating attractive habitats for ungulates, but with low carrying capacity. Hunting affect both deer numbers and space use, but differently from natural predators, lacking the same ecological functionality. The large areas covered in artificial forests for forestry purposes, the lack of natural predators, and the recent increase in ungulate populations in several areas of the world, caused a disequilibrium in the ecosystems that, in the light of recent researches, may be solved by applying close-to-nature silviculture techniques and trying to restore a functional ecological network.

INTRODUCTION

The effects of deer on forest ecology have been the focus of a lot of studies throughout the world (Rooney 2001, Danell *et al.* 2006, Takatsuki 2009, Kuijper 2011, Gerhardt *et al.* 2013). Particular attention has been given to this topic in Europe and North America, where in the last decades deer populations have shown a strong increase both in number and in spatial distribution (Coulson 1999, Apollonio 2010). This range expansion and raise in densities caused, in turn, an increase in their impact on forests. In spite of the huge amount of work done, the relationship between deer and environment is not clear yet, due to its complexity. Human activity, from forestry to hunting, have add another layer of complexity to this relationship, affecting both environment and animals on several aspects. The effects of deer on the forest are well studied and may include changing in species composition and forest structure (Joys, Fuller & Dolman 2004), limiting or preventing regeneration (Ammer 1996), decreased revenue for high plant mortality or decreased timber quality (Welch *et al.* 1992, Gill, Webber & Peace 2000, Ward *et al.* 2004), up to ecological changes that can affect other wildlife species or groups as birds (Fuller 2001) and invertebrates (Feber *et al.* 2001, Stewart 2001). Deer density is often point at as the primary cause of deer damage, but it is now clear that it is neither the only nor the major cause of it (Kuijper 2011, Gerhardt *et al.* 2013). Moreover, deer can have positive effects for the environment too, given that the environment itself is managed in a way that considers ungulates part of the ecosystem rather than outsider disturbance. Looking at ungulates-forest interaction with an holistic view, that includes and considers all the actors involved, would not only provide a better understanding of the phenomenon, but would allow for a more efficient planning of management actions for both wildlife and forest. The aim of this review is to look at ungulate-forest relationship with a wider perspective, trying to place it into its proper position in the ecological network.

DEER AS PREDATORS OF PLANTS

Herbivory is the most advocated direct effect of deer presence for the alteration in species composition and forest structure (Welch *et al.* 1992, Ammer 1996, Partl *et al.* 2002, Miller *et al.* 2010, Chianucci *et al.* 2015). The most apparent reason for this to happen is plant species palatability, based on which deer can choose to feed preferentially on some particular plant species, causing a strong decline in their abundance and/or spatial distribution (Long, Pendergast & Carson 2007, Mason *et al.* 2010). A lot of studies considering exclosures, showed that inside the fenced area (where ungulates where excluded from) both the number of saplings and the number of species were higher than outside the fences (Marquis & Grisez 1978, Opperman & Merenlender 2000, Cutini *et al.* 2011). On the other hand, other studies (Pellerin *et al.* 2010) find out that plant species and diversity were reduced, outside fences, only during the first year of the study, while after 3 years the negative effects of browsing disappeared. Nonetheless, even if effect on species richness was recovered after 3 years, browsing by deer altered species composition in the plant communities, where palatable species were reduced in favor of unpalatable or browsing-resilient species (Pellerin *et al.* 2010). Less linked to palatability of the plant species are the modifications of forest structure. Deer browsing, especially when present at high levels, can reduce – and in extreme cases prevent- plant regeneration and growth (Caudullo *et al.* 2003). This, in turn, change the structure of the forest, reducing the understorey level and interfering with the growth patterns of the stand, to the point of influencing other wildlife groups as birds (Fuller 2001), invertebrates (Feber *et al.* 2001, Stewart 2001), and other mammals (Flowerdew & Ellwood 2001). Sometimes the changes in forest structure are exacerbated by the choice of the economically interesting plant species that are managed, as those species are often exported to locations outside their natural distribution areas, so they face environmental factors they are not evolutionarily prepared for, included diverse browsing patterns (see Kuijper 2011). This is particularly true for conifers species, as they result to be more sensitive than broadleaves species to ungulate browsing, as they are less capable of build up reserves in the roots (Edenius 1993). When ungulate impact is too high for a particular site, it can prevent tree regeneration altogether, turning mixed plant communities into grass-dominated ones (Welch 1986, Trumbull, Zielinski & Aharrah 1989, Schreiner *et al.* 1996).

The effects of ungulate impact turn into damage when they affect economically important species in managed forests (Reimoser, Armstrong & Suchant 1999, Ward *et al.* 2004). Multiple stemming, delayed rotations, growth loss, and a general decrease of timber quality are some of the problems that forest managers have to face when deer are present; if and how this represent a damage depends on the aims of the management plans (Ward *et al.* 2004). These aspect are often interconnected: as Welch *et al.* (1992) stated, in his study multiple stemming was a more serious impact than loss of increment, which on average was estimated as one year. Gill *et al.* (2000) suggested that browsing damage, at high deer densities, can cause a loss up to 5 years of growth, but on the other hand, because of compensatory growth the consequent extent of rotation was only 2 year. The same ungulate impact can then be seen as a more or less pronounced damage depending on the silvicultural techniques applied. When deer are considered part of the ecosystem, and when forest management plans are devised holistically – taking into account all the characteristics of the ecosystem, from soil proprieties to wildlife behavior- they can have a positive effect on the ecosystem (Reimoser & Gossow 1996). When a close-to-nature silviculture is applied, deer can increase biodiversity by regulating plant competition (Kramer, Bruinderink & Prins 2006), can increase seedling presence, maybe because of seed spreading through coat, feces or trampling (Pellerin *et al.* 2010), and even have a positive effect on soil, fertilizing it with droppings and helping gas circulation by trampling or scrape-marking (Persson, Danell & Bergström 2000). The most often referred to cause of deer damage is deer overabundance (Peterken & Tubbs 1965, Caudullo *et al.* 2003, Senn & Suter 2003), and several authors found deer density to be positively correlated to deer impact (e.g. Chianucci *et al.* 2015). Nonetheless, deer density is not the only factor regulating deer impact, as different habitats suffer differently for the same deer density. Several studies stated that, for a given deer density, browsing impact shows substantial variation (Reimoser

1986, Gill 1992). For example, Bergquist and Örlander (1998) found that, while comparing two different sites in Southern Sweden, the one with the lowest density suffered the highest damage. As mentioned before, a variety of factors can influence the outcomes of deer presence, and density is just one of those. Still, when deer densities are too high, they can overcome the other environmental factors. Gerhardt *et al.* (2013) "[…] found evidence that most factors are modifiable by silvicultural means but can e overruled where deer density […] (is) locally in excess.". Other authors drawn the same conclusion (Peterken & Tubbs 1965, Caudullo *et al.* 2003, Senn & Suter 2003), but the definition of "locally in excess" remains vague. Some authors (Putman 1996, Vospernik & Reimoser 2008) theorized the existence of a density-threshold, above which all the action took to mitigate deer impact will be overruled, but the value of this threshold, despite some attempts (see Putman 1996) remains unknown, even because –as we'll see in the present review- this value is strongly site dependent.

SITE CHARACTERISTICS

Natural characteristics

The characteristics of the site have a strong influence on the predisposition of the forest to browsing. Some of this proprieties are not modifiable by human actions, such as morphology and climate, but they have a role in determining the forest productivity and development, and they can influence animal behavior on different temporal scales. Light conditions in which saplings grow up is one of the factor that influence both forest development and animal behavior. When a sapling grows in dim light condition, it will be a better quality forage for deer, as the C/N ratio will be low, and it will grow mostly in height as it will be trying to reach for more light. On the other hand, when a sapling grows in full light condition, it will be a low quality forage, because the C/N ratio will be higher (Bryant 2003), due to elevated photosynthetic activity, resulting in lower digestible forage for deer (Molvar, Bowyer & Van Ballenberghe 1993, Hartley *et al.* 1997). The latter sapling will grow less in height and have more twigs, resulting in a more bushy plant. This difference can be found between tree saplings growing in small openings in a close forest and those growing in a wider gap, like a clear-cut. The different way in which those saplings will grow can change the browsing pressure they will receive, as an intense growth in height can quickly take the sapling out of the browsing zone (e.g. Cutini *et al.* 2011). In temperate forests, deer prefer to feed on saplings growing in full light, despite the fact that they represent a lower quality forage (Kuijper *et al.* 2009). The reasons for this choice are not known yet, but it seems that on temperate climates deer choose quantity over quality (see Kuijper 2011). Moreover, some authors suggested that the bushy shape of the saplings growing in full light may have a role in deer preferences (Edenius 1993). Habitat productivity is most probably affecting the deer choice of forage quantity or quality, as several works show that in a low productive environment, as the boreal forest, the plant chemical quality has a role in determining the foraging behavior of ungulates and smaller herbivores (Crawley 1983, Ball, Danell & Sunesson 2000, Bryant 2003). In high productive environment, as temperate forests, we found deer feeding preferentially on low quality forage in forest gaps (Welch *et al.* 1990, Reimoser & Gossow 1996, Campbell *et al.* 2006, Kuijper *et al.* 2009), showing the opposite behavior and selecting forage quantity over quality. Moreover, for a given browsing pressure, a high productive environment will of course suffer less the biomass loss.

Another aspect that can influence browsing pressure on a very fine scale is terrain morphology. Convex relief, as ridges, allow the animal to have a better view, hence a better control, over the proximity, enhancing vigilance performance. Usually, convex reliefs are more exposed to wind, which during winter time can reduce the amount of snow on the ground, leading to easier access to forage and earlier snow melt. Even if terrain morphology is not usually considered, some authors found that rough reliefs are preferred by deer, and trees in those areas are more prone to browsing (Reimoser *et al.* 2009, Nopp-Mayr, Reimoser & Voelk 2011). On the other hand, concave reliefs accumulates more snow, and are usually avoided and visited only when climatic protection is more important than foraging. An exception are valley bottom at low altitudes, when the amount of forage is higher and climatic conditions are less severe, and, in fact, those are generally the places chose for wintering. Climatic conditions can affect animal behavior, and thou forest predisposition to deer impact on many levels. Deer are shown to prefer relatively warmer and drier climate, and this influence their choices from stand level to wintering areas, i.e. landscape, level. Snow cover is a good example of how climate can influence animals' choices, as high level of snow on the ground hinder movement, cover forage, and cause thermal stress. Deer will then prefer stands with dense canopy cover, which intercept snow and allows for less severe condition at ground level. Ground snow cover can have two opposite effects on browsing pressure, as it can hide trees from deer, resulting in a protection layer even for taller trees (Stankovski *et al.* 1998), but, on the other hand, single trees that emerge from the snow cover are visually striking, and are more likely to be browsed (Pépin *et al.* 2006). Intuitively, altitude is strongly related to climatic conditions, as usually at higher altitudes the climate is colder and snow cover is deeper than at lower altitudes. The same stands for aspects, as stands looking at south-west will experience a different micro-climate condition than those looking at north-east, which affects animal choices about where to linger, and in turn their impact on the different located stands (see Gerhardt *et al.* 2013). In natural conditions, lower altitudes' forests are the destinations of winter migrations, and are therefore more prone to deer impact during that season (Nopp-Mayr *et al.* 2011). When this is prevented, e.g. human disturbance as settlements, artificial barriers, etc., deer are forced into sub-optimal habitats, i.e. higher altitudes, and stands at those areas will be subjected to a strong browsing and strip-barking pressure (Motta 1996).

Human-induced characteristics

The way in which humans modified the landscape has an effect in forests predisposition to browsing too. Preventing migrations or destroying deer natural habitat are the most apparent factors that influence deer behavior, and consequently its influence on forest development, but less evident modifications of the environment can have strong impact on forest predisposition to browsing. For example, dimension and spatial distribution of clear-cuts inside a forest can modify not only the predisposition to browsing of the clear-cut, but even of the surrounding stands. If clear-cuts are wide and isolated, their forage offer will attract a high number of deer that will exert a high browsing pressure on clear-cut regeneration (Reimoser & Gossow 1996, Kuijper *et al.* 2009). If deer number is too high, or if deer are often disturbed, they will retreat in the forest stands in the proximity of the clear-cut, that in turn will suffer a high browsing pressure, often disproportioned in respect to their forage offer. The opposite situation, where a small patch of forest is surrounded by open areas, as in mixed agricultural landscapes, can cause an excessive browsing pressure on the forest patch. Agricultural lands are a good source of forage, and forest patches offer visual and thermal protection, so this landscape is attractive for deer (Reimoser 1986, Gill 1992, Reimoser & Gossow 1996, Tufto, Andersen & Linnell 1996, Mysterud 1999). But agricultural forage is often seasonal, and disturbance is usually high in this habitat, so deer resolve to feed in the forest patches, causing a high level impact (see Gerhardt *et al.* 2013). Human made infrastructures, such as roads and railways, can have an effect on spatial distribution of browsing pressure, as they provide open areas but are a source for disturbance (Nopp-Mayr *et al.* 2011). Reimoser *et al.* (2009) stated that high road density increases the vulnerability of forests to deer impact. Some species are attracted by striking edges, e.g. roe deer (Reimoser & Gossow 1996), and will therefore feed in the proximity of roads, but all deer species are sensible to the disturbance caused by vehicles, and this will cause them to avoid areas close to roads or railways. They will linger further back in areas where disturbance level is lower, but they will still be disturbed by road traffic, which will increase their energy demand (Nopp-Mayr *et al.* 2011) and in turn make their impact higher. Deer tendency to avoid high traffic roads and railways, can hinder seasonal migration too, forcing animals into a sub-optimal habitat that will suffer a high impact (Motta 1996).

FOREST MANAGEMENT

The human activity that exert the widest control over forested environment is forest management. Through forest management, several characteristics of the ecosystem, such as species richness or composition, age structure, spatial distribution of regeneration, can be almost completely controlled by foresters. The modifications of the environment can lead to alteration in animals' behavior, which in turn changes the level of browsing impact, most likely increasing it (see Kuijper 2011). Of the several environmental factors affected by forest management, three are the most relevant to explain why ungulate impact will likely be larger on managed forests: i) the size of the forest gaps, ii) the change in tree species composition towards ungulate-intolerant species, and iii) the creation –through forestry - of an unbalanced habitat, highly attractive but with a low carrying capacity (Kuijper 2011). In old-growth temperate forests, the gaps are usually due to occurrences of single trees falling down, and their mean size ranges between 40 to 190 m^2 (Tanaka & Nakashizuka 1997, Henbo *et al.* 2004, Kenderes, Mihók & Standovár 2008, Kenderes *et al.* 2009), and the majority of the gaps have a size between 20 and 50 m^2 (Kenderes *et al.* 2009). In managed forests, artificial gap size can vary, and it strongly depends on the silvicultural techniques applied and on which country or region the forest is located into. Kuijper (2011) reports the mean clear-cut sizes for some countries in Europe to range from 0.02 ha to 12 ha. While this information is not representative for the world-wide variation in clear-cut sizes, it helps to understand the difference between the two phenomena. There is a positive relationship between the dimension of the gap and the modifications in some micro-climatic conditions, such as air and soil temperature, soil humidity and solar radiation (Latif & Blackburn 2010). These environmental factors can influence the way in which vegetation develops, and in turn - as seen previously- animals use of space. Kuijper *et al.* (2009) found a positive linear relationship between gap size and number of ungulates visiting the gap. That can be due to the higher amount of forage that can be found in the gap, which attracts the ungulates in the surrounding areas. Several authors (see Scotter 1980, Kay 1993) suggest increasing gap size to mitigate ungulate impact. Increasing the gap size can mitigate ungulate impact in two ways: on one hand the impact is spread over a wider area, so it will be diluted, and on the other hand a wider open area means for ungulates being more exposed to predators and, possibly, being further from hiding places. The chance for this to work depends on the number of ungulates present and the species they belong to. If the number of ungulates is too high, the impact will still be high on the whole gap, and while the landscape of fear drawn by the gap can be challenging for certain species, e.g. roe deer, other species may not feel so exposed or in danger in the open areas, e.g. fallow deer and red deer (Kay 1993). Moreover, wide clear-cuts create striking edges between different biotopes, like close forest and meadow, which are strongly attractive for some species of deer, such as roe deer (Reimoser & Gossow 1996). The forage offer in the clear-cuts is not only limited to tree species, as the high light level favors the growth of ground vegetation, such as bushes, herbs and grasses. Ground vegetation is appreciated by deer, and when present, sometimes preferred over tree species as forage, but if the gap attracts too many deer, and the impact increases, ground vegetation won’t be able to support the browsing pressure, which will fall on tree saplings (Bergquist & Örlander 1998, Kramer *et al.* 2006). Bushes, herbs and grasses, can have a negative effect on seedlings by altering micro-site condition, both by modifying light and humidity levels - simply by shading the emerging seedlings-, and through inter-specific competition, as limiting available resources, as it happens with ferns (Kuijper 2011). On the other hand, some authors suggest that ground vegetation can favor tree seedlings by protecting them from deer (Putman 1994, Bergquist & Örlander 1998, Ramos *et al.* 2006). Opposites conclusions have be drawn on this topic, mostly based on the development stage of the growing tree plant and, again, on site micro-conditions. Ground vegetation can shelter seedlings and saplings by hiding them, visually, and by hindering herbivores movements. More than only a physical barrier, bushes can be noisy to walk through, and thou alert predators of herbivore presence (see Bergquist & Örlander 1998). Other studies, however, have found that ground vegetation protection last only as long as the plant is smaller than ground vegetation (Pellerin *et al.* 2010). Once the saplings have outgrown ground vegetation, the visual protection ends, and the saplings become visually striking, which –similarly as how it happens with snow cover- can enhance ungulate impact.

Another factor that can enhance deer impact in managed stands is the shift of species composition towards browsing-intolerant species. Browsing-intolerant species means that those species are more reduced in growth following browsing events, compared with tolerant species. The most economically interesting species in many temperate areas are coniferous species, such as *Picea Abies*, *Pinus sylvestris*, *Pseudotsuga menziesii*, *Abies grandis*, *Picea sitchensis*, *Larix kaempferi* (Kuijper 2011). The increasing amount of coniferous species, even out of their natural range, is a well-documented phenomenon in temperate regions of Europe (Spencer & Kirby 1992, Jedrzejewska *et al.* 1994). Nowadays, one of the aims of foresters throughout Europe is to convert those stands – often mono-specific and even-aged- into mixed stands with broadleaves species (Ammer, Bickel & Kölling 2008), but the question if those mixed stands are more economically attractive than monocultures is keeping many private owner from converting their stands (Knoke *et al.* 2008). Economically interesting species are often a second-choice for herbivores, as there are not nutritionally attractive, but this means that they're evolutionally unprepared to suffer elevated browsing impact. Conifers, as an example, are expected to be less tolerant to browsing, due to a strong apical dominance. To our knowledge, however, there are no studies that compare tree species regrowth capabilities after browsing events. Several studies about relationships between deer impact and species composition found that browsing pressure reduced the amount of preferred tree species, but Kuijper *et al.* (2010) show us a different scenario. In their study they found that oscillations in ungulates densities causes shifts in tree species composition, favoring unpreferred and browsing intolerant species increase during periods with low densities of ungulates. When, on the other hand, ungulates densities were high, browse preferred species increased in abundance. The reason for this probably rely in the natural conditions where the study took place, Bialowieza forest, one of the least disturbed temperate forests in Europe, where the forest is not managed, so regeneration occurs naturally, and large predators are present (Cromsigt & Kuijper 2011). Moreover, studies from Bialowieza forest show that the most preferred tree species may also be the most browsing tolerant (Kuijper *et al.* 2010). It seems reasonable, from an evolutionary point of view, that those species more affected by browsing pressure developed a more efficient response to it than species that suffered that pressure only occasionally. When the abundance of browsing sensitive species, such as conifers, is artificially increase for economic purposes, ungulates will have few other foraging options, and the stands will strongly suffer browsing impact (Jedrzejewska *et al.* 1994). Plants show three ways of responding to browsing pressure: tolerance, resistance, and phenological response. Tolerance means that the plant recovers quickly after being browsed, for example through compensatory growth, while resistance means that the plant develops a specific defense, physical (e.g. thorns) or chemical (e.g. alkanoids, tannins), to result less palatable to ungulates. The phenological response can be found in those ecosystems where herbivores are absent from the area for certain periods of time, like during seasonal migrations. The plants take advantages of herbivore absence and quickly grow during this time window.

The third factor that may enhance ungulate impact on managed forest is the creation of an unbalanced habitat, which is an outcome of the previous two factors considered. In a forest where the proportion of unpalatable species is very high, and the forest lacks heterogeneity of structure because of even-aged stands, the opening of a clear-cut works as a food trap for ungulates. The elevated forage availability in the clear-cut attracts ungulates, as mentioned before, but the surrounding homogenous forest provides food-independent settling stimuli which are more important than food-related stimuli (Reimoser & Gossow 1996, Vospernik & Reimoser 2008). The food-independent settling stimuli are those habitat characteristics able to satisfy the need for shelter and thermal cover. Of course, climate and disturbance characteristics in the area play an important role in shaping those needs. Gerhardt *et al.* (2013) stated that the presence of hiding places, escape cover, and thermal cover increase forest predisposition to browsing impact, and that a dense canopy cover is a strong settling stimulus, because it provides the aforementioned protection from disturbance or climate. When the forage offer in the clear-cut will decline, ungulates will found themselves in a habitat that satisfy their needs for protection, but has no nourishment to offer, and they will probably start damaging adult trees through bark stripping or move to another clear-cut. This shows another feature of the unbalance habitat, which is the uneven distribution of food resources. When food resources are concentrated in a relatively small area, may it be a clear-cut or a poorly planned artificial feeding station, the high number of ungulates will exert a unnaturally high browsing pressure both on the area and its surroundings. Forest managers seem to have a way to achieve their aims and, at the same time, reduce ungulate impact, and it’s represented by the use of thinning and shelter-cut. Those techniques creates small but abundant gaps, in this way the regeneration, and thou the forage offer, is more spatially distributed. Simulating, or at least resembling, natural gap formation dynamics, those techniques favor the presence of ground vegetation quite homogenously in the forest, which represent an alternative forage source that can be found forest-wide (Reimoser *et al.* 2009). A reduced browsing pressure on tree species can also favor the development of a forest with several layers of vegetation –un-even aged forest- which on one hand creates an ecologically healthier environment, which will more easily support wildlife populations, and on the other hand will provide a constant revenue for managers. Having different layers in the forest, every year there will be trees ready to harvest. Of course, the yearly yield will be lower, and that should be compensated by higher timber quality –due to reduced damage from herbivores- and a wider offer in terms of tree species (Reimoser & Gossow 1996, Reimoser *et al.* 2009). This kind of management resemble the natural dynamics found in not-managed forests, where the heterogeneity caused by gap formation offers regeneration opportunity for virtually all plant species, while supporting a substantial population of large ungulates, as in Bialowieza forest (Bernadzki *et al.* 1998, Bobiec *et al.* 2000, Bobiec 2007). Studies that have tested close-to-nature forestry techniques, found that even at high deer densities, the herbivores impact can have a low effect on regeneration (Madsen & Hahn 2008). In this scenario, ungulates should not be considered a problem, but should be seen and managed as a functional part of the ecosystem (Kuijper *et al.* 2010). Thinning, selection cutting, and other close-to-nature techniques are, of course, not the one solution for the issue of ungulate impact. Several studies show negative effects of those techniques, or difficulties in their application. Kramer *et al.* (2006) show that the increase in ungulate biomass due to the increase in herbs and grasses, can cause in turn an increase in browsing pressure even in distant areas, which are managed differently. Reimoser and Gossow (1996) found that single tree selection has high predisposition to browsing damage, but on the other hand, that group selection has not. Caudullo *et al.* (2003) found that, at high deer density, close-to-nature forestry is failing and regeneration is severely limited and sporadic. Similarly, Kamler *et al.* (2010) stated that the conversion of a traditionally managed forest towards a more close-to-nature management can be hampered by too intense herbivory. These negative effects, however, seem to be due to the lack of several control mechanisms, in managed forests, which interact with herbivore top-down effects (Kuijper 2011). These mechanisms, profoundly altered or even absent in human-modified forests, need time to establish and operate, depending on how much the ecosystem is altered.

DISTURBANCES

Amongst the aforementioned mechanisms that interact with ungulates top-down effect, disturbances are probably the most human-affected. Apart from the direct disturbances caused by humans, such as hunting, roads and railroads construction, tourist activities, forestry work, humans are directly responsible for the absence of a functionally important disturbance such as carnivores. Large carnivores have a strong ecological role in shaping herbivores populations, both in terms of individual numbers and behavior. Their pressure on herbivores populations causes a cascade effect which has consequences on other trophic levels (Fortin *et al.* 2005, Beyer *et al.* 2007, Beschta & Ripple 2009, Terborgh & Estes 2010). Carnivores direct effect is exerted through predation, which lower the number of individuals in the prey population, in turn partially relieving plants from herbivore pressure (Fretwell 1987, DeAngelis 1992). Carnivores top-down effect on prey communities have been the object of several studies, both within and outside Europe (Messier 1994, Jedrzejewska *et al.* 2005, Ripple & Beschta 2005). This effect is, however, dependent on the productivity of the environment. In fact, in low productive environment, carnivores have a strong regulating effect on prey populations, while in highly productive environments they have a smaller effect (Jedrzejewska *et al.* 2005, Melis *et al.* 2009). Studies conducted on Bialowieza National Forest show how carnivores do not regulate ungulate abundance, but limit the populations under the carrying capacity of the ecosystem at a given time (Jedrzejewski *et al.* 2002, Jedrzejewska *et al.* 2005). The indirect effects of the carnivores presence seems to be at least as important as the direct lethal effects on population densities (Schmitz, Beckerman & O'Brien 1997, Creel & Christianson 2008). Carnivores' presence modifies the behavior and resource selection of prey populations, because they exert a constant pressure on virtually the whole landscape through the risk of predation, which creates what has been called 'landscape of fear'. A well-known example of indirect effects is represented by the studies conducted on Yellowstone National Park, where after wolf (*Canis lupus*) reintroduction, habitat selection of its main prey item, elk (*Cervus elaphus*), changed to avoid high risk areas (Creel *et al.* 2005, Fortin *et al.* 2005, Mao *et al.* 2005). Prey populations try to avoid predation risk by carefully selecting the environment they will linger into, and they do this at different scales. On a coarse scale, they tend to avoid areas frequently used by predators, like river valleys, while on a finer scale they avoid places with physical or visual barriers that can hinder their flee or hide predators (Halofsky & Ripple 2008). The shift in habitat use caused a change in browsing pressure distribution, which favor an increase of plant regeneration in areas where elk use markedly before wolf reintroduction (Beschta & Ripple 2009). Those changes led to a localized increased in ecosystem structure and quality, which favored other wildlife communities, such as birds. Recently, there has been an increasing debate about the possibility of large carnivores reintroduction in those areas of Europe where they've been eradicated since decades, as a means to counteract the increasing ungulate populations and the consequent impact on forests (Manning, Gordon & Ripple 2009). But the environmental condition in which they would be reintroduced in Europe are very different from the ones where the studies reporting those effects have been performed. As mentioned before, in highly productive environments, as most of the temperate forests in Europe, the direct effect of predators is quite limited (Jedrzejewska *et al.* 2005). On the other hand, most of our knowledge on indirect non-lethal effects comes from North America (Beschta & Ripple 2009), those effects on Europe ecosystems are still poorly studied (Manning *et al.* 2009). The studies conducted in North America were located in wide national parks, with large landscape heterogeneity. The aforementioned example, of wolf and elk interactions, was located in Yellowstone National Park, which is almost 9,000 km^2 wide, and comprises dense forests, wide open areas, river valleys and mountain ridges. In Europe the landscape is highly fragmented and strongly altered, moreover large carnivores would be reintroduced in natural preserves, which extent cannot be compared to those of the national parks in North America. In fact, Wilson (2004) stated that the reintroduction of large carnivores may not be feasible at all in many areas, due to ecological or socio-economical reasons. In Europe, the most often advocated solution for control ungulate populations pressure on forest is hunting. Hunting may be a way to regulate ungulate populations on a relatively small area, or to a wider extent if the efforts are coordinated (Hothorn & Müller 2010), but there's little empirical evidences that wildlife management is able to control ungulates population on a larger area (McShea, Underwood & Rappole 1997, Milner *et al.* 2006). But even if that was the case, hunting would be a poor substitute for large carnivores because it cannot resemble their ecological function (Berger 2005). Direct effects of hunting on populations are quite different from the one exerted by natural predators (Kuijper 2011). The individuals that are targeted by these two disturbances are, in fact, different. Hunting usually is perform with the aim of maximize the trophy, so it targets the biggest or most beautiful animals, which often are the strongest. In the case of deer, usually only males have trophies – i.e. antlers- and though hunting may modify the structure of the population, shifting the sex-ratio towards females. Hunting effects are thou very different from natural predation's one, as the latter usually focus on the easiest individuals to be preyed, which often are the weakest, such as old, debilitated, or very young individuals (Okarma 1984). Moreover, indirect effects of carnivores and hunting are quite different too, both spatially and temporally. The changes in ungulate behavior caused by hunting are mostly determined by the type of hunt they're subjected to. Where natural predators roams over wide areas of hundreds of square kilometers (Okarma, Jędrzejewski & Schmidt 1998), hunters usually select hunting grounds based on accessibility –e.g. area close to forest roads-, presence of hunting structures, such as hunting towers, and on habitat type that provide profitable conditions (Proffitt *et al.* 2009). This of course turns into a very different spatial risk gradient for ungulates, that will reflect a different browsing pressure on the environment (Proffitt *et al.* 2009). If we consider a situation where a protected area has been instituted, this will be reflected in ungulates behavior with what is known as reserve effect, where species that are targeted by hunting concentrate in within the boundaries of the protected area, to avoid harassment. That will cause a spatial concentration of individuals that may reach very high densities, and in turn will locally increase browsing pressure. Moreover, whereas natural predator pressure is constant in time, all day every day of the year, hunting pressure is not. Most countries have hunting seasons which last for some months, sometimes divided into two smaller periods in which it is allow to hunt only one of the sexes. Some hunting techniques require several hunters to gather, as drive hunts, and those are usually performed during weekends, and mostly at dawn or dusk (Proffitt *et al.* 2009). Other hunting techniques, which do not require groups of hunters, may provide a more timely-homogenous pressure, as different single hunters may occur frequently in the same or in a close area. All those regulations create a temporally and spatially highly discontinuous landscape of fear, which strongly contrasts with the continuous one created by natural predators (Manning *et al.* 2009). This allows herbivores to select the most profitable foraging areas, avoiding spatially or temporally human-related risks, and to exert a strong browsing pressure on regenerating plants in those areas.

CONCLUSIONS

The view in which the relationship between deer and forest has been studied changed quite a lot in the last decades, expanding from a single factor relationship towards a more holistic multi-factor frame of investigation. The results obtained are showing that the relationship between deer and forest includes many other actors, both biotic and abiotic, that help our understanding of the ecological network that lies beneath the phenomenon. Once gained a more comprehensive view of all the interactions and dynamics that shape deer impact, it seems apparent that a single factor solution probably wouldn't work. Herbivores are not a problem *per se*, but part of an ecosystem that is failing to fit in place because of the extensive modification both of the environment and of its dynamics. In such an artificial environment, the straight solution would be the eradication of the herbivores, but in today's world this is –fortunately- unacceptable. There has been an increasing number of stakeholders regarding forested habitats, composed now not only by foresters and hunters, but by tourists, environmentalists, and all the related category, from tourism-related shop owner to politicians. As a single solution for the issue seems not to exists, the way to solve the problem seems to be the one of restoring a functional ecosystem, changing the management aims to be able to reach the same economic goals, whilst still satisfying the requests of all categories involved. As mentioned before, it will take time to restore the functionality of an altered system, but in several areas, at least in Europe and North America, managers have already started working in this direction. In the meanwhile, researchers should aim at conducing multi-factor studies, which will clarify the role of the different actors in the ecosystem, and so help managers improving ecological and functional restoration while using ecosystem resources in a sustainable way.

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Chapter 2

Application of three census method for roe deer density estimation in a mountainous environment in the Apennines

Manuscript

Application of three census method for roe deer density estimation in a mountainous environment in the Apennines

Marcon A.[1], Battocchio D.[1], Grignolio S.[1], Apollonio M.[1]

1 Department of Science for Nature and Environmental Resources, University of Sassari, Sassari, Italy

ABSTRACT

Roe deer is the most abundant and distributed ungulate in Italy , and it has a considerable impact over managed forests . To understand the impact and effects it can have on forest development, and plan a proper management, it’s fundamental to know the abundance of its population in the area, to the best precision and accuracy it is possible to reach. We tested 3 methods, one direct – drive census-, and two indirect – pellet-group count and camera trapping -, during two following years, for their accuracy and applicability in estimating roe deer abundance in a broadleaved mountainous forest in the Apennines. The density estimation returned were consisted across the methods (for year 2012 - drive census 21.89±12.74 ind./100 ha and pellet-group count 18.74±2.31 ind./100 ha; for year 2013 – drive census 19.32±11.12 ind./100 ha and camera trapping 27.67±7.48 ind./100 ha. The methods showed to have a wide range of precision, with coefficient of variation estimation ranging from 0.12 (pellet-group count) to 0.58 (drive census). We weren’t able to assess accuracy of the methods, as the real number of animals in the area is unknown. Drive census resulted to be the most demanding method, because of the elevated number of operators needed to perform the drives, and it returned the less precise results. Pellet-group count returned the most precise results, and requires a very small number of operators, but the sampling effort is quite high. The R.E.M. method resulted to have an intermediate precision compared to the other two methods, and the lowest sampling effort. The ease of field protocol of each method is considered and discussed, in the light of the increased probability of the census being performed by volunteers, instead of technicians, in the next future.

INTRODUCTION

Population size estimate is mandatory to planning wildlife management. More than the mere number of individuals in a population, long term census programs may provide information on population status and trends, habitat requirements for the species, and on anthropogenic impacts. Those information are particularly important when regarding species, such as deer, that may have a marked economical impact on humans societies, both through hunting and interaction with managed forests. An ideal situation for a proper evaluation of a population status, and to appropriately plan management actions, would be knowing the exact number of deer present in the area of interest. As it is often unfeasible to count all the individuals in a populations, especially for wild populations, sampling techniques are used to estimate animal density in a given area (Putman *et al.* 2011).

Census methods can be subdivided into two category, direct and indirect methods. Direct methods require the operator(s) to directly see the animals, as in drive censuses or line transect, while indirect methods rely on signs left by animals while moving, eating or defecating. Direct methods, as they imply observing the animals, can provide additional information other than the number of individuals, for example population structure, such as proportions of sex- and age-classes, groups composition, and sometimes behavioral information. On the other hand, those methods present logistical issues, as they are demanding and time-consuming, and so are often restricted to specific sampling periods (Mayle, Peace & Gill 1999, Marques *et al.* 2001). This can be an issue when the target species has a strong seasonal behavior or distribution, or its abundance change easily, and quickly, due to environmental conditions. Moreover, the presence of the operator(s), if perceived by animals, can alter their behavior leading to biased results, e.g. fleeing. The environment where the census is performed, and the consequent detectability of the species, must be taken into account when choosing the census method. As an example, (Andersen 1953) found that direct observations from vantage points for roe deer (*Capreolus capreolus*) in broadleaved woodland estimated a density that was one-third of the actual one, and Bongi *et al.* (2009) on a study in the Apennine found that about the 70% of a tagged sample of animals known to be in the drives were actually observed. In response to those difficulties, several indirect methods have been proposed and tested in the last decades, to assess the abundance of animals population through the analysis of persistent signs, like tracks, bite marks on vegetation, or fecal count. The reliability of those methods is not yet consensual (Putman 1984, Anderson 2003), but they're usually less demanding or time-consuming, and causing a lower disturbance, are less prone to the aforementioned bias of modified behavior.

During this study we focus on the roe deer, as it is the most abundant and distributed ungulate in Italy (Apollonio 2010), widely diffused in the Apennines, and the focus of both hunters interests and foresters concerns. We applied three different census methods in a mountainous area of the Northern Apennines, to test their relative performance on a forested habitat. During two different years we applied drive census, pellet-group count, and camera trapping, to estimates the density of roe deer population. Drive census technique was developed in the 40s by the USDA, refining an earlier technique used since the 19th century (Leopold 1933). Drive census is a direct method, as it requires the operators to see and count the animals. Drive censuses are conducted under the direction of Arezzo Province every year, to monitor the population and refine the culling plans, if needed. The pellet-group count is an indirect methods, where the estimate of the population number is calculated from the number of dung groups found during the sampling. This technique has been applied for various species of deer, and in different countries, since the 40s (Bennett, English & McCain 1940, Acevedo *et al.* 2008, Periago & Leynaud 2009, Koda *et al.* 2011). This technique can be divided into two category, the first - fecal standing crop – needs a parallel study on decay rate of the dung, i.e. how long the drops remain in the environment. The sampling areas are visited only once, and the density is estimated as a function of the number of pellet-group found and the decay rate. The second category - fecal accumulation rate or clearance count – requires two visit at the sampling areas, one for cleaning the area from the pellet-groups, and the second visit to count the pellet-groups. The last method we applied is camera trapping. This is an indirect method, as the operator is not present when the camera triggers, but recording images or videos, it allows for the gathering of other information, e.g. behavior, that other indirect methods cannot provide. The method was developed in the early 80s, and have been used for monitoring cryptic or rare species in several different environments (McCallum 2013). If the target species has individual marks, natural or artificial, that the camera is able to capture, this technique can be used to estimate animal abundance through capture-mark-recapture technique. Of course this is not possible for species that naturally lack those individual marks, and are difficult to catch. For those species, the use of trapping rate (i.e. number of pictures for unit of time) as a proxy for species abundance has been proposed more than a decade ago (Carbone *et al.* 2001). This approach received criticisms, as the trapping rate may easily be influenced by other factor than the animal density alone (Jennelle, Runge & MacKenzie 2002, Stephens *et al.* 2015). Rowcliffe *et al.* (2008) developed a method which does not require individual recognition (Random Encounter Method, R.E.M.), and solves the issues related with trapping rate biases by modeling the underlying dynamic of the encounters between animals and cameras. Even if this methods received some criticisms (Foster & Harmsen 2012), several tests on the field show the good performance it can achieve (Rowcliffe *et al.* 2008, Rovero 2009, Zero *et al.* 2013, Cusack *et al.* 2015). We decided to test the R.E.M. method for a small forest dwelling ungulate, the roe deer, in the heterogeneous habitat of the Northern Apennines, to try and understand if it's a suitable method for this environment. Aims of the study were to test the precision and applicability of those methods in the broadleaved forests of the Apennines for roe deer, and to field test the new approach of R.E.M. method in this environment. Moreover, we try and understand if the demands of each method are proportionate with the quality of the results it delivers.

METHODS

Study area

The study area encompasses 13’800 ha of the Casentino valley, Tuscany, Italy (Fig. 1). It is located in a mountainous regions in the Northern Apennines, and it covers an altitude range between 248 m and 1’414 m a.s.l.. The study area comprises a protected area of 2’760 ha, which lays at the highest altitudes (Fig. 1). The climate in the area is continental, with hot and dry summers and cold and rainy winters, with high humidity rate. The mean annual precipitations in the area are between 900 and 1’500 mm.

Forest covers the 67% of the area, while urban areas covers 4% of it, the remaining is composed by agricultural areas (18%) and scrubs (11%). Forest is mostly comprised by broadleaves species, the most abundant of which are oaks (*Quercus* spp.), beech (*Fagus sylvatica*), chestnut (*Castanea sativa*) and hornbeam (*Ostrya carpinifolia*), while for conifers are white fir (*Abies alba*), black pine (*Pinus nigra*), Douglas fir (*Pseudotsuga menziesii*), and maritime pine (*Pinus pinaster*).

Four ungulate species are present in the study area: roe deer, wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). Roe deer and wild boar are abundant and present in the whole study area, while the densities of red deer and fallow deer are lower and they are heterogeneously distributed. Two predators are present in the area, wolf (*Canis lupus*) and red fox (*Vulpes vulpes*). Our study area encompasses parts of territories of at least two wolf packs (mean number of individuals in a pack, estimated by means of wolf howling is 4 individuals, unpublished data), that use roe deer as one of the main prey items (Bassi *et al.* 2012). Fox is commonly present in the area, and while uses roe deer as a prey item, its use is focused on fawns (Bassi *et al.* 2012).

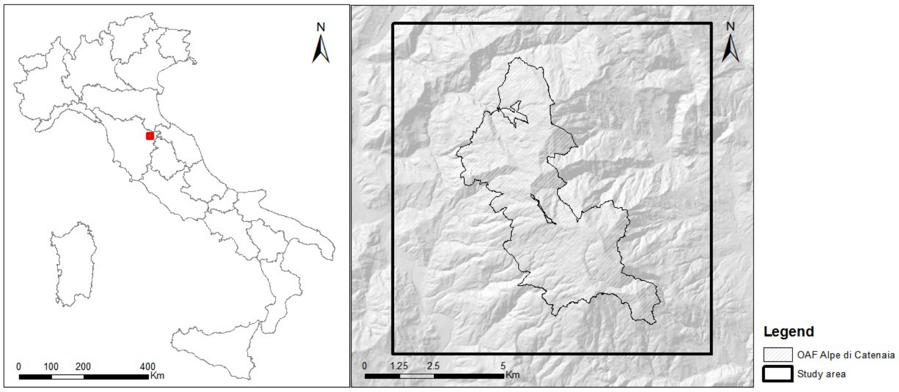

Figure 1 Hillshade of the study area and boundaries of the protected area it comprises

Census techniques

Drive census

During our study, 15 drive censuses have been performed inside our study area between April and May 2012 and 2013. Drive censuses are conducted annually by the Arezzo section of URCA, the association of the Apennines hunters, in the whole area where roe deer hunting is allowed. Of the 15 drive censuses considered, 6 were inside the protected area, and were performed by URCA hunters under the logistic direction of the researchers.

Drive census is a direct method, that aims at the total count of the animals present in a certain area. The method requires a large number of operators, as the area – at least some hectares wide- must be surrounded by operators that maintain visual contact. After the area has been surrounded, a line of operator – which length encompasses the total length of one of the axes of the area- walks throughout the area, scaring away the animals. The distance between operators along the line should be short enough that no animal present in the area is missed, so it depends on the vegetation density and structure of the site. The operators that surround the area are in charge of counting the animals that flee out of it. If some animals happen to flee from outside to inside the area, those are counted and then subtracted from the final count, as they were not inside the area at the beginning of the census.

Drive census areas have an average extension of 34.92±6.79 ha, and their locations have been chosen in order to be representative of the different vegetational categories in the area. Drive censuses are usually conducted between April and May, following the protocol described in Jedrzejewska *et al.* (1994); the density of operators for each drive census is on average of 110 operators/100 ha (Mattioli *et al.* 2004).

C.E.M.A.G.R.E.F. (1984) – now IRSTEA, the French National Institute for Environmental and Agricultural Science and Research - indicates that only forested areas should be selected for this technique, but in a heterogeneous habitat this might lead to biased estimates. For example, if drive census area is the only forested patch in an otherwise extensive agricultural land, all roe deer that live in that area will be inside the forested patch seeking for hiding. If we consider those animals to live only inside the forested patch, our density estimates will be highly inflated and not representative of that area, because when not disturbed, those same animals will roam the extensive agricultural land. For this reason, we applied a correction factor that takes into account the percentage of forested area in the surroundings of the drive census area. We calculated an 1 km buffer around the census area, and use the percentage of forest cover of this new area as a multiplier - our correction factor - for the density estimation of that particular census area (Davis *et al.* 2012). The overall density estimation is calculated as the averaged density across all the census areas within our study area (C.E.M.A.G.R.E.F. 1984).

Pellet group count

The pellet group count census took place between May and July 2012. We used the F.A.R. method (Fecal Accumulation Rate), which require two visits for each sampling plot (Neff 1968, Buckland 1992, Webbon, Baker & Harris 2004). The first visit for clearing the area of all pellet groups present, and the second visit to count the pellet groups deposed in between the two visits. This technique requires to choose an appropriate time window between the two visits, long enough to allow animals to visit the area and, at the same time, short enough to guarantee that no pellet group will decompose and not be counted. By empirical observations we estimated that, in our study area in late spring-early summer, roe deer drops decompose completely after a minimum of 28 days, so we choose a time window of 21 days between the two visits.

For the mean defecation rate for roe deer, needed for the density estimation, we used data from Mitchell *et al.* (1985), which found the daily defecation rate for roe deer to be between 17 and 23 groups of pellet, based on the productivity of the environment. As we do not have data that allows us to precisely defined a productivity level of our environment for roe deer, we decided to use the mean value of 20 pellet groups per day.

For the sampling design and the subsequent analysis we followed the methodology described by Fattorini *et al.* (2011), to obtain statistically more robust results. We supposed that roe deer density would differ between habitats, so starting from CORINE Land Cover dataset (2006), we grouped land use categories to obtain sets of habitats that would likely host similar roe deer densities (Tab. 1). As Sutherland (1996) stated, one of the most common mistakes in censuses is to sample few big areas instead of a many smaller ones. For this reason, we clipped the CORINE map by overlaying a 500 m grid, so that the widest land use polygon would be 25 ha. Moreover, we stratified the sampling plots between habitat sets, based on their extent (Tab. 1). The land use polygons to sample have been chosen randomly, with a probability of been extracted proportional to their extent, i.e. wider polygons had a higher probability to be extracted. This was performed because, in the subsequent analysis, the data collected in each polygon selected for sampling would contribute to the density calculation proportionally to the polygon extent, i.e. wider polygons will have higher weights in density calculations (Fattorini *et al.* 2011). For a better estimation of the density of each selected polygon, 5 sampling plots have been located within each of them. Instead of randomly place the 5 plots inside the polygons, we divided each polygon in 5 areas of equal extent and similar shape, and then randomly placed a single sampling plot within each of those areas. The splitting procedure was performed using Brus algorithm, implemented in an R procedure (Brus, Spätjens & De Gruijter 1999, R

Core Team 2014). This was done to maximize the representativeness of the results for the sample area –i.e. the land use polygon- following Barabesi, Franceschi and Marcheselli (2012).

This led us to a theoretical sampling effort of 300 plots, 6 of which were impossible for operators to reach, resulting in 294 monitored plots. Each plot was displaced through a GIS software (ArcGIS 10.0, E.S.R.I.) and located on the field through a handheld GPS device. Each plot consisted of a circular area with a radius of 5 m, covering an area of 78.54 m^2 each. A pellet group was defined as a group of at least 10 fecal pellet, and two pellet groups were considered as distinct if they were separated by at least 1m (Koda *et al.* 2011).

Stratum	Area (ha)	Area %	Number of polygons	Number of plot
Coppice	3818,473	28,79	17	85
Beechwood	2741,095	20,66	12	60
Oakwood-Chestnutwood	1973,863	14,88	9	45
Conifers	755,0715	5,69	4	20
Shrubs	1524,954	11,50	7	35
Agricultural	2451,207	18,48	11	55
Total	13264,66	100	60	300

Table 1 List of the vegetational strata considered, their extent in hectares, percentage of the total area, and number of sampling plots for each stratum.

R.E.M. – Random Encounter Method

The census by means of camera-traps has been performed between April and May 2013. The R.E.M. method (Rowcliffe *et al.* 2008) allows density estimations from camera traps data for species for which individual recognition is not possible. The method requires the encounters between animals and cameras to be random, and several sampling designs meet these assumptions (Rowcliffe *et al.* 2013).

For our study, we stratified our camera placement over the same vegetation categories used for pellet-group count method, and we deployed our cameras randomly on 60 locations. The minimum distance between location was set at 500 m, to minimize the risk of spatial correlation between closely located cameras. We used 15 cameras, 9 MultiPR-12 and 6 Bushnell HD. Locations have been identified by means of a handheld GPS device, and cameras have been set pointing toward North, at an approximate height of 50 cm on trees or bushes present at the location. The bearing the cameras were facing has been chosen to minimize the interference of the sunlight, which can cause triggering of the camera without any animal present, or can "burn" the image making it unusable. The height of the displacement was choose to be far from ground vegetation, which can interfere with camera performance, but not so high to miss the animals passing by. So we choose a value, 50 cm, that was a bit lower than the average shoulder height for the species in our area, which is 72 cm (unpublished data). Being the vegetation very thick in some locations, we choose positions for the camera that would have some vegetation-free space in front of it.

It may happen that an animal, or a group, trigger the camera multiple times in a row, because it's walking slowly, lingering in the area, or simply because there are several animals. All those pictures are relative to a single encounter event, between the animal and the camera, and so they actually count as one. Some authors set a delay after the triggering of the camera before another picture can be taken, to prevent multi-triggering for a single encounter event (Rowcliffe *et al.* 2008, Zero *et al.* 2013, Cusack *et al.* 2015). We did not set any delay after a picture was taken, so we identified the independent encounter events by looking at all the pictures (Rowcliffe pers. comm.). The formula used to calculate the density estimation is the following (Rowcliffe *et al.* 2008):

$$D = \frac{y}{t}\frac{\pi}{vr(2+\theta)}$$

The *y/t* variable is the trap rate, which is the number of independent event of encounter (i.e. pictures) of a species divided by the days of monitoring effort (i.e. trap-days), *v* is the average daily speed, and *r* and θ are the radius and angle of the detection area of the camera. The averaged daily speed was found in the literature to be 1 km/day (Carbone *et al.* 2005). The radius and angle for the detection area have been extracted from the cameras technical specifications, resulting in 20 m and 80° for the Multi-PIR12 model, and 15 m and 50° for the Bushnell model. To obtain single values for each parameter to use into the R.E.M. model, we calculated a weighted average of both radius and angle of cameras detection area, using as weights the number of camera locations in which each camera model was used, 24 and 36 for Multi-PIR12 and Bushnell respectively. The resulting parameters are 17 m and 62°. Roe deer is usually wrongly considered a solitary animal, but along the year it shift its social structure from solitary and territorial, mostly during spring and summer, to social groups, mostly in winter (Andersen, Duncan & Linnell 1998). For this reason we used random encounters data collected between 2008 and 2012 during the research activities in the area (n=208), for the same months of the monitoring effort (i.e. April and May), to calculate an independent estimate of the mean number of individuals in a group, which resulted to be 1.22. The R.E.M. model does not return an estimate of the error of the result, so following Rowcliffe *et al.* (2008) we use non-parametric bootstrap on camera locations, with 10’000 replicates, to estimate a standard error and calculate the 95% confidence interval.

RESULTS

Drive census

Drive census were performed between April and May 2012 and 2013, on the same battue areas in both years. The mean extension of census areas was 34.92 ± 6.79 ha, covering a total extent of 523.80 ha.

The density estimations for the single drive areas, weighted by the forested-area index of the buffered area, range between 6.81 and 46.14 individuals per square kilometer, for the year 2012, and between 6.34 and 45.20 for the year 2013. Following C.E.M.A.G.R.E.F. (1984) the density estimation for the whole study area is calculated as the averaged density of the drives performed. This led to the estimation of 21.89±12.74 and 19.32±11.12 individuals for square kilometer, for years 2012 and 2013 respectively (Fig. 3, Tab. 3).

Drive census area	Drive census extent (ha)	2012		2013	
		Animals observed	Density estimation	Animals observed	Density estimation
Fonte S.Francesco	41.24	9	19.34	5	10.75
Monte Sovaggio	36.65	15	29.72	15	29.72
Santa Mama	32.65	11	13.81	9	11.30
Il Casale	43.6	22	41.43	24	45.20
Casina della Burraia	35.61	12	28.50	11	26.13
Sopaccia	41.6	10	15.05	7	10.54
Fonte Galletta	30.6	15	46.14	11	33.84
Capanno del Lupo	29.01	15	42.99	10	28.66
Trecciano	31.94	8	17.04	9	19.17
Pian D'Acero	38.88	6	14.83	8	19.78
Caselline	29.24	5	15.85	2	6.34
Eremo della Casella	20.83	2	8.75	2	8.75
San Luigi	43.96	7	15.00	6	12.86
La Crocina	40.51	8	13.11	8	13.11
Fosso Cupo	27.48	2	6.81	4	13.62

Table 2 List of drive census areas, their extent, the number of roe deer observed and the density estimate for each area for both year 2012 and 2013.

Pellet-group count

We monitored 294 plots, each covering 78.54 m^2, between May and July 2013. The number of pellet groups found in a single plot ranges from 0 to 7, with a frequency distribution markedly shifted towards the lower end of the range (Fig.2).

The method developed by Fattorini *et al.* (2011) returns an estimate of the number of pellet groups present in the monitoring time window for each of the strata considered in the sampling design. The sum of those estimates, divided by the span of the time window, by the defecation rate of the species, and the extent of the study area, gives the density estimates for the area. In our study area, considering a daily defecation rate of 20 pellet groups, the returned density estimate is 18.74±2.31 individuals for square kilometer (Fig. 3, Tab. 3).

The estimates returned by this method are quite precise, as can be seen from the low coefficient of variation, i.e. 0.12 (Tab. 3).

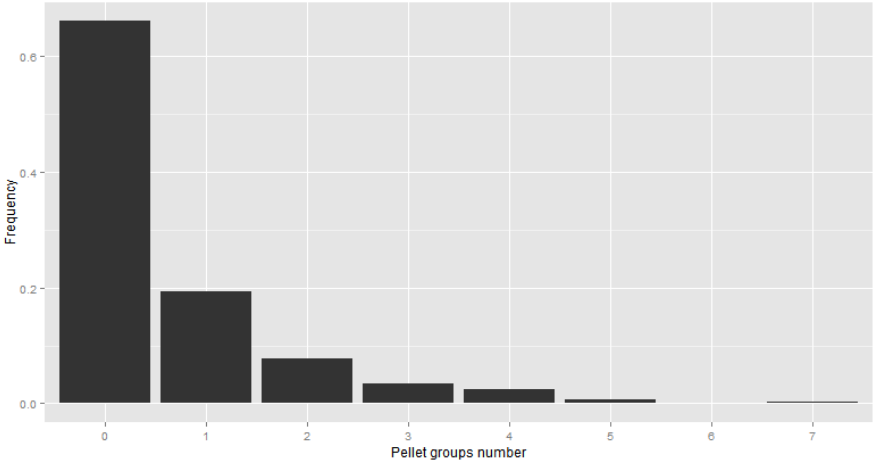

Figure 2 Distribution of the number of pellet groups found for each plot

R.E.M. – Random Encounter Method

We deployed 15 cameras on 60 locations between April and May 2013, for a total of 782 trap-days, during which they recorded 2098 pictures containing animals of different species.

Roe deer is the second most recorded species, with 850 pictures which, once visually analyzed, identified 296 independent encounters of the species. Those numbers gave us a trap-rate of 0.379 encounters per day. The density estimates calculated using the R.E.M. method, setting a daily speed of 1 km/day and a radius and angle for the detection area equal to 17 m and 62° respectively, resulted to be 27.67±7.48 ind/sqkm (Fig. 3, Tab. 3).

Method	Density (100 ha)	Variance	C.V.	95% C.I.
Drive census 2012	21.89	162.31	0.58	46.86-0.0
Pellet-20	18.74	5.34	0.12	23.27-14.21
Drive census 2013	19.32	123.65	0.58	41.12-0.0
R.E.M.	27.67	55.95	0.27	42.33-13.01

Table 3 Density estimates with coefficient of variation and 95% confidence interval for each method considered.

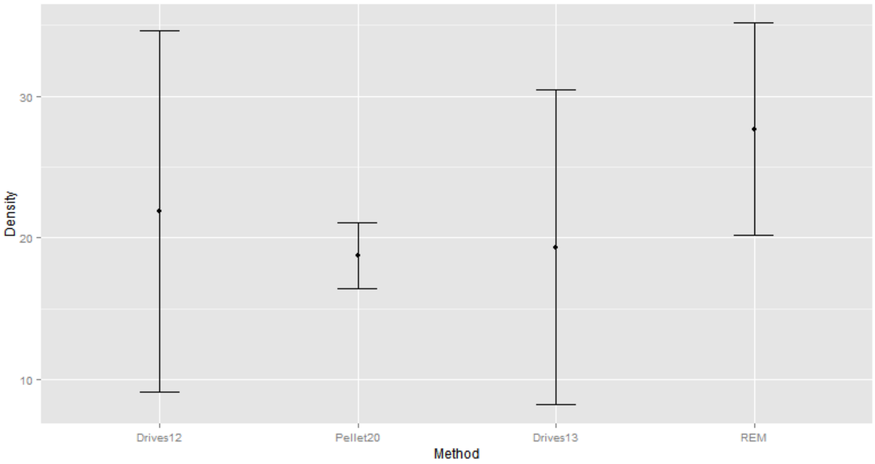

Figure 3 Density estimations with relative standard deviation for the methods considered

DISCUSSION

Our results show that the three methods applied return congruent estimates of roe deer population, but different levels of precision of the estimates (Fig. 3). As often happens with free ranging wildlife, we do not know the real number of animals in the area, so we are not able to evaluate the accuracy of the density estimates.

Drive census resulted to be the method with the lowest precision (C.V. 0.58 in both years), due to the high variability in animal counts between different census area. Several factors may have influenced the counting performance of the operators, such as weather conditions, to vegetation closeness or thickness, different level of noise during the disposition of the operators before the drive – which could make some animals flee the area-, and the time of the day the drive is performed (e.g. Bongi *et al.* 2009). Census areas have been chosen to be representative of the whole study area, so the difference in animals numbers counted between drives may of course be a genuine indication of the heterogeneous spatial distribution of the species. Despite this uncertainties, drive censuses return a certain minimum number of animals present in the area, because they’ve been seen and counted. This method is widely used both in Tuscany and in Italy to estimate the density of roe deer populations, moreover Bongi *et al.* (2009) found it to be the method that returned the highest densities in an Apennine environment, so we considered it as a reference value.

The pellet-group count method, performed following the protocol explained in Fattorini *et al.* (2011), returned the most precise results, with a C.V. of 0.12 (Fig. 3, Tab. 3). Both methods applied in 2012 include in their 95% c.i. the estimate returned by the other method (Tab. 3). The density value returned by pellet-group count, estimated considering a defecation rate of 20 groups per day, is slightly lower that the estimation returned by drive census (Tab. 3), and the reason for this difference may be due to a failure in finding all the pellet-group present in a plot, caused by environment characteristics. The pronounced slope of certain areas may have influenced the persistence on the ground of the fecal pellets, which rolled downhill. On the other hand, dense ground vegetation, such as herbs, grasses and bushes, may have affected the capability of the operator to locate all the pellet-group present, despite the effort. A pilot study about the effect of vegetational composition of the plot on the ability to locate artificially displaced pellet-group, shown that the percentage of the plot covered by grass or bushes is an important factor that influence the number of pellet-group found (unpublished data).

The R.E.M. method returned a density estimate that is congruent with the one returned by drive census for 2013, and each method includes in its 95% c.i. the estimate returned by the other technique (Fig. 3). The R.E.M. method returned a higher estimate, but as mentioned before, we are not able to measure its accuracy. Still, we can address some sources of uncertainty on our estimates, related to the parameters of the detection area of the camera and the daily speed of the species. The issue of the detection area parameters have been raised before (Kelly & Holub 2008, Tobler *et al.* 2008), and the reason for this to happen may be a different camera trap sensitivity between animal species, between camera models, or related to environmental conditions, like humidity or vegetation density. During our study we used two different camera models, and calculate the detection area parameters as a weighted average of the values reported in the technical specification for each model. We acknowledge this as a potential source of bias for our estimate. Cusack *et al.* (2015) performed a sensitivity analysis of the effect of the variation of those two parameters on the density estimation, and found that a 1% variation in detection radius and angle values resulted in a change in density of 1% and 0.3% respectively. Referring to this results, our density estimate may be biased of 13-15% due to the averaging of the data from the two camera models. The other source of bias may be the average daily speed of the species. Lacking fine movement data for the species in our study area, we extract the value from the literature (Carbone *et al.* 2005). The value comes with no error estimation, so it has not been possible to insert its uncertainty in the variance calculation of the final estimate. Moreover, the given value of 1km/day seems to be quite low for our study area, where animals are often disturbed by human activities and where there's a resident healthy population of wolves.

Despite the aforementioned biases pertaining each method, the density estimates were consistent with each other. Pellet-group count returned the lowest estimate, but with the highest precision, while drive census returned the lowest precision, with R.E.M. somewhat in the middle, even if it's worth remember not all sources of uncertainty have been considered for the latter.

Drive census required the highest number of operators needed, as it is performed with a density of 110 operators for 100 ha of census area. Bongi *et al.* (2009) would recommend an even higher density of operators, stating that below 200 op/100 ha the amount of observed animals drops sensibly. Intuitively, the organization of such a crowded event is not easily done, the suitable days to perform the drives are limited, as are the number of drives that can be performed in a single day. In addition, it's worth noting that the hunters population's trends are decreasing, as the majority of hunters is composed by elder people, and the new generations seem not to be interested in hunting practice. This will probably make it more difficult to organize large group of people together to census the number of areas required for a good representation of extended territories such as hunting districts.

Pellet-group count method has lower operator requirements, 4 operators were needed to perform our sampling, but it's time consuming, as visiting twice our 300 plots –as the F.A.R. requires-, took 3 whole months of everyday work. On the other hand, the sampling design and the subsequent data analysis are quite complicated, and necessitated the help of a statistician.

The R.E.M. method required the lowest number of operators, only 2, and 2 month of field work, at alternated weeks. Ideally, R.E.M. method would benefit of a parallel study on daily movement of the target species, during the same time window as the census is performed, as to avoid seasonal or annual differences in daily range. Both sampling design and subsequent analysis are quite easily performed, but the method requires an initial economic investment in terms of camera traps which, depending on camera models and number, can be quite consistent.

As the resulting estimates of all methods are congruous, the choice of the method to apply, in a mountainous forested environment, seems to be dependent on resources and logistic issues of the single study area. Pellet-group count gave the most precise estimates, and with some specific study in the area on pellet visibility it may be possible to calculate a correction factor for pellet-group that are not located, to increase method accuracy. The R.E.M., with a study on the daily range of the target species in the area, would provide *ad-hoc* and data-based parameters, calibrated on the species and the environment the study is being performed on. Once that study is performed, the R.E.M. is the easiest and fastest of the methods we tested. The latter characteristics, while of questionable scientific relevance, assume great importance in a context where the censuses are performed by hunters or volunteers, instead of by researchers and technicians. The application of these methods gives adequate results only if their protocols are properly followed, and as the performing agents in the next future will probably be volunteers, the ease of field practices will increase the quality of the results. Anyway, if reliable results are requested, the methods cannot transcend adequate knowledge of some species- and site-related parameters - such as daily defecation rate, or daily range- that should be acquired through appropriate studies performed by technicians or researchers. Some of those studies are quite demanding or expensive, but fortunately, they do not need to be repeated every time the censuses are performed.

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Chapter 3

Early and long-term impacts of browsing by roe deer in oak coppiced woods along a gradient of population density

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Research paper

Early and long-term impacts of browsing by roe deer in oak coppiced woods along a gradient of population density

Francesco Chianucci[1*], Luca Mattioli[2], Emilio Amorini[1], Tessa Giannini[1], Andrea Marcon[3],
Roberta Chirichella[3], Marco Apollonio[3], Andrea Cutini[1]

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Abstract - Over the last few decades, wild ungulate populations have exhibited relevant geographic and demographic expansion in most European countries; roe deer is amongst the most widespread ungulate species. The increasing roe deer densities have led to strong impact on forest regeneration; the problem has been recently recognized in coppice woods, a silvicultural system which is widespread in Italy, where it amounts to about 56% of the total national forested area.

In this study we investigated the effect of roe deer browsing on the vegetative regeneration of Turkey oak few years after coppicing, along a gradient of roe deer density. A browsing index revealed that browsing impact was high at any given roe deer density but increased at higher density, with the browsing rate ranging from 65% to 79%. We also analyzed the long-term impact of browsing six and eleven years after coppicing under a medium roe deer density. Results indicated the early impact are not ephemeral but produced prolonged impacts through time, with an average reduction in volume of -57% and -41% six and eleven years after coppicing, respectively. Based on these results we proposed integrating browsing monitoring with roe deer density estimation to allow identifying ungulate densities which are compatible with silvicultural and forest management objectives. The proposed browsing index can be regarded as an effective management tool, on account of its simplicity and cost-effectiveness, being therefore highly suitable for routine, large scale monitoring of browsing impact.

Keywords - *Capreolus capreolus*, Turkey oak, forest damage, stool, coppice forest

Introduction

The coexistence of ungulates and forest ecosystems has gaining growing attention, mainly because of the steady increase in wild ungulate populations observed in the last few decades. This is a particularly relevant issue for roe deer (*Capreolus capreolus* L.), i.e., the most widespread European deer species, with an estimated 10 million individuals occurring in the continent (Apollonio et al. 2010, Linnell et al. 1998). Roe deer population densities have been growing notably during the last few decades (Cederlund et al. 1998, Gill 1990) due to the abandonment of rural areas, changes in human land use, restocking and lack of predators (Apollonio et al. 2010). In addition, changes in silvicultural systems have entailed a general decline in wood exploitation, improving productivity, biomass accumulation and structural complexity of forest ecosystems (Cutini et al. 2013). The reduced pressure on wood also resulted in a lower human disturbance on ungulates in general and roe deer in particular.

The increasing roe deer densities have led to conflicting interests between game and forest management (Apollonio et al. 2010, Cutini et al. 2011, Gill 1992). A land-owner aiming at silviculture and wood production may see his goals frustrated by high densities of ungulates permitted on neighbouring grounds (Kramer et al. 2006). The problems of deer browsing have long been recognized in conifer species (Gill 1992, Motta 1996, Mysterud and Østbye 1999). Recently, the problem of deer impact has also been observed in coppice woods (Cutini et al. 2011), a silvicultural system which is widespread over Mediterranean countries. In Italy, coppice is the most frequently adopted silvicultural system in private forests, and it amounts to about 56% of the total forested areas in Italy (National Forest Inventory, www.infc.it). Deciduous Turkey oak (*Quercus cerris* L.) occupies the intermediate vegetation belt between sclerophyllous and mountain broadleaved forest over one million hectares (Di Matteo et al. 2014). This species represent an economically relevant species with regard to coppice management and also a potentially key food resource for roe deer (Cutini et al. 2011). Despite such a large diffusion

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[1] Consiglio per la Ricerca e la sperimentazione in Agricoltura, Forestry Research Centre (CRA-SEL), Arezzo, Italy
[2] Province of Arezzo, Arezzo, Italy
[3] Department of Sciences for Nature and Environmental Resources, University of Sassari, Sassari, Italy
[*] corresponding author: francesco.chianucci@entecra.it

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and importance, few studies have focused on roe deer browsing on coppice wood, probably because the problem of deer impact on coppice regeneration in Italy is relatively recent (Cutini et al. 2011). After coppicing, stems are cut down close to ground level, where the growing shoots are exposed to deer browsing, expecially during the early years following cutting. Because the browsing incidence can heavely be influenced by ungulate density (Chevrier et al. 2011) it is important to evaluate density-related effects of browsing. In addition, because browsing can delay the growth of vegetative regeneration (Motta 2003), it is important to evaluate the long-term browsing influence on coppice growth. Indeed, as browsing impact are expected to be limited to the early phase of coppice rotation, since shoots are more exposed to browsing, an important question is whether the effects of browsing are likely to be permanent, or simply ephemeral due to changes associated with stand maturity (Gill and Beardall, 2001).

The objective of this study is twofold:

i) to assess the effects of roe deer browsing on vegetative regeneration of Turkey oak (stands after coppicing, along a gradient of ungulate density;

ii) to evaluate the long-term effects of browsing through time (i.e., six and eleven years after coppicing).

Both information are nowadays strongly needed for sustainable planning of deer density and for assessing economic impact of deer on coppice (e.g., for refunding purposes).

Material and Methods

The study was carried out in the Province of Arezzo (Tuscany, Italy). Suitable study areas were individuated by integrating a series of information on roe deer densities and forest data available in the Province. Roe deer densities were obtained by means of drive censuses conducted by the Fish and Wildlife Service of the Province of Arezzo (Cutini et al. 2013, Mattioli et al. 2004, Davis et al. 2012). Data were collected from 2011 to 2013 on a network of 187 permanent sample plots (43.9 ± 26.0 S.D. ha of mean surface and 8116 ha of total area) uniformly distributed along the Province. Roe deer density at local scale was calculated by spatial interpolation using the inverse distance weighting method (Li and Heap 2008) in ARCMAP 9.2 ESRI package. The setting used was: $p = 2$ and the minimum number (n) of sampled points used for estimation was 5, within a radius of 5 Km, and the pixel size of the output was 1 ha. Roe deer density was calculated for each study area as a mean of the values of each hectare included in the area, and for each plot inside the study areas was calculated as a mean of the values in a buffer of 1 km around the centre of the plot. Data of geographical distribution and size of coppiced areas were obtained from "ARTEA" dataset of Regional Administration (www.artea.toscana.it).

Study areas were only deemed suitable if other deer species influence was absent. Also, a similar wooded and coppice coverage were considered to ensure comparability between the study areas; this was a major determinant in the choice of study areas and consequently after experimental design. Three study areas were selected representing a gradient of roe deer population densities which was representative of hilly and mountain areas of Central Italy (hereafter scenarios; Tab. 1). The observed mean roe deer densities were comparable to that indicated by the Italian National Institute for Environmental Protection and Research (ISPRA) as low (i.e., between 10 and 15 individuals per km^2) , medium (i.e., between 20 and 25 individuals per km^2) and high (i.e, more than 25 individuals per km^2) roe deer densities in Apennines and Mediterranean environments.

Within each study area, a number of oak coppice stands aged 0-2 years with minimum size of 2500 m^2 were individuated. Within these plots, we randomly sampled 744 stools, of which half stools were located near the centre of each stand and half stools were located along the border of each stand. The observation period ran between October 15 and November 15, i.e. close to the end of the growing season. For each stool, we recorded the number of sprouts, top height of sprouts (i.e., the height of the tallest sprout of each stool), and number of recently browsed sprouts. The cover area of each stool was estimated by the geometric mean of the maximum and minimum diameter of projected area (assuming an elliptical shape). The browsing index was calculated as the ratio of browsed sprouts over the total number of sprouts for each surveyed stool. Browsing estimates were then averaged for each plot. Differences in oak browsing, top height, and cover area in the three different scenarios were compared by means of ANOVA. If ANOVA indicated that a significant difference existed between them in the variable of interest then Tukey's pair-wise comparison test was used to compare results from the three scenarios. We used R version 3.0.2 (R Development Core Team 2013).

To evaluate the impact of browsing on

Table 1 - Study areas

Study area	Average roe deer (n km-2)	Scenario
Valdambra	38.3 (2.6)	High
Alpe di Poti	13.9 (0.9)	Low
Alpe di Catenaia	22.6 (0.5)	Medium

Table 2 - Mean value of browsing ratio, top height and cover area in the different roe deer density scenarios.

Roe deer density	Browsing	Top height (cm)	cover area (m^2)
Low	0.65 (0.02)	110.0 (3.3)	1.28 (0.1)
Medium	0.77 (0.01)	88.1 (3.2)	1.18 (0.1)
High	0.79 (0.01)	90.2 (3.0)	0.99 (0.1)

Table 3 - Main mensurational parameters in protected (P) and non-protected (NP) Turkey oak coppiced areas.

Year	area	N (shoots)	dm (cm)	hm (m)	G (m^2ha^{-1})	V V (m^3ha^{-1})
2008	P	6768	3.8 (0.1)	3.5 (0.2)	8.83 (0.10)	27.61 (2.23)
	NP	3330	3.8 (0.1)	3.2 (0.3)	3.75 (0.07)	11.95 (1.27)
2013	P	6907	5.6 (0.1)	6.5 (0.2)	18.11 (0.22)	57.07 (5.12)
	NP	4826	6.0 (0.1)	6.2 (0.2)	14.23 (0.13)	33.76 (3.51)

the long term, additional data were collected from permanent monitoring plots previously established in the Alpe di Catenaia (Cutini et al. 2011), i.e., the medium density scenario. The permanent plots were located within three 1-ha stands dominated by Turkey oak, which were coppiced in 2002. Two sampling plots sized about 200 m^2 were established within each stand, one of which was fenced (protected, P), while the other was left accessible to browsing (non-protected, NP). Within each plot, we measured diameter at breast height and total height of sprouts. Volume was then estimated by applying a formula developed in a previous study for Turkey oak coppices in Tuscany (Amorini et al. 1998). We compared difference in growing stock (basal area and volume) between P and NP by two inventories made in 2008 (i.e., 6 years after coppicing) and 2013 (11 years after coppicing).

Results

The incidence of ungulate browsing was high in all the three different scenarios. The percentage of browsed sprouts ranged from 65% to 79% (Table 2). Damage was not uniformly distributed over all height classes of sprouts, but rather concentrated in those at the browsing height, i.e. between 20 and 130 cm (Figure 1). Moreover, browsing was negatively correlated with top height ($r=-0.46$, $p<0.001$) and cover area ($r=-0.35$, $p<0.001$).

ANOVA and Tukey's test indicated that browsing was significantly higher and height and cover area were significantly lower in the higher density scenario, compared with the others (Tukey's HSD test, $p < 0.05$). By contrast, medium and higher density scenarios did not exhibit significant differences in these attributes (Table 2).

Analysis of browsing impact 6 years after coppicing in Alpe di Catenaia (2008) revealed that growing stock in not-fenced areas was lower than that in fenced areas, with an average reduction in basal area and volume of -58% and -57% respectively, a consequence of the steady reduction in the number of shoots (Table 3). These differences were lower 11 years after coppicing (2013), even though browsing still reduced basal area and volume by- 21 % and -41 %, respectively (Table 3).

Discussion

The study revealed that browsing by roe deer has a significant impact on oak during the early years after coppicing. The observed browsing pressure was noticeably high even at lowest deer density, in which about two third of the sprouts were browsed. The browsing impact showed a density-dependency because significantly higher impacts were observed at medium and high density, compared with the low density scenario. Results are in agreement with previous studies, which reported a strict relationship between browsing and deer density (Chevrier et al. 2011). The negative relationship trend observed between browsing incidence and top height of sprouts further confirmed that the early years after coppicing are particularly critical, because the emerging shoots grow beneath the browsing height and are therefore exposed to sustained and prolonged impacts (Rooke et al. 2004).

On the other hand, we demonstrated that the effects of early browsing were not ephemeral but produced prolonged impacts through time; although the trend decreased between 2008 and 2013, the average reduction in volume observed eleven years after coppicing is noticeably high to heavily retard shoot growth, with relevant ecological as well as economic consequences. Based on the observed

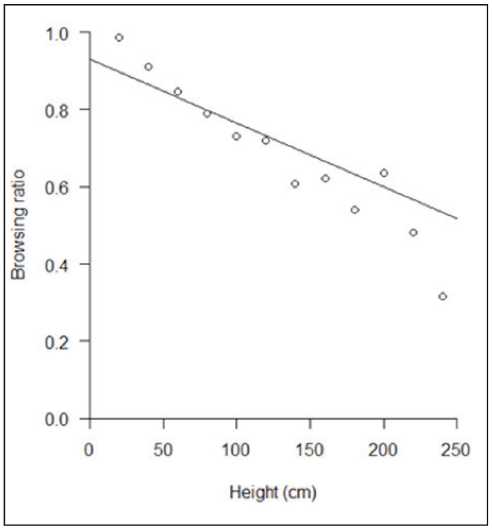

Figure 1 – Relationship between browsing ratio and top height of stools.

impacts and trends we could expect a reduction of -25% in volume at the end of the coppice rotation period, which may also imply a prolongation in the minimum rotation period (which is 18 years in Tuscany according to regional laws) to achieve a profitable harvesting, under the observed medium roe deer density.

Regardless economic considerations, both the early and long-term results indicated the browsing impacts are sustained in a range of roe deer density regarded as "normal" (ISPRA 2013) and regularly occurring in Apennines. In addition, roe deer in Italy is frequently sympatric with other deer species, e.g., fallow deer and red deer; hence, taking into account the current deer densities and their browsing pressure, we could expect that browsing intensity can seriously compromise forest dynamics in coppice woods. In these situations, the sustainable planning of ungulate densities should consider all the deer species on the whole. For example, Mattioli (2010) proposed a general ungulate density threshold based on roe-deer-equivalent conversion factors. The author individuated a maximum carrying capacity of 18 roe-deer equivalent individuals in Apennines, with red deer and fallow deer having a roe-deer-equivalent factor of 4.5 and 2.3, respectively (i.e., 1 red deer = 4.5 roe deer; 1 fallow deer = 2.3 roe deer. However, as Reimoser and Putman (2011) correctly noted, if a relationship between deer density and browsing impacts exists, the relationship is complex and not linear, making the identification of a critical ungulate density complex. Indeed, at any given deer density, sustained impact levels are affected by a wide range of other factors such as site conditions, landscape mosaic, availability and quality of alternative food resources, ungulate sympatry etc (Ward et al. 2008, Gill and Morgan 2010, Reimoser and Putman 2011). Therefore, it is important to move beyond single-factor approach (e.g., ungulate density) to embrace the complexity of fauna-forest interactions (Weisberg and Bugmann 2003). An integrated forest-fauna management is frequently advocated by many authors as an effective way to consider the interactions among ungulates and vegetation (Bianchi et al. 2014, Cutini et al. 2013, Weisberg and Bugmann 2003). To accomplish this purpose, there is a need for rapid and objective indicators to monitor the impact of roe deer on vegetation (Reimoser et al. 1999). The browsing index proposed in this study can be regarded as an useful management tool on account of its fast, simple and cost-effective procedures, it being therefore highly suitable for large scale monitoring of the effects of deer browsing on vegetative regeneration. Integrating browsing monitoring with deer density estimation can be regarded therefore as an effective option for sustainable forest-fauna management (Cutini et al. 2013), i.e., to determine whether the relationships between ungulates and forest ecosystems are consistent with meeting silvicultural and forest management targets (Keigley and Frisina 2011, Reimoser et al. 1999). We also advocate the need to collect information on deer impact over large areas because ungulate effects on forests cannot be generalized to the spatial and temporal scales that are relevant to management. Integrating information on deer impact and deer density in e.g., regional and national forest inventory alongside with the definition of rigorous and systematic long-term monitoring programs to measure the interaction forest-ungulates can be a decisive step towards the definition of appropriate protection measures in landscape and large scale planning.

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Chapter 4

Effects of forest management and roe deer impact on a mountainous forest development in the Apennines: a modeling approach using LANDIS-II

Manuscript

Effects of forest management and roe deer impact on a mountainous forest development in the Apennines: a modeling approach using LANDIS-II

Marcon A.[1], Mladenoff D.[2], Apollonio M.[1]

1 Department of Science for Nature and Environmental Resources, University of Sassari, Sassari, Italy

2 Department of Forest Ecology and Management, University of Wisconsin-Madison, Madison, Wisconsin, USA

ABSTRACT

Forest development is a complex phenomenon, that for the number of actors involved, and the response time express by forests, is difficult to understand and explore. Forest in Italy, as in several areas of Europe, are experiencing a strong control by forestry practices, and recently an increasing impact by ungulates. The effects on the forest development of this two disturbances combined are difficult to predict, and though to properly manage the environment. We used a landscape development model, LANDIS-II , to simulate forest development, and forestry and roe deer impact, for 200 years in a mountainous forest of the Apennines. We found that each disturbance alter forest development, in terms of species richness, forest types abundance distribution and forest structure. When considered combined, the two disturbances show additive behavior, enhancing or moderating each other effects. Forest harvesting seems to drive the species richness, which shows a negative trend. Forest types abundance distribution and forest structure resulted to be influenced, but it doesn’t seem that one of the disturbances is driving the change. We expected roe deer to have a negative effect on harvest yields, but it resulted significant only for two harvesting treatment. On the other hand, roe deer presence had a positive effect on biodiversity. All the simulation scenarios returned some extent of forest loss, and even if probably partially caused by model constrains, the presence in all scenarios suggest that it is not a model artifact. The amount of the forest loss is minimum in the scenario without disturbances, and maximum when both disturbances are considered. The two disturbances combined, to the extent modeled in our simulations, do not seem to be an hazard for the forest functionality in our study area. LANDIS-II resulted to be useful for identify the trends of forest development, and to help understand the dynamics that lay beyond it. We suggest it to forest and wildlife managers as a tool to help in the planning of management actions.

INTRODUCTION

Developing a better understanding of how human activities and ungulate impact interact with each other for the development of the forests, is of major concern for forest managers, game managers, conservationists and stakeholders. The pressure, often combined, of these two disturbances can affect biodiversity, natural resource sustainability and important economic interests (Reimoser & Gossow 1996, O'brien 2003, Joys, Fuller & Dolman 2004, Ward *et al.* 2004). Species composition, stand structure and landscape heterogeneity, often artificially created by forest management, can have a strong influence on shaping ungulate impact, which in turn modifies the vegetation condition of the area they live in (Reimoser & Gossow 1996, Gough & Grace 1998, Moore, Hart & Langton 1999, Kramer, Bruinderink & Prins 2006, Hurley *et al.* 2012, Gerhardt *et al.* 2013, Schippers *et al.* 2014). Human activities are the first cause of forest modification and shaping in wide areas of the world (Sanderson *et al.* 2002). Since ancient times, the need for wood and for rangelands to breed livestock, brought man to shape the extent and composition of the forest to match his needs. In the last centuries, the human population increase and its spread, had caused an even stronger effect on forest extent and composition, causing - in certain parts of the world – the development of a completely artificial forest (Hannah, Carr & Lankerani 1995, Bengtsson *et al.* 2000, Johann 2004). Wild ungulates populations had to face a rapidly changing environment, different from the one they evolved in. As long as hunting and habitat reduction kept wild ungulate populations at low densities, their effect on forest development was most likely low. In the last half-century, however, wild ungulate populations strongly increased their number, especially in Europe, North America and Japan (Coulson 1999, Kaji *et al.* 2000, Côté *et al.* 2004, Kaji *et al.* 2004, Apollonio, Andersen & Putman 2010), becoming environmental engineers able to shape forest structure and development (Hobbs 1996, Husheer, Coomes & Robertson 2003, Rooney & Waller 2003, Weisberg & Bugmann 2003, Gill & Morgan 2010). A lot of studies were devoted to the effects of ungulate populations on forests, with special reference to high densities of ungulates (Putman 2012, Chollet *et al.* 2013, Perea & Gil 2014, Shelton *et al.* 2014). These effects can vary from affecting or driving species abundance and composition, to deforestation (Kuijper *et al.* 2010, Bressette, Beck & Beauchamp 2012, Endress *et al.* 2012, Hegland, Lilleeng & Moe 2013). Those studies, however, mostly focused on the effects of ungulates, and only few of them on the development of the forests in the presence of ungulates (Jorritsma, Van Hees & Mohren 1999, Newton *et al.* 2011, White 2012). Forest development is a very complicated ecological process, in which several factors – biotic and abiotic- interact at different scales. The tools used to understand and simulate those dynamics are the ecological models. As these dynamics are so complicated and intertwined, several types of models have been developed and used in ecology (Mladenoff & Baker 1999, He, Larsen & Mladenoff 2002, Fyllas *et al.* 2007, Seidl *et al.* 2011), which focus on different aspects of the same phenomenon. In this investigation we used the LANDIS-II (LANDscape DIsturbance and Succession) model framework, which simulates the development of forested landscapes taking into account ecological processes, such as succession, seed dispersal, harvesting, and a set of biotic and abiotic disturbances (Scheller *et al.* 2007). It is ideally suited to such problems because it models multiple ecological and anthropogenic processes such that the interactions of these processes are an emergent property of the simulations (Mladenoff 2004). LANDIS-II is a process-based and spatially explicit model framework, which operates on raster maps, where every cell contains information about tree species, environment and disturbance. This software has been used to explore forest landscape dynamics in many parts of the world (He, Mladenoff & Crow 1999, Scheller & Mladenoff 2005, Scheller *et al.* 2007, Gustafson *et al.* 2010, Karam *et al.* 2013, de Bruijn *et al.* 2014), but, to our knowledge, only once considering ungulates (Newton *et al.* 2011), and it has been only occasionally used in Italy (Mairota *et al.* 2014).

The current study was performed on a mountainous region of Italian Apennine, focusing on a heavily managed forested area, including three protected areas where ungulate harvesting is banned. Four ungulate species inhabit the area, two of which are overall abundant (*Capreolus capreolus* and *Sus scrofa*). LANDIS-II has been used to simulate forest development with or without the presence of the two disturbances “Harvesting” and “Roe deer”, considered both individually and in conjunction. The other ungulate species have not been included because of limited distribution and/or limited knowledge of their effect on the ecology of the forest in the area. The analysis of the model output examined the impact of the different disturbances on forest structure, composition, species richness and extent. While the outputs of the model simulation cannot be taken as a precise prediction of the forest development, they can be used to understand interactions between disturbances, and to identify the ecological trends that would emerge from those interactions. The questions searched in the present study are:

i) are the two disturbances interacting?

ii) is one of the two disturbances leading the shaping of forest development?

iii) can analyses of disturbance regimes, performed through process modeling, help in the development of management policies?

METHODS

Study area

The study has been performed in the Casentino valley, in Arezzo Province, Tuscany, Italy (Fig.1). The study area is located in a mountainous region of the northern Apennines, and its altitude ranges from 200m to 1655m a.s.l.. The climate is continental, characterized by hot and dry summers and cold and rainy winters, with a high humidity rate. Due to the wide altitude range covered, mean temperatures can vary a lot between the mountain tops and the valleys. The mean January and July temperatures are reported for both highest and lowest areas, respectively: January 1.3°C and 4.2°C; July 19.3°C and 22.5°C. The mean annual precipitation ranged, in the last 12 years (2000-2012), from 900 mm to 1500 mm. The area is 82614 ha wide, 67.6% of it is covered by forest, while urban areas cover only 1% of the surface. Agricultural lands represent a small percentage of the area and are mostly found close to urban areas, at the lowest altitudes. The study area intersects three protected areas, a national park and two protected areas: Foreste Casentinesi National Park (13845 ha – only the extent that overlaps the study area), Pratomagno OAF (5379 ha) and Alpe di Catenaia OAF (2760 ha). Until the mid ‘60s of the past century, this area was heavily used by local residents, mostly with agricultural and livestock production purposes, and forest was present only at the highest altitudes. After the end of WW2, the population moved towards lowlands and cities, and the land use in the study area shifted towards forestry. Nowadays, almost the totality of the forest in the study area is managed, mostly as coppice. Other management techniques applied are selection cutting and thinning, mostly in the protected areas. At the lowest altitudes, broadleaves monoculture patches dominate the landscape, and at mid-altitudes some conifers patches, coming from artificial afforestation, are present. At the highest altitudes, the forest is composed by semi-natural beech monocultures. The most abundant broadleaves species are oaks (*Quercus* spp.), beech (*Fagus sylvatica*), chestnut (*Castanea sativa*), and hornbeam (*Ostrya carpinifolia*), while for conifers are white fir (*Abies alba*), black pine (*Pinus nigra*), Douglas fir (*Pseudotsuga menziesii*), and maritime pine (*Pinus pinaster*)(Fig.2). Four ungulate species are present in the study area: roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), fallow deer (*Dama dama*), and red deer (*Cervus elaphus*). Roe deer and wild boar are present in the whole study area, while red deer and fallow deer are sparsely distributed in high-density but localized areas. Two predators are present in the area, wolf (*Canis lupus*) and red fox (*Vulpes vulpes*).

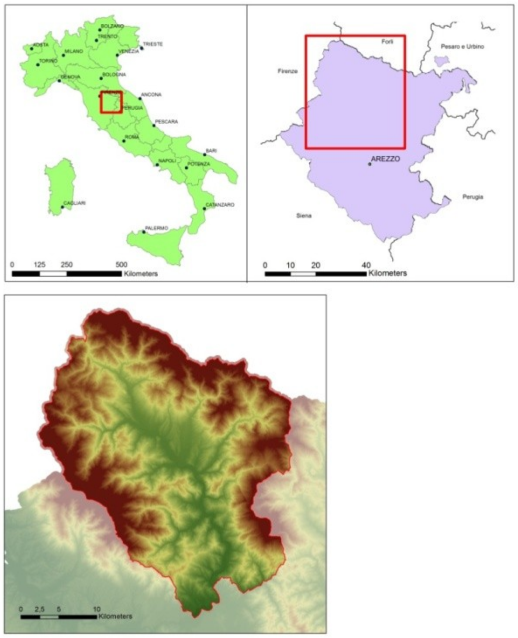

Figure 1 Study area, Casentino valley, in Arezzo province, Tuscany, Italy.

Model description

LANDIS-II is a software that models the development of a forested landscape on wide spatial and temporal scales. The model is spatially explicit and raster-based (i.e. the landscape is represented by a grid), and it's used to simulate the ecological dynamics involved in landscape development, by modeling processes such as forest succession and disturbances. There are several extensions that can be used to model the latter, from harvesting to windthrow to biological disturbances. The software allows the user to choose between different level of modeling complexity, based on the starting data and the research questions. A detailed description of the LANDIS-II model framework can be found in the literature (Mladenoff 2004, Scheller & Mladenoff 2004, Scheller *et al.* 2007). We choose to model forest development for 200 years, with a 3 year time step. For our study we choose to use the Age Only Succession v.3.0 extension, which models the tree species as presence or absence of species, and their age cohorts, inside each cell of the grid that represents the study area. To model forest management and roe deer impact we use the Base Harvest v.2.2 extension (Gustafson *et al.* 2000). We defined 4 different scenarios, to compare the effects of disturbances on forest development and composition. The scenarios are: *No Disturbance*, *Harvesting*, *Roe Deer*, and *Harvesting & Roe Deer* combined. All spatial elaborations have been performed with ArcGIS v.10 (ESRI) and all statistical elaborations and analysis with R v.3.0 (R Core Team 2014).

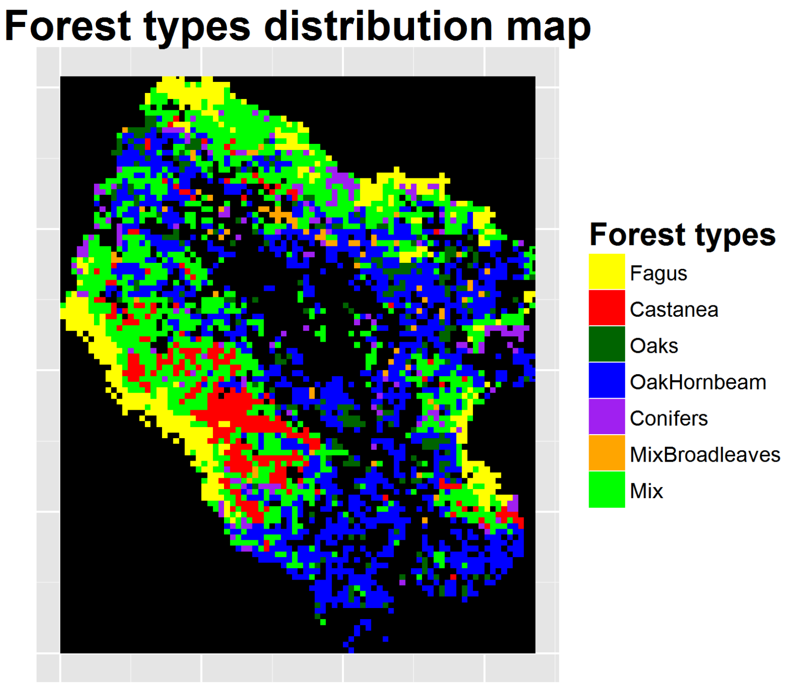

Figure 2 Spatial distribution of major forest types in the study area at the beginning of the simulation.

Datasets

Species assemblages and dominance have been extracted from a regional dataset (Tuscan Forest Survey, *Inventario Forestale Toscano,* IFT, Regione Toscana, 1998). From this grid-structured dataset, with 400m sided cells, we extracted data about the canopy cover of the cell (as percentage), and the three most abundant tree species ranked in order of abundance. Tree species physiological data have been collected from literature (Grime, Hodgson & Hunt 1988, Burns & Honkala 1990, Brzeziecki & Kienast 1994, Bugmann 1994, Bernetti 1995, Verdú 2002, Diaz *et al.* 2004, Ordóñez García & Alumbreros 2004, Lischke *et al.* 2006, Niinemets & Valladares 2006, Schumacher *et al.* 2006, Vittoz & Engler 2007, Fernandes *et al.* 2008, Paula *et al.* 2009, Henne *et al.* 2013) and extracted from TRY database (the TRY initiative: Kattge *et al.* 2011). Soil composition data and soil water content have been extracted from the pedological dataset of the watershed of the Arno river. Climatic data have been extrapolated from data sets granted by Corpo Forestale dello Stato (Pratovecchio and Pieve Santo Stefano stations). Ungulate distribution data have been collected by Arezzo section of URCA (Apennine hunting association) and granted by Wildlife and Hunting Department of Arezzo Province. Roe deer impact data have been extracted from literature, from studies conducted in the same area (Cutini *et al.* 2009, Cutini *et al.* 2011, Chianucci *et al.* 2015).

Input data

Initial communities map

Our original tree species dataset was too coarse for the extent of our study area (400m sided cells), so we halved the cell side, obtaining four times the number of cells in the area. The data contained in each of the four new cells, were copied directly from the original cell. The downscale didn't improve the initial dataset precision but was performed to obtain higher resolution results. We use the canopy cover data in the IFT to exclude from the analysis and modeling the cells that were not forested (overall canopy cover <5%). To select the tree species for the modeling, we used the presence data for each species, weighted for the rank they have in each cell, to calculate an index of abundance. Calculating the cumulative percentage of tree species abundance, we found that 9 species account for more than 97% of the overall forest cover. We add to those 9 species other 3, *Acer pseudoplatanus*, *Fraxinus ornus* and *Robinia pseudoacacia*, the formers because highly preferred by ungulates and the latter because it's an alien species considered a pest. The list of the 12 tree species we used can be seen in table 1.

Species	Long evity	Sexual Maturity	Shade Tol.	Fire Tol.	Seed dispersal distance		Vegetative reprod. prob.	Min sprout age	Max sprout age	Post-fire Regen.
					Effective	Max.				
Abies	300	70	4	3	50	160	0	0	0	None
Acer	300	15	4	2	100	300	0.8	1	100	Resprout
Castanea	600	15	3	2	20	30	0.9	1	600	Resprout
Fagus	300	60	5	2	25	50	0.75	1	100	Resprout
Fraxinus	200	20	3	2	50	140	0.8	1	80	Resprout
Ostrya	150	30	4	2	80	180	0.8	1	100	Resprout
Pinus_nig	300	30	2	3	40	100	0	0	0	None
Pinus_pin	200	15	1	4	40	300	0	0	0	None
Pseudotsuga	700	20	3	5	100	250	0	0	0	None
Quercus_cer	350	40	2	3	20	40	0.9	1	80	Resprout
Quercus_pub	350	50	2	3	20	40	0.75	1	80	Resprout
Robinia	100	15	2	1	30	120	0.9	1	100	Resprout

Table 1 Life traits parameters for the selected species. Shown values are: Longevity (years), Sexual Maturity age (years), Shade Tolerance (ranked increasingly from 1 to 5), Fire Tolerance (ranked increasingly from 1 to 5), Effective and Maximum seed dispersal distance (meters), Probability of Vegetative Reproduction, Minimum and Maximum re-sprout age (years), type of Post Fire Regeneration (Seronoty, Resprout or None).

We use the information about the ranking of the three most abundant species inside each cell to extrapolate the most representative species assemblages (forest types), with an abundance driven method. Tree species age data have been extrapolated from the Forestry Management Plans produced by Casentino Municipality Union, the institution that manage the regional owned forests. For each species of our cells, we assigned the age recorded for the closest parcel to our cell that contains that particular species, in the Forestry Management Plan.

Ecoregions map

The model also requires an ecoregion map, a raster map that identifies ecologically homogenous regions in the study area. Ecologically homogenous here refers to those ecological conditions that influence tree species establishment. To identify the ecologically homogenous regions we used a clustering technique on a dataset containing 6 variables: altitude, available water content, soil pH in the firsts 50 cm, PAR (Photosynthetic Active Radiation), organic matter content in the firsts 50 cm, and average annual precipitations. We apply a PAM clustering method (Partitioning Around Medoids, Kaufman & Rousseeuw 1990, package cluster: Maechler, Rousseeuw & Struyf 2015), with several different *k* parameters. Then we assessed the most reliable value for *k* through bootstrapping and then calculating the mean Jaccard index for each cluster of each *k* value (Jaccard 1901). The highest *k* values with all clusters having a mean Jaccard index value higher than 0.75 has been chosen. That analysis led to 5 clusters, which in turn led to 5 ecoregions. LANDIS-II requires a probability of establishment value for each species in each ecoregion. To calculate those values we used the software PnET-II for LANDIS-II (Aber *et al.* 1995, Xu, Gertner & Scheller 2009).

Species	Ecoregions 1	2	3	4	5
Abies alba	0.5	0.7	0.5	0.3	0.1
Acer pseudoplatanus	0.5	0.7	0.7	0.4	0.2
Castanea sativa	0.1	0.6	0.6	0.2	0.1
Fagus sylvatica	0.9	0.7	0.5	0.2	0.1
Fraxinus ornus	0.1	0.4	0.7	0.7	0.6
Ostrya carpinifolia	0.1	0.7	0.7	0.7	0.7
Pinus nigra	0.1	0.4	0.6	0.4	0.1
Pinus pinaster	0.1	0.2	0.3	0.4	0.6
Pseudotsuga menziesii	0.1	0.7	0.6	0.2	0.1
Quercus cerris	0.1	0.8	0.7	0.4	0.1
Quercus pubescens	0.1	0.2	0.4	0.6	0.9
Robinia pseudoacacia	0.1	0.7	0.7	0.7	0.7

Table 2 Establishment probabilities of each species for the 5 ecoregions considered.

This software uses ecological characteristics of a region and some physiological parameters of the tree species to calculate the probability of the species to establish in that region. We use the medoids of our clusters as ecological data representative of each ecoregion, and calculate the monthly mean data for temperature, precipitation and PAR, starting from a 20 years-long daily raw dataset for temperature and precipitation, and GIS elaborations on a DEM file for PAR data. As PnET-II for LANDIS-II is a model developed for the eastern U.S., we ask the forest manager of our study area to check the establishment probabilities for our species. They slightly modified some of the values, for a better representation of the local situation. The establishment probability values can be found in table 2.

Harvesting prescriptions

The Base Harvest extension needs a Management Areas map, a raster map that identifies areas on which the same set of harvesting prescriptions are applied (Fig.3). Management areas have been extrapolated from the parcel map of the study area. Each parcel contains information about the species presence, the prevalent age and the type of management applied. The most widely applied management method is coppice, especially by private owners, while in region or state owned forests, thinning and selection cutting prescriptions are applied

(Fig.3). Based on that, we divided our study area in three management areas: coppice management area, selection management area (with selection cutting and thinning prescriptions), and no-prescriptions management area, were no management prescriptions were applied. We defined several prescriptions, to simulate the forest management practice. Those prescriptions target certain age cohorts of certain species, on the basis of the type of management practice they simulate. The harvesting prescriptions have been defined and calibrated to simulate a static application of current forest management prescriptions, and to fulfill the present forest management objectives. A list of the prescriptions applied can be found in table 3.

Prescription	Target species	Target age cohorts	Management area	Target area (%)
Quercus Coppice (planting oaks)	*Quercus cerris* *Quercus pubescens*	20-40 20-40	Coppice	4.3%
Castanea coppice	*Castanea sativa*	20-40	Coppice	1.7%
Broadleaves coppice	*Ostrya carpinifolia* *Fagus sylvatica*	20-40 20-40	Coppice	1.3%
Conifers reduction	*Abies alba* *Pinus nigra* *Pseudotsuga menziesii*	All All All	Coppice	5%
Thinning	*Castanea sativa* *Fagus sylvatica* *Ostrya carpinifolia* *Quercus cerris* *Quercus pubescens* *Pseudotsuga menziesii*	40-50 40-90 40-60 40-80 40-90 All	Selection	1%
Selection cutting	*Castanea sativa* *Fagus sylvatica* *Ostrya carpinifolia* *Quercus cerris* *Quercus pubescens* *Pseudotsuga menziesii*	50-100 90-140 60-150 80-200 90-200 All	Selection	1%
Conifers eradication	*Abies alba* *Pinus nigra* *Pseudotsuga menziesii*	All All All	Selection	0.9%
Roe deer	*Castanea sativa* *Fagus sylvatica* *Quercus cerris* *Quercus pubescens* *Abies alba* *Acer pseudoplatanus* *Fraxinus ornus*	1-3 1-3 1-6 1-6 1-6 1-6 1-6	All Management Areas	100%

Table 3 List of prescriptions applied in *Harvesting* and *Harvesting & Roe Deer* scenarios.

The same extension has been used to model roe deer impact on forest development. Data about roe deer impact have been extracted from existing literature (Cutini *et al.* 2009, Cutini *et al.* 2011, Chianucci *et al.* 2015). The prescription that models roe deer impact targets the youngest age cohorts of its preferred tree species. Base Harvest v.2.2 prescriptions work removing completely the targeted species' age cohorts, so we have to model roe deer impact as it completely removes some age cohorts of its preferred species. The target age cohorts of that prescription are the youngest, from 0 to 6 years for the most affected species, and from 0 to 3 years for the least preferred species (Tab.3). Being the roe deer present in the whole study area, this prescription is applied to the 100% of the area. Base Harvest v.2.2 extension does not allow multiple prescriptions to be applied in a single cell at the same timestep. This makes sense for management prescriptions, but it is a theoretical error if we consider roe deer prescription, i.e. cutting old pines does not prevent roe deer to feed on young oaks in the same area. To get around this problem we added the roe deer effect to all the other prescriptions, so when a certain prescription is applied, it automatically implies the application of roe deer impact on the same cells.

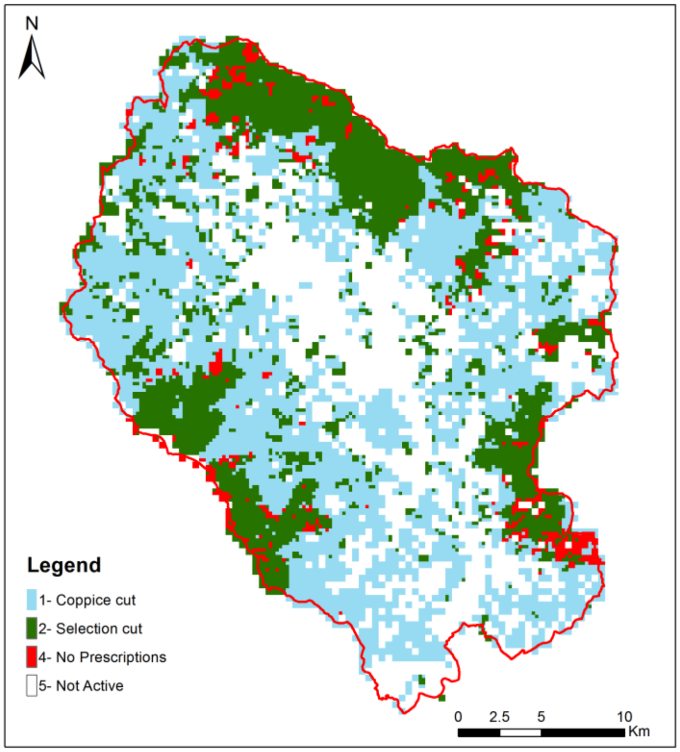

Figure 3 Spatial distribution of management areas

Model Outputs

Output Cohort Statistics v.2.1 extension has been used to produce output of maximum age across all species in each cell, species presence/absence for each cell, and total number of tree species in each cell. Through Output Age Reclass v.2.0 extension, we reclassified the raw data about species presence in each cell into forest types. This extension consider both species presence and dominance to classify a cell into user-determined groups, representing ecologically meaningful species assemblages for the area (Tab.4). Base Harvest v.2.2 extension produce a table which shows, for each time step, how many cells were targeted by each prescription applied in that scenario, grouped by management area. LANDIS-II outputs consist of raster maps produced at a user-defined time step, each map containing one of the selected output information. We used a 20 years timestep for output maps production. The maximum age across all species in each cell has been used to examine forest structure: ages have been binned in 40 years wide bins (<40 years, 40-80 years,… , >200 years) for clarity purpose, and then the proportion of cells falling into each bin has been calculated. To better understand the regeneration dynamics, we made a second step analysis only on those cells which maximum age was lower than 100 years. Species presence/absence maps have been used to calculate the abundance for each species, expressed as the percentage of all active cells which contains that particular species. Species richness has been analyzed by calculating the number of cells that contains a certain number of species (range 1-5) at the end of the simulation (i.e. at year 200). The percentage cover of each forest type across the landscape has been calculated as the percentage of active cells that contains that forest type, for each output time step. The Base Harvest tables have been used to quantify the harvested extent for each prescription, allowing us to evaluate the differences in harvesting extent when roe deer was considered. Being the roe deer impact simulated as a prescription too, the same table allowed us to evaluate the extent of the area affected by roe deer, and the differences in impact between management areas. We compared the extent of the forested area at the beginning and at the end of the simulations, to check for forest loss.

Data Analysis

The chi-square test has been used to test the differences of forest structure and species richness between all the scenarios. When considering scenarios with harvesting management areas, we used the chi-squared test to check for the significance of differences between forest structures of each management area. Friedman's test and its post-hoc tests have been used to test the significance of the differences for most of the other output analyzed, as our data were neither normal nor homoscedastic. We used it to test i) differences in abundance of forest types between scenarios, ii) changes in harvesting extent with and without considering roe deer impact, iii) different roe deer impact on different management areas, and iv) differences in species abundance with and without considering roe deer presence.

RESULTS

No disturbance scenario

At the end of our simulation, the *No disturbance* scenario is dominated by the OakHornbeam forest type (Tab.5, Fig.4), followed by Mix, MixBroadleaves and Fagus forest types. The remaining forest types cover around 6% of the forest area all together. At the beginning of the simulation, OakHornbeam was the most abundant forest type, and it remained more or less stable throughout the simulation (Fig.4). Mixforest type had a sharp decline in abundance, especially in the last 50 years, while on the other hand Fagus and MixBroadleaves showed a constant increase. The other forest types showed a constant decrease, but overall with a smaller magnitude (Fig.4). The forest structure at the end of the simulation is markedly unbalanced towards older age classes (Fig.5). The cells with maximum age over 160 years represent the 94% of the whole study area, while the younger classes cover the remaining 6% (Tab.5). Looking at the per-cell species richness, there’s a clear prevalence of cells containing 3 species (40.1%), while the rest of the area is mostly composed in equal parts by cells with 1 or 2 species (Fig.9). It’s worth noting the presence of cells containing 4 or 5 different species, although in a small percentage (Tab.10).

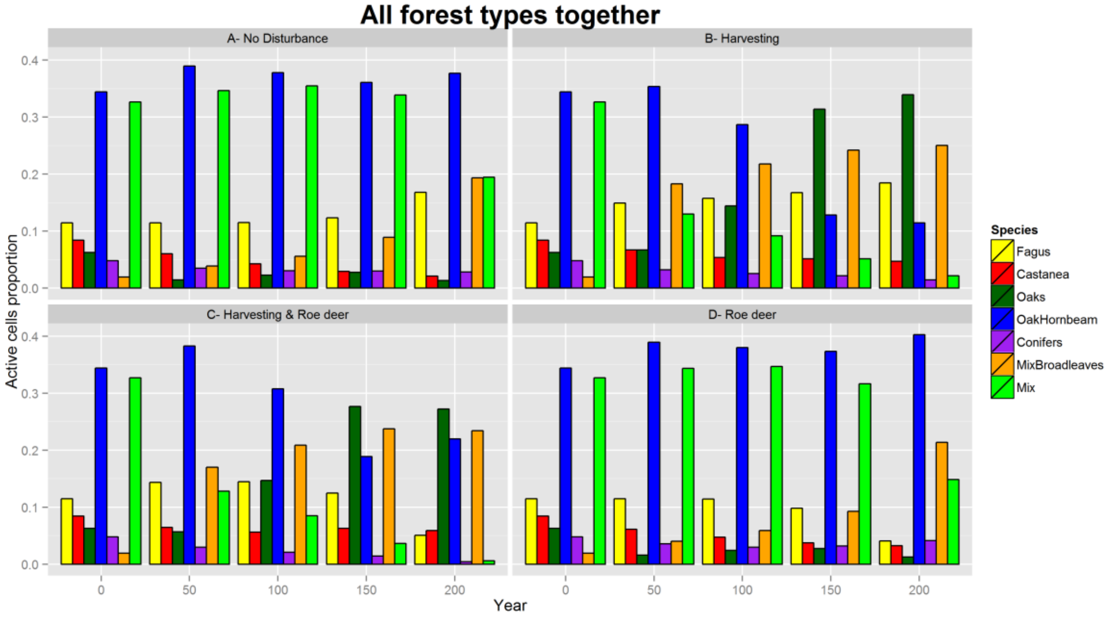

Figure 4 Proportions of Major Forest Types between different scenarios, at 50-years steps.

Forest Type	Species assemblage
Fagus	*Fagus sylvatica*
Castanea	*Castanea sativa*
Oaks	*Quercus cerris, Quercus pubescens*
OakHornbeam	*Quercus cerris, Quercus pubescens, Ostrya carpinifolia*
Conifers	*Abies alba, Pinus nigra, Pinus pinaster, Pseudotsuga menziesii*
MixBroadleaves	*Fagus sylvatica, Castanea sativa, Quercus cerris, Quercus pubescens, Ostrya carpinifolia*
Mix	*Fagus sylvatica, Castanea sativa, Quercus cerris, Quercus pubescens, Ostrya carpinifolia, Abies alba, Pinus nigra, Pinus pinaster, Pseudotsuga menziesii*

Table 4 Species assemblages used to create forest types.

Harvesting scenario

The most abundant forest types at the end of the *Harvesting* scenario simulation were Oaks, MixBroadleaves and Fagus (Tab.5, Fig.4). All of them showed a constant increasing trend throughout the simulation, ending up to represent the 34.7%, 25.6%, and 18.9% of the forested study area respectively. The other forest types showed a constant decreasing trend (Fig.4). The Friedman's test and the post-hoc tests returned the difference of forest types abundance between the two scenarios as significant, for all the forest types (Tab.14). The forest structure produced by the *Harvesting* scenario simulation is shifted to younger ages, if compared to the *No Disturbance* scenario (Fig.5). Cells with maximum age above 160 years old comprise 84.1% of the study area, this clear shift respect to *No Disturbance* scenario is mostly due to the ">200 years" class. All the other age classes show an increase respect to *No Disturbance* scenario, especially the class "120-160 years" (Tab.6). The difference in forest structure between the two scenarios resulted to be statistically significant ($\chi^2_{(5,N=\ 12)}$= 8089.8, p< 2.2 e-16). Due to the application of different prescriptions, different management areas resulted to have different forest structures. Coppice management area has an age structure shifted towards older ages, while Selection management area shows a more balanced distribution (Fig.7, Tab.8). In No Prescription management area, almost all the cells have a maximum age above 160 years. The differences in age distribution between management areas resulted all to be significative (Coppice *vs* Selection: $\chi^2_{(5,N=\ 12)}$= 5132.4, p< 2.2 e-16; Coppice *vs* No Prescription: $\chi^2_{(5,N=\ 12)}$= 45, p= 1.49e-8; Selection *vs* No Prescription: $\chi^2_{(5,N=\ 12)}$= 258.5, p< 2.2 e-16). The species richness in this scenario resulted to be the lowest between all scenario, with the highest percentage of cells containing a single species (31.3%), and a general shift towards lower values of per-cell species richness (Tab.10). The difference with the *No Disturbance* scenario is statistically significant ($\chi^2_{(3,N=\ 8)}$= 7669.1, p< 2.2 e-16).

Scenarios	Fagus	Castanea	Oaks	Oak-Hornbeam	Conifers	Mix-Broadleaves	Mix
No Disturbance	16.9	2.1	1.3	37.8	2.8	19.4	19.5
Harvesting	18.9	4.8	34.7	11.7	1.5	25.6	2.2
Harvesting & Roe deer	6.0	6.9	32.1	25.9	0.5	27.6	0.7
Roe deer	4.6	3.6	1.4	45.1	4.6	23.9	16.6

Table 5 Percentages of study area coverage, by major forest type and scenario.

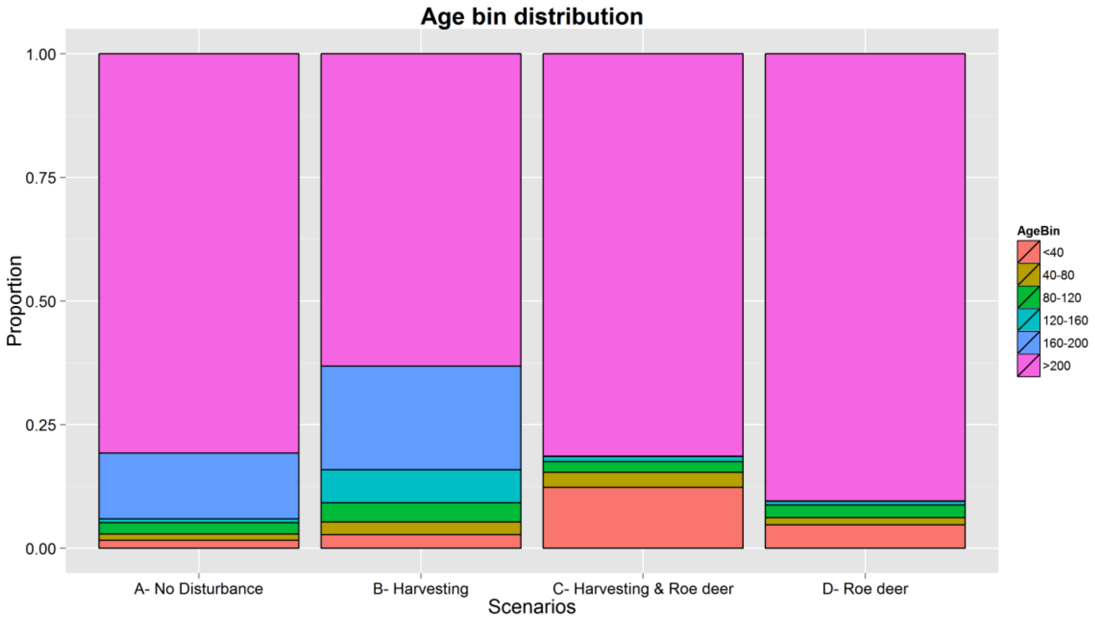

Figure 5 Proportion of age bin distribution between scenarios.

Roe deer scenario

OakHornbeam forest type resulted to be the most abundant throughout the *Roe deer* simulation, followed by MixBroadleaves and Mix forest types (Fig.4, Tab.5). These three forest types cover the 45.1%, 23.9%, and 16.6% of the forested study area respectively. Conifers forest type seems to remain quite stable along the simulation, while the other forest types have decreasing trends, especially Fagus and Castanea (Fig.4). The forest types abundance distribution in *Roe deer* scenario differs significantly from the *No Disturbance* scenario's one, except for forest type Oaks and Conifers (Tab.14). The forest structure at the end of the *Roe deer* simulation is markedly shifted towards older ages, as cells with maximum age over 200 years comprise 90.4% of the forested study area (Fig.5, Tab.6).

Scenarios	<40	40-80	80-120	120-160	160-200	>200
No Disturbance	1.6	1.3	2.2	0.8	13.3	80.8
Harvesting	2.8	2.6	3.9	6.7	20.9	63.2
Harvesting & Roe deer	12.3	3.0	2.2	1.0	0.0	81.4
Roe deer	4.8	1.4	2.6	0.7	0.1	90.4

Table 6 Percentages of study area coverage, by age bins and scenario.

The second most abundant age class is "<40 years", which includes 4.8% of the forested study area. The forest structure of this scenario resulted to be significantly different from the one of *No Disturbance* scenario simulation ($\chi^2_{(5,N=12)}$= 2191.0, p< 2.2 e-16). The per-cell species richness in *Roe deer* scenario resulted to be the highest amongst our simulations, even thou there are no cells containing 5 different species (Tab.10). Even if the distribution of the per-cell species seems to be similar between this scenario and the *No Disturbance* scenario, the chi-squared test confirmed the significance of the difference ($\chi^2_{(3,N=8)}$= 300.2, p< 2.2 e-16).

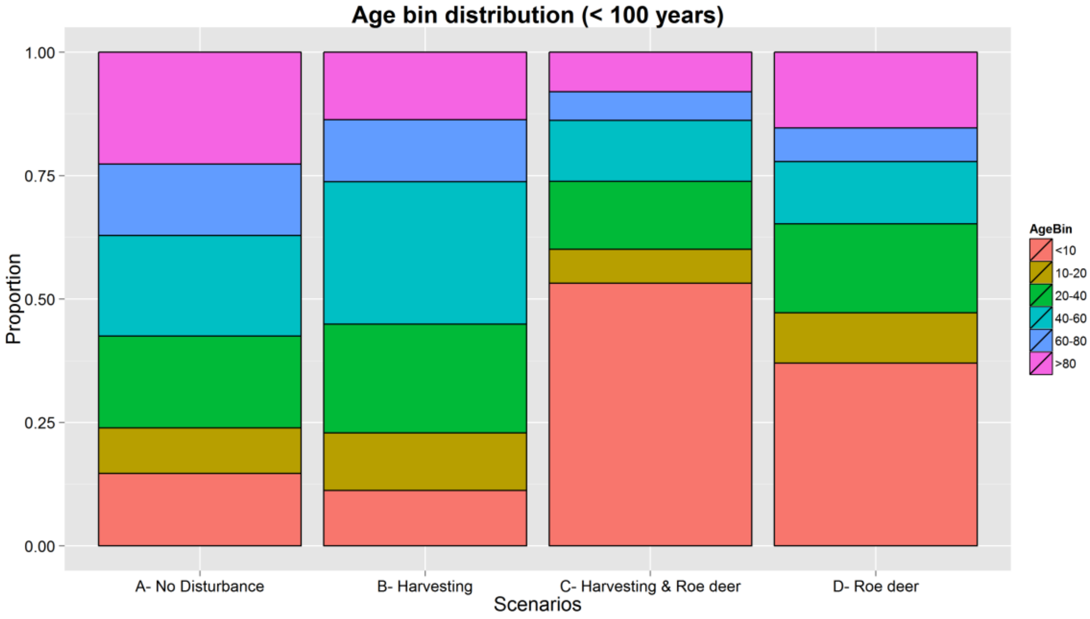

Figure 6 Proportion of age bin (less than 100 years) distribution between scenarios.

Harvesting & Roe deer scenario

At the end of the simulation of the scenario that considers both disturbances, the most abundant forest types are Oaks, MixBroadleaves, and OakHornbeams, respectively covering 32.1%,27.6%, and 25.9% of the forested study area (Fig.4, Tab.5). The others forest types represent very low percentages of the study area. Except for Oaks and MixBroadleaves, which had an increasing trend, and Castanea, which remained quite stable, all the other forest types had decreasing trends. Even OakHornbeam, in spite of being one of the most abundant at the end of the simulation (Fig.4). The forest types' abundance distribution is significantly different from the one of the *No Disturbance* scenario, even if for Fagus we're at the significance limit (Tab.14). The difference resulted significant even for the comparison with *Roe deer* scenario, for all forest types (Tab.14). On the other hand, in the comparison with *Harvesting* scenario, Castanea and Oaks distributions did not result to be significantly different (Tab.14).

Scenarios	<10	10-20	20-40	40-60	60-80	>80
No Disturbance	14.6	9.3	18.6	20.4	14.5	22.7
Harvesting	11.2	11.7	22.0	28.8	12.6	13.7
Harvesting & Roe deer	53.2	6.9	13.7	12.4	5.8	8.0
Roe deer	37.0	10.2	18.0	12.6	6.8	15.4

Table 7 Percentages of study area coverage, by age bins and scenario, for cells with maximum age lower than 100 years.

The forest structure is showing a prevalence of older age trees, as cells with maximum age above 200 years covers the 81.4% of the study area. On the other hand, this scenario has the highest percentage of cells which maximum age is below 40 years, 12.3%. The other four age classes represent minor percentages of the study area (Tab.6). The difference between the age structure of this scenario, compared with *No Disturbance* scenario, resulted to be statistically significant ($\chi^2_{(5,N=\ 12)}$= 11058, p< 2.2 e-16). Moreover, the age structure resulted to be significantly different from the ones of the scenarios considering only one of the two disturbances considered in the current one, harvesting and roe deer impact. The chi-squared tests conducted both returned significative results, $\chi^2_{(5,N=\ 12)}$= 8173.6, p< 2.2 e-16 against *Harvesting* scenario's age structure, and $\chi^2_{(5,N=\ 12)}$= 906.9, p< 2.2 e-16 against *Roe deer* scenario's age structure.

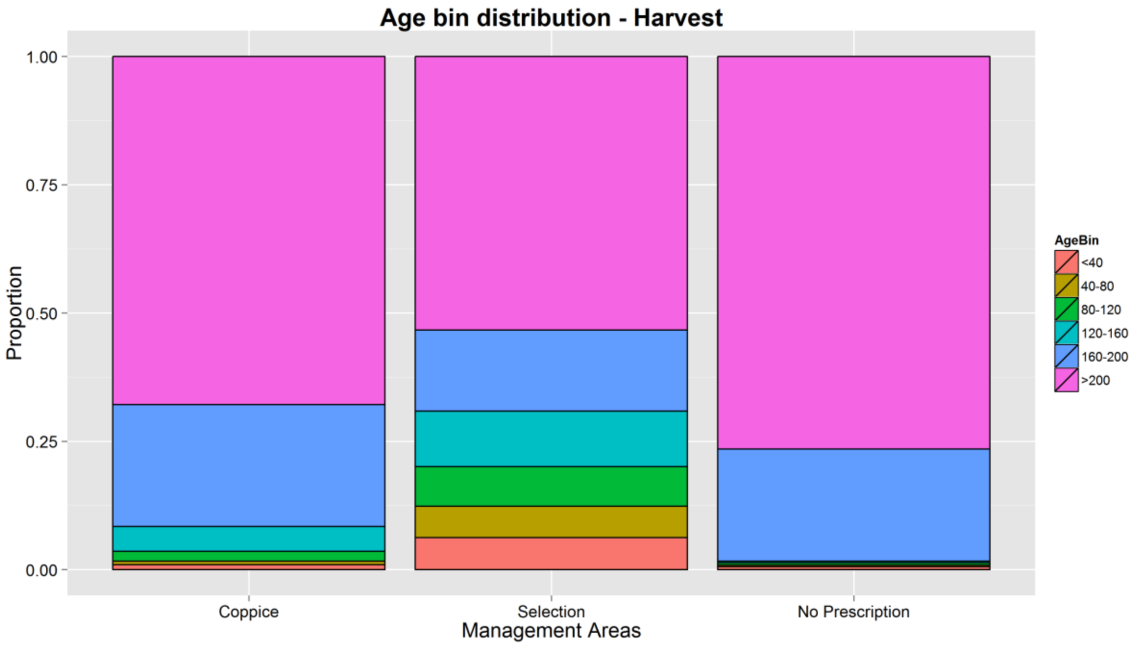

Figure 7 Proportion of age bin distribution between Management Area, relative to *Harvesting* scenario.

The application of harvesting prescriptions caused a difference in forest age structure between management areas (Fig.7). Selection management area resulted to have a higher percentage of young forest, as 27% of cells have a maximum age lower than 120 years (Tab.8). Coppice and No Prescription management areas have a quite similar age structure, markedly shifted towards older ages, as the ">200" age class includes at least 85% of the cells. Nevertheless, the chi-squared tests returned the differences as significant, for all the management areas: $\chi^2_{(4,N=\ 10)}$= 514.3, p=1.96e-10 for Coppice against No Prescription, $\chi^2_{(4,N=\ 14)}$= 4902.1, p< 2.2 e-16 for Selection against Coppice, and $\chi^2_{(4,N=\ 10)}$= 166.4, p< 2.2 e-16 for Selection against No Prescription.

Management Area	<40	40-80	80-120	120-160	160-200	>200
Coppice	1.0	0.7	1.9	4.9	23.7	67.8
Selection	6.3	6.1	7.7	10.8	15.8	53.3
No Prescription	0.6	0.3	0.5	0.3	21.8	76.5

Table 8 Percentages of study area coverage, by Management Areas' age structure, relative to *Harvesting* scenario.

In the current scenario, the per-cell species richness is shifted towards lower values, with the highest percentage falling in the "2 species" class. The remaining percentage is almost equally divided between the "1 species" and the

"3 species" classes (Tab.10). The distribution of species richness resulted to be significantly different from the ones of the other scenarios, the chi-squared test results are $\chi^2_{(3,N=8)} = 6051.3$, $p < 2.2$ e-16 against *No Disturbance* scenario, $\chi^2_{(3,N=8)} = 346.0$, $p < 2.2$ e-16 against *Harvesting* scenario, and $\chi^2_{(3,N=8)} = 27385$, $p < 2.2$ e-16 against *Roe deer* scenario.

Management Area	<40	40-80	80-120	120-160	160-200	>200
Coppice	12.6	0.9	0.5	0.4	0.0	85.6
Selection	13.2	8.1	5.9	2.6	0.0	70.1
No Prescription	2.4	0.4	0.8	0.2	0.0	96.3

Table 9 Percentages of study area coverage, by Management Areas' age structure, relative to *Harvesting & Roe deer* scenario.

Roe deer presence effects

Effect on Harvest Extent

We applied the Friedman's test, and its post-hoc tests, to the harvesting extent data from the two scenarios considering harvesting, to test for the significance of the differences in harvesting yield due to the presence of roe deer. The tests have been run for each management area. Only two tests, for CastaneaCoppice and ConifersReduction prescriptions in Coppice management area, reported significant results (p=1,25e-07 and p=7.5e-05 respectively). QuercusCoppice prescription in Coppice management area reported results are at the significance limit, p=0.058. All the other tests run for the other prescriptions, in all management areas, reported non-significant results (Tab.15).

Impact per Management Areas

Simulated roe deer impact depends on species and age-cohort presence, so we supposed it would differ between management areas. To test those differences, we used the Friedman's test, and its post-hoc tests, on the roe deer impact data of *Harvesting & Roe deer* scenario. The impact, expressed as proportion of management area affected, resulted to be highest on Coppice management area, followed by No Prescription and Selection management area (Fig.10). Those differences resulted all to be statistically significant, as returned by the post-hoc tests: p=0 for Coppice against Selection, p=1.38e-08 for Coppice against No Prescription, and p=5.66e-08 for Selection against No Prescription.

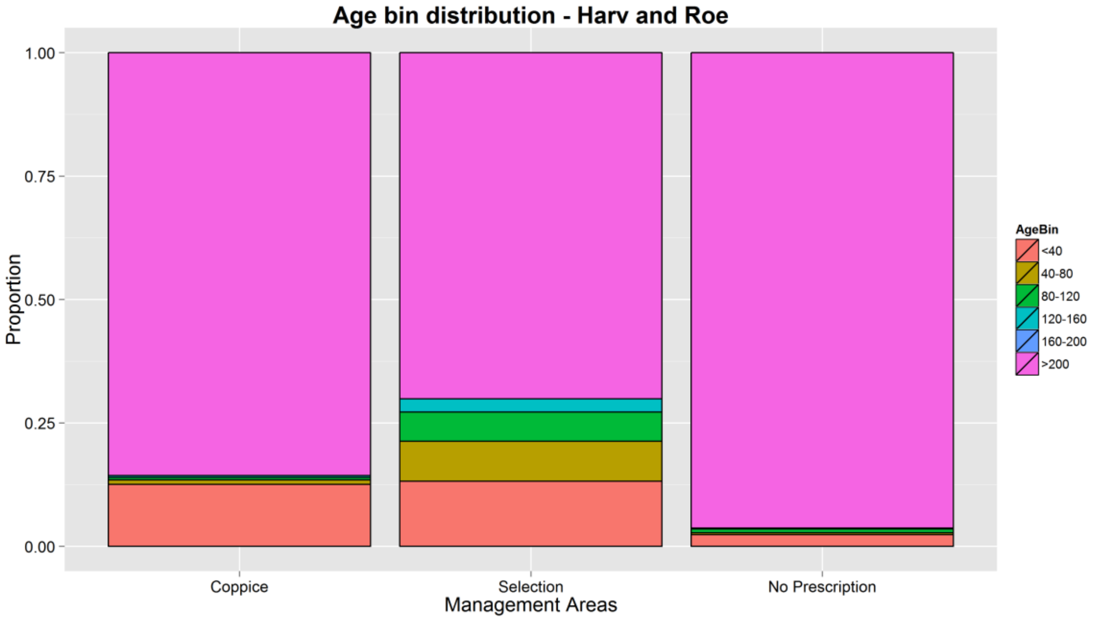

Figure 8 Proportion of age bin distribution between Management Area, relative to *Harvesting & Roe deer* scenario.

Effect on species abundance

The comparisons have been conducted between *No Disturbance* scenario's and *Roe Deer* scenario's data about species abundances. Five species out of the 12 considered are not significantly affected by roe deer presence: three of those species are considered not palatable in the simulation (*Pinus nigra*, *Pinus pinaster*, and *Robinia pseudoacacia*), while the other two are, (*Castanea sativa* and *Quercus cerris*; Tab.11). The latter has a p value on the significance limit: p=0.058. Most of the palatable species have a decreasing trend in *Roe Deer* scenario, if compared to *No Disturbance* scenario: *Abies alba, Acer pseudoplatanus*, *Fagus sylvatica*, and *Fraxinus ornus*. Two species show increasing trends (*Ostrya carpinifolia* and *Pseudotsuga menziesii*), while the remaining show a quite stable trend (Fig.11). *Quercus pubescens* seems to be an interesting case, as its trend looks stable, while the difference between scenarios results to be statistically significant, p=0.025 (Tab.11).

Scenarios	1 Spp	2 Spp	3 Spp	4 Spp	5 Spp
No Disturbance	25.6	26.0	40.1	8.1	0.2
Harvesting	31.3	53.2	15.0	0.4	0.0
Harvesting & Roe deer	25.7	54.1	20.0	0.3	0.0
Roe deer	19.7	28.7	44.5	7.1	0.0

Table 10 Percentages of study area coverage, by per-cell species richness and scenario.

Forest structure <100 years old

The age structure of the forest younger than 100 years is quite homogenously distributed between age classes for both *No Disturbance* and *Harvesting* scenarios (Tab.7). When roe deer is considered, there is a clear shift towards younger age classes (Fig.6). The youngest age class (<10 years) comprise up to 53.2% of the young forest in *Harvesting & Roe deer* scenario, and up to 37% in *Roe Deer* scenario (Tab.7).

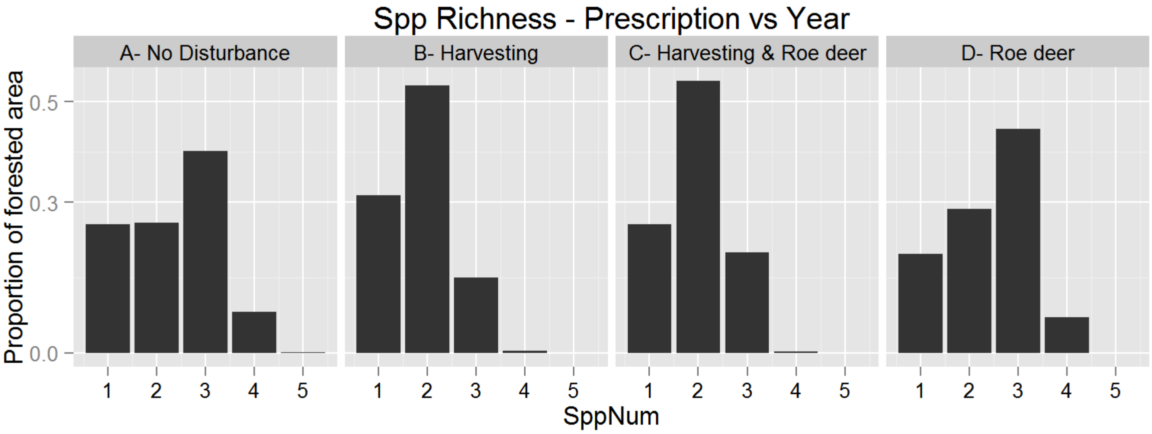

Figure 9 Species richness distribution for each scenario at the end of simulations.

Forest loss

At the end of the simulation, our forested area showed a reduction in extent, in all 4 scenarios. The magnitude of the reduction change for each scenario, from 0.3% of *No Disturbance* scenario to the 15.2% of *Harvesting and Roe Deer* scenario (Tab.12). It seems that most of forest loss concentrated along the outmost areas of the study area (Fig.12). Even if harvesting has an effect on forest loss, it seems that roe deer presence markedly affects forest extent. The cells subjected to forest loss were covered, in *No Disturbance* scenario, mostly by Fagus forest type, with 75.5% and 89.6% coverage for *Harvesting & Roe deer* and *Roe deer* scenario respectively (Fig.13). Conifers and Mix forest types covers respectively 12.3% and 6.4% for *Harvesting & Roe deer* scenario, and 5.8% and 2.0% for *Roe deer* scenario. OakHornbeam and MixBroadleaves are represented by smaller proportions (Tab.13). Around 1% of the lost forest cells resulted as not-forested in the *No Disturbance* scenario too (Tab.13).

DISCUSSION

Our study shows the utility of using LANDIS-II and its extensions for understanding dynamics and interactions between forest succession and disturbances, that are difficult to measure empirically, especially if considered on large-scale and long-term. At the end of the simulation of the No Disturbance scenario, conifers-related (Conifers and Mix) and shade-intolerant (Oaks and Castanea) forest types show a marked decrease in abundance. The former is most probably due to the decrease in conifers abundance, as those species are not native in the area so they're not present in the second growth forest. They resist to some degree until the end of the simulation because of the longevity of the species, which is for almost all species is higher than the simulation's length. Oaks and Castanea forest types are probably hindered by the low shade tolerance and dispersal capabilities, which don't allow them to survive under shade tolerant species and reduce their ability to colonize neighboring areas.

Species	*P*-values	Trend (No Dirturbance *vs* Roe deer)
Abies alba	0.002	Decreasing
Acer pseudoplatanus	0.002	Decreasing
Castanea sativa	NA	Stable
Fagus sylvatica	0.005	Decreasing
Fraxinus ornus	0.002	Decreasing
Ostrya carpinifolia	0.002	Increasing
Pinus nigra	0.48	Stable
Pinus pinaster	0.65	Stable
Pseudotsuga menziesii	0.011	Increasing
Quercus cerris	0.058	Stable
Quercus pubescens	0.025	Stable
Robinia pseudoacacia	1	Stable

Table 11 Table of trends for each species, and p-values for the significance of the difference of abundance between the two scenarios. NA values are indicating that there are no differences to test.

The forest structure indicates the presence of a mature forest, as more than 96% of the cells have a maximum age higher than 160 years. The absence of any disturbance certainly plays a role in shaping forest structure, but on the other hand the time span of our simulation is shorter than the longevity of the majority of the species considered. Species richness increased at the end of simulation, indicating a shift towards a landscape composed of mixed deciduous species assemblages, similar to the one existing before anthropogenic disturbances of the last centuries that introduced coniferous species in the area. Nonetheless, if the time span of our simulation were wider, we would probably see some shade-tolerant species monopolize wide areas of the map, due to some constrained applied by the succession extension choose for the modeling (Mladenoff & He 1999). On the other hand, modeling the development of forests for a long time span (i.e. 800 years) ignoring the climatic and socio-economical changes that will occur in that time span, would probably return a simulation so disconnected from the real course of events that the results would be meaningless.

Harvesting causes a shift of both forest structure and forest types distribution. By targeting some species and aiming at maximizing the harvest yield in the long run, harvesting causes directly or indirectly a shift in species composition. That happens by both planting the desired species and eradicating the undesired ones that can compete for resources, and changing the inter-specific competition by deeply modifying the environment. This, in turn, will probably cause a loss in species richness. Despite the fact that introducing a disturbance in a scenario generally causes an increase in species richness, by creating openings that can be colonized, our results do not show this dynamic. That is most probably due to model constrains, such as that species establishment is prevented in a cell if a species is planted, and that the removal of a species cohort does not create an opening in a cell, unless that species was the one with the highest shade tolerance in that cell (Gustafson *et al.* 2000). The application of harvesting prescriptions changed the forest types distribution, reducing Conifers and increasing Oaks distribution. Eradication of coniferous alien species is one of the aims of the current management plan, so it was explicitly applied into prescriptions. Oaks increased distribution is due to the high commercial value of those species, which in our prescriptions is emphasized by planting oak species at the end of the prescription that deals with oaks coppice management. In LANDIS-II framework, as mentioned before, planting (or re-sprouting), prevent any other form of establishment of species (Gustafson *et al.* 2000).

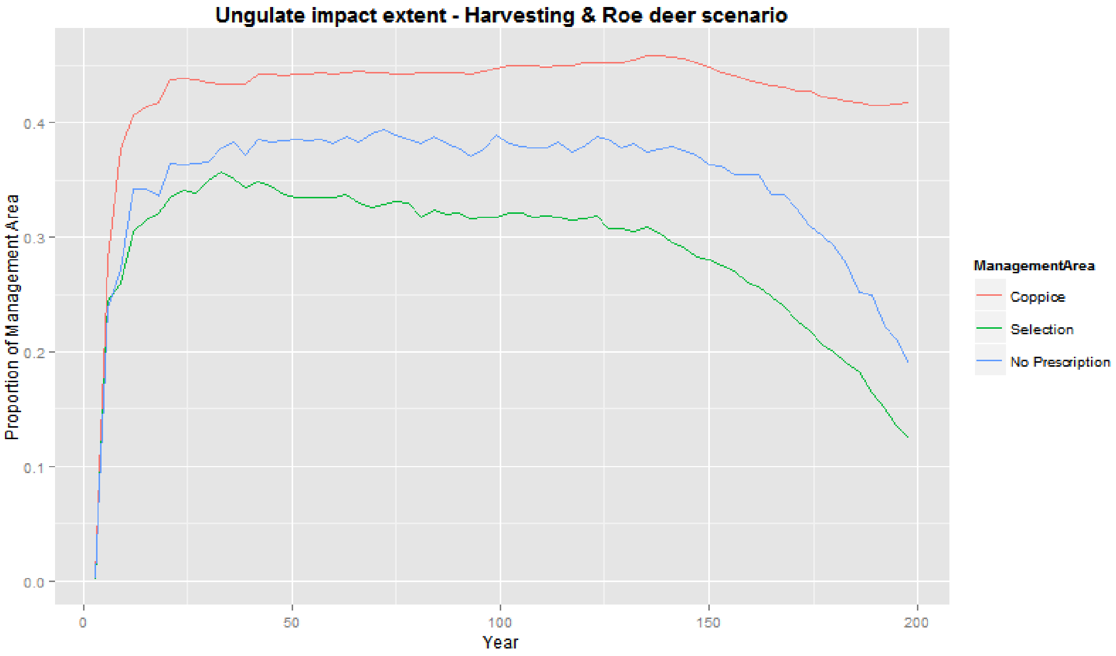

Figure 30 Extent of roe deer impact, expressed as proportion of management area affected for each time step.

Preventing the establishment of other species will, in the long run, increase the number of cells dominated by oak species. The decrease of Castanea along the simulation, in spite of its being of economic interest, is probably due to its low shade tolerance, which doesn't allow to colonize new cells while, on the other hand, allows for the invasion by more shade-tolerant species. Fagus, for the same reason, shows a different behavior: having the highest shade-tolerance value, it's able to colonize new cells while other species with lower shade-tolerance values can't establish under its canopy. The age structure of a managed forest will strongly depend on the management practice applied. Forests managed as coppice will have a different structure from those managed with selection cutting. Our results show a shift of the forest structure towards younger ages, which is due to the selection cutting in the Selection management area. The prescriptions applied in Selection management area targeted older cohorts, increasing the number of cells composed by younger trees. Coppice management area, on the other hand, shows an age structure where more than 90% of cells host trees older than 160 years. This seems counter intuitive, but the prescriptions in this management area target only young trees, leaving the older ones –inside the same cells- aging without disturbances. The management area where no prescriptions were applied has the highest percentage of cells containing old forest, as less than 2% of the cells have oldest trees younger than 160 years. Species richness results to be affected by harvesting prescriptions too, as it shows a shift towards smaller values. The presence of openings in the forest, as the ones created by some forest management practice, usually favors the establishment of species different from the ones present in the canopy, increasing -locally- species richness (Nicholas 1982, Busing & White 1997). This does not happen in our simulations for two reasons: first, in LANDIS-II framework the cell is the smaller entity, and it's considered homogeneous. In other words, openings smaller than the cell's size do not exists in the simulation. Moreover, shade-tolerance constrains limits cells colonization. The second reason, as mentioned before, is that planting prevents the establishment of other species in that cell.

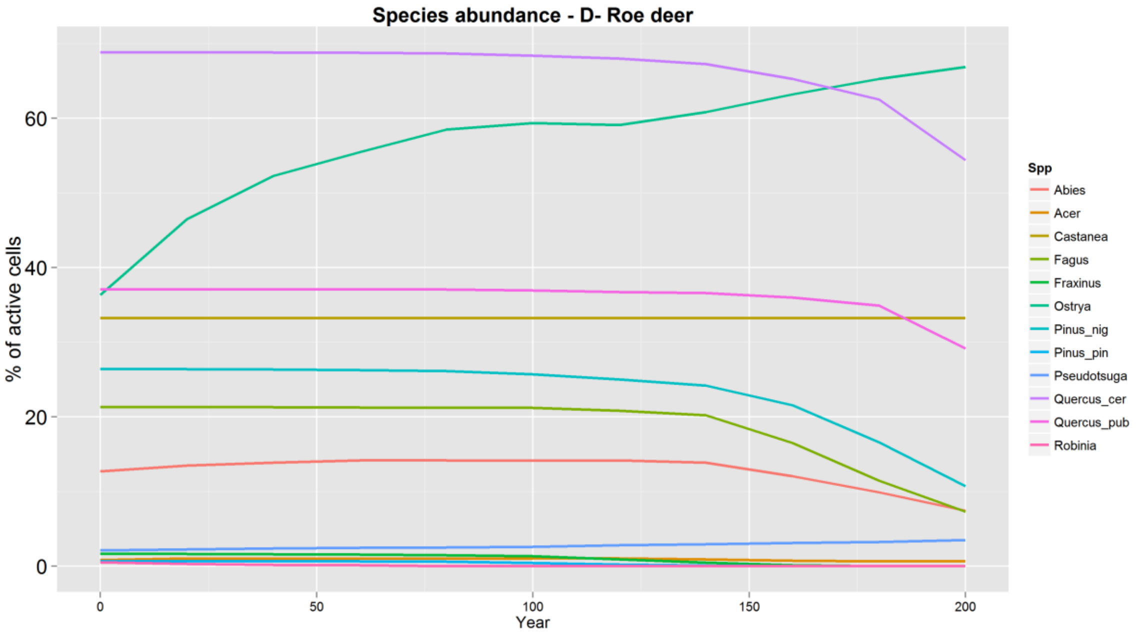

Figure 11 Species abundances, defined as percentage of active cells in which the species is present, for all the considered species throughout the simulation.

Ungulate impact in the literature is shown to alter the species abundance, as preferred (palatable) species are subject to a selection. In situation of high ungulate densities, this selection can result in a strong decline of the preferred species, while other non-palatable species can take advantage of the resulting openings and resources (Ammer 1996, Pellerin *et al.* 2010). In some extreme situations, some tree species can be almost eradicated from the landscape, and the forest structure can be severely shifted towards older ages, as most of the saplings are not able to survive ungulate impact (Caudullo *et al.* 2003). Our simulation results are in accord with literature findings, as they show a clear decrease of the forest types composed by roe deer preferred species. Two forest types increased during the simulation, OakHornbeam and MixDeciduous, most probably because of the introduction of not-preferred species, as hop hornbeam, in oak mono-cultural cells in the first case, and conifer reduction for the latter (Mix forest type, which contains coniferous species, shift to MixBroadleaves when conifers are removed/lost). This hypotheses seem to be confirmed by the fact that Oaks and Conifers forest types are not significantly different from No Disturbance scenario. That leads to the conclusion that changes in forest types distribution, by effect of roe deer impact, are more related to an increased richness in per-cell species rather than a reduction in the abundance of single species across the landscape. The results of species richness analysis seem to confirm this conclusion, as this is the scenario with the highest values. Even if the maximum number of species in a cell is 4 in this scenario, the distribution of species richness is strongly keen towards the highest values. This would suggest a positive effect of roe deer impact on species diversity, as suggested by several authors for ungulates (Reimoser & Gossow 1996, Pellerin *et al.* 2010). If compared with No Disturbance scenario, the increase in species richness appears around the end of the simulation, suggesting that the magnitude of the phenomenon may have an increasing trend that goes beyond the end of the simulation. The forest structure in this scenario is strongly shifted towards older ages (90% of cells have trees older than 200 years), probably because most of the saplings are removed from the landscape by roe deer impact along the simulation, causing – in time - a gap in forest structure between very young and very old ages. Nevertheless, the youngest ages (up to 10 years) are very well represented, about twice the abundance returned in the No Disturbance scenario. This is probably due to the “providing-openings-and-resources” effect of the ungulate impact, but we have to take into account the model framework. Ungulates can have an effect on saplings only, so most probably there have been other dynamics involved that removed the oldest cohorts already present in those cells. Natural mortality (i.e. aging) and dispersal/establishment capabilities are the only other dynamics explicitly present in the model framework, so probably is in those that we shall look for the cause of lack of older trees. The roe deer impact then, consuming the palatable saplings, keeps the maximum age of the cell low.

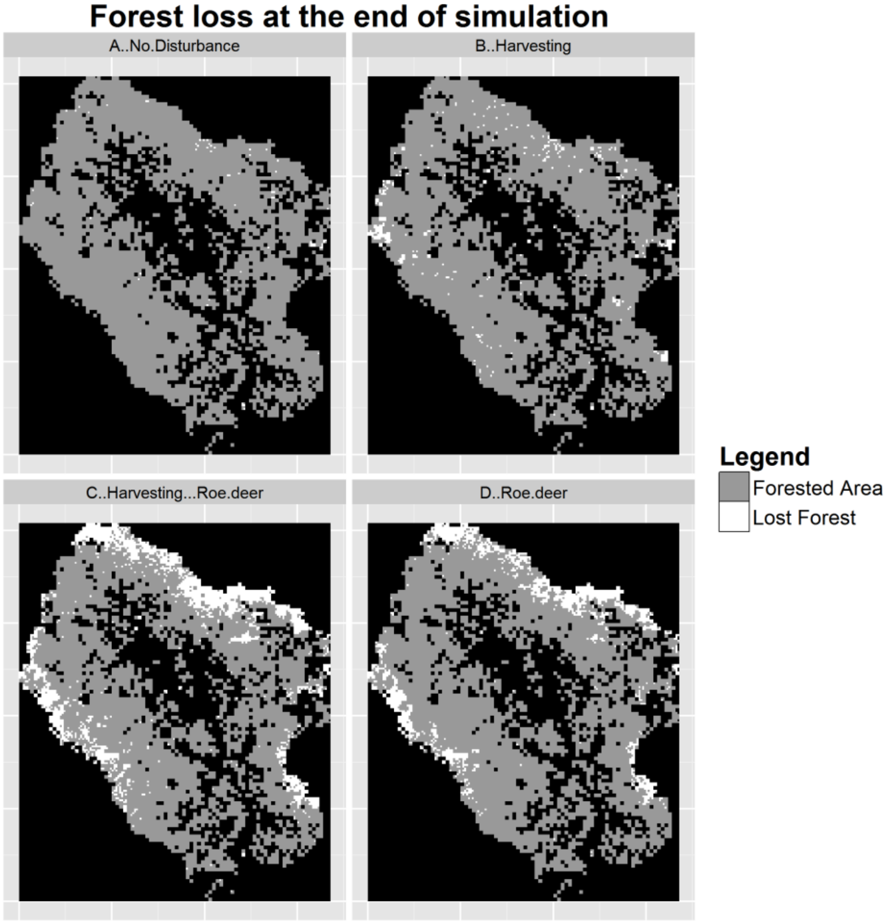

Figure 42 Forest loss areas at the end of simulation in all 4 scenarios.

Scenarios	Forested area loss (percentage)
No Disturbance	0.27%
Harvesting	2.27%
Harvesting & Roe deer	15.19%
Roe deer	10.74%

Table 42 Forest lost at the end of simulation for each scenario, expressed as percentage of initial forested extent

When the two disturbances are combined, we expected them to markedly change the face of the landscape, and to interfere with each others. We predicted that roe deer impact would reduce the harvest yield, as the species targeted by harvesting prescriptions are some of roe deer's preferred species. The species richness would decrease, as harvesting will plant and select for target species, and the forest structure would shift towards older ages, as they're not affected by either of the disturbances. The forest types distribution at the end of simulation shows the effects of both disturbances: the increase of Oaks forest type in spite of OakHornbeam, and the strong decrease of Mix and Conifers forest types are due to harvesting disturbance; on the other hand the decrease of Fagus abundance and the relatively high value of OakHornbeam are due to roe deer impact. It's interesting to note that this is the scenario where Castanea is most abundant, this is probably due to the colonization by *Castanea sativa* of the cells left vacant by Fagus. As can be noted, roe deer impact causes a strong decrease in Fagus forest types, such as it leads to the deforestation of some areas previously occupied by Fagus (Fig.14).

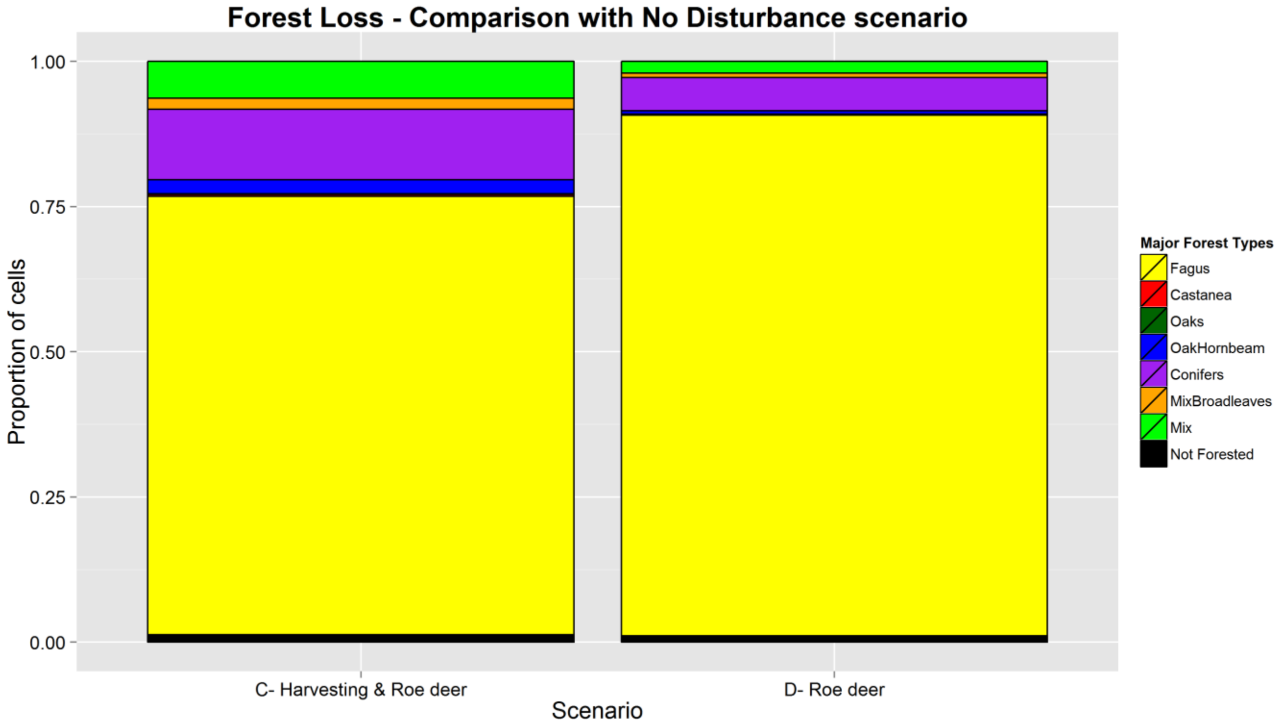

Figure 53 Proportions of forest types loss in the scenarios considering roe deer, compared to *No Disturbance* scenario, at the end of simulation.

Disturbances	Fagus	Castanea	Oaks	OaksHornbeam	Conifers	MixBroadleaves	Mix	Not Forested
Harv&Roe	75.5%	0.3%	0.1%	2.4%	12.2%	1.9%	6.4%	1.3%
Roe deer	89.6%	0%	0.2%	0.6%	5.8%	0.7%	2.0%	1.1%

Table 13 Percentage of forest type coverage of cells that are lost forest on *Harvesting & Roe deer* and *Roe deer* scenario.

At the end of our simulations, the presence of roe deer did reduce the harvested area, but only for the coppice one. That makes sense, as it is the one with the shortest rotation, and therefore the highest amount of cells with saplings, being the most affected by roe deer impact (which target trees up to 6 years old). The presence of roe deer in the other management areas, where the ages targeted by harvesting prescriptions are older, didn’t cause a significant difference in harvest yield. For the same reason we found that roe deer impact is significantly different between management areas, as coppice management creates conditions that favor roe deer’s impact. The forest structure at the end of the simulation is shifted towards older ages indeed, but there is a surprisingly high proportion of very young trees. When we look in detail the proportion of trees younger than 100 years (Fig.6), we can see that this scenario is the one where the proportion of trees younger than 10 years is the highest. Harvesting prescriptions are still planting oaks, and roe deer are still creating openings for other species to colonize, but such a high proportion still raises a question, as roe deer impact is applied to 100% of the study area, and to explain this high proportion of untouched saplings the increase of un-palatable species should be stronger. The same dynamics mentioned above about roe deer impact are most probably acting in this scenario too, but the disturbance cause by harvest prescriptions seems to favor those situations leading to area (i.e. cells) composed only by very young trees. Species richness seems to be influenced more by harvesting than by roe deer impact. The distribution of the number of species per cell resulted to be shifted towards lower values, resembling the distribution obtained when harvesting only was considered. The influence of roe deer impact can be seen in the light shift towards higher values in respect to Harvesting scenario species richness distribution, but this effect is not enough to shift the distribution closer to the No Disturbance or Roe deer scenario’s ones.

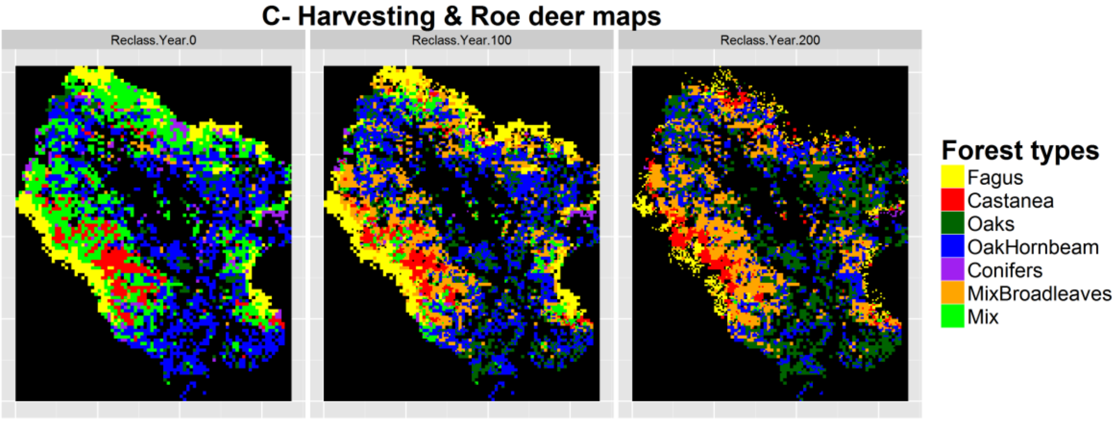

Figure 64 Spatial distribution of major forest types along the scenario considering Harvesting and Roe deer impact. The three maps shows the forest distribution at year 0, 100 and 200 of the simulation.

Our results show the loss of some areas of forest in all 4 of our scenarios, but the extent of this loss shows a quite wide range. It seems apparent that roe deer impact has a major effect on this phenomenon, as the scenarios considering roe deer are the ones that experienced the loss to the widest extent. Harvesting has a certain effect too, as when considered alone, it returns a forest loss which is several times the one returned by No Disturbance scenario. The two disturbances, when considered combined, have an added up effect, which leads to the loss of wide areas of forest, mostly along the edges of the study area. The fact that the lost areas are located mostly along the edge suggests that the phenomenon is biased by a modeling artifact, which is the presence of a *vacuum* beyond the borders of the study area. If that bias were to be removed, the outer cells of our study area wouldn’t be “isolated”, and maybe the extent of forest loss would be smaller. This would explain why the majority of cells, which comprise the forest loss areas, would be hosting Fagus forest type. We obtain this data from a comparison with No Disturbance scenario, looking for which forest types are present in those cells which are “lost” in the deforestation process of other scenarios. Fagus forest type seems to be the forest type most affected by forest reduction in the landscape. This is probably due to the location of this forest type, mostly spread along the borders of the study area, and to the high shade-tolerance value of the species. Moreover *Fagus sylvatica* finds its ecological niche at higher elevations, which in our case are located on the edges of the study area. On the other hand, *Fagus sylvatica* has the highest shade-tolerance value in the modeling, which means that no other species (except for *Abies alba*) is able to establish under its canopy.

Fagus	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	2.8e-09		
Harvesting & Roe deer	0.043	2.6e-03	
Roe deer	2.5e-03	0.0	2.4e-09
Castanea	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	1.9e-15		
Harvesting & Roe deer	0.0	*0.95*	
Roe deer	9.8e-03	1.2e-06	8.7e-08
Oaks	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	0.0		
Harvesting & Roe deer	5.7e-10	*0.11*	
Roe deer	*0.73*	1.1e-13	6.8e-07
OakHornbeam	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*

Harvesting	5.3e-13		
Harvesting & Roe deer	6.5e-04	2.9e-03	
Roe deer	0.036	0.0	1.2e-10
Conifers	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	8.6e-08		
Harvesting & Roe deer	0.0	0.028	
Roe deer	*1.0*	2.1e-07	0.0
MixBroadleaves	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	0.0		
Harvesting & Roe deer	1.4e-11	5.4e-03	
Roe deer	5.4e-03	9.5e-12	1.8e-03
Mix	*No Disturbance*	*Harvesting*	*Harvesting & Roe deer*
Harvesting	3.5e-12		
Harvesting & Roe deer	0.0	7.3e-03	
Roe deer	2.8e-03	1.7e-03	2.6e-11

Table 54 Table of p values of Friedman's post-hoc tests for the comparison of forest types abundance between different scenarios. P-values in italic font are not significant.

So when the species is eradicated from the cell, it remains empty, and it can't be colonized by beech again because its high shade tolerance prevent it from colonizing openings. Moreover, this forest type is targeted by both disturbances. This combined conditions, and the simplification inherent in the modeling process, lead to a isolation of the outermost cells, which most probably has an effect in the modeled forest loss. On the other hand, results show that several areas where forest was lost are far from the edges of the study area, indicating that the forest loss is an actual effect of the disturbances, despite the bias concerning the study area borders.

Management Area	Prescriptions	Friedman's test *p*-value
Coppice Management Area	BroadleavesCoppice	NA
	CastaneaCoppice	1.25e-07
	ConifersReduction	7.5e-05
	QuercusCoppice	*0.058*
Selection Management Area	ConifersEradication	*0.083*
	SelectCut	NA
	ThinCut	NA

Table 65 Table of p values of Friedman's post-hoc tests for the comparison of harvesting yields for each prescription between *Harvesting* and *Harvesting & Roe deer* scenarios. P-values in italic font are not significant.NA values are indicating that there are no differences to test.

CONCLUSIONS

Working with models always implies simplifications and generalizations (Burnham & Anderson 2002). Our simulations provided some insight on the development of the forest under the effects of the two disturbances considered, nonetheless they should be viewed more as indications of the resulting trends than actual future predictions. Our results show that the two disturbances are interacting, in all aspects of forest ecology we analyzed. Forest types distribution and forest structure are affected by both disturbances, but it doesn't seem that one disturbance has a stronger influence on those aspects. On the other hand, the species richness seems to be strongly driven by harvesting. The deforestation depicted in the results should be look at with caution. Even if the trend seems to be present in all four scenarios considered, model constrains and simplifications could have had a stronger effect on this aspect of forest ecology. Besides the "edge effect" mentioned in the discussion – beyond the borders of the study area there's an artificial vacuum- it must be reminded that LANDIS-II does not model shrubs, which can have a shield effect against browsers pressure, favoring saplings survival and so limiting deforestation (Bergquist & Örlander 1998). The combination of the two disturbances, with the magnitude simulated in the modeling, does not seem to be an hazard for the forest functionality in our study area. None of the ecological traits examined, compared to the simulation without disturbances, showed alterations that raised concerns. On the contrary, the two disturbances act additively, compensating and balancing each other effects. The presence of ungulates, advocated by forest managers as causing a marked loss in revenues due to browsing impact, does not seems to significantly affect harvesting yield, and apparently increases biodiversity. The effects of ungulate presence, based on the simulated impact magnitude, seem to have an overall positive effect when applied to a context where forest management is present to the extent reported by our simulations. Despite the constraints imposed by the modeling effort, LANDIS-II is a very flexible tool, which allows to simulate a wide variety of ecological situations at different –user selected- level of complexity. The ability to show the trends the landscape will face under different situation is very useful for virtually testing managing options and different scenarios. Moreover, the results of the simulations are quite rich of details, enabling scientists or managers from other disciplines to use those results as a base for their analysis (e.g. Shang *et al.* 2012). The complexity of the phenomenon the model deal with, reflects in the complexity of the use of the software itself, which together with a lack of knowledge about some tree species life-traits parameters, can slower the spread of this useful tool amongst managers and researchers.

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THESIS CONCLUSIONS

This thesis was devoted to the analysis of the complex ecological network that surrounds and influences ungulates and forests. While reviewing the existing literature on the topic (Chapter 1), it became quickly clear that the extent of that network goes well beyond the limited context of animal abundances that is usually addressed. Usually, managers that have to deal with ungulates, both from a wildlife and a forestry point of view, have jurisdiction over a small area, and so the solutions they apply to mitigate the conflict are rarely effective. Moreover, some very important factors that influence ecosystem dynamics are often ignored. Some of those factors cannot be modified in the short terms by human actions, such as climate – e.g. temperature, humidity, snow accumulation -, site productivity, terrain morphology – e.g. aspect and elevation. However other factors can be controlled, or at least influenced by forestry practices at different spatial scales. The tree species composition, the dimension and spatial distribution of the clearings due to harvesting, the number of vegetation layers in the forest, and the structure of the landscape mosaic are all strongly influenced by the forest management. All those factors have a role in shaping ungulate impact, as they can affect the forest sensitivity to browsing, by creating attractive habitats to ungulates. Those areas attracts an elevated number of herbivores , but once the amount of forage drops – due to consumption, or plant growing and escaping the browsing line – ungulates must turn to surrounding area for forage. But the extensive even-aged stands created by most forestry practices do not provide it, so that these stands are called "ecological traps" (Reimoser & Gossow 1996). Missing both vegetation layers – such as herbaceous and bushy species – and age and species heterogeneity, those stands are unable to sustain ungulate population pressure without suffering strong impacts like bark stripping or saplings browsing.. A more naturalistic approach to forest management would help mitigate this effect, because shelter cutting and single-tree selection could favor the development of diverse vegetation layers and a more homogenous spatial distribution of food resources. In doing so, ungulate impact would be distributed over a wider area and several vegetational groups, i.e. trees, bushes and herbaceous vegetation. The application of these techniques, paired with the restoration of large predators and their ecological functionality, would allow for a economically proficient exploitation of the forests, while enhancing biodiversity, ecosystem functionality and, not less importantly, a strong mitigation of herbivores damages to forestry. Nevertheless, when an ungulate population is overabundant, the action taken to mitigate their impact may be overruled, and there would be the need for a demographical control That bring us to the unsolved problem of estimating how many deer are in a certain area, to proper planning the management actions and to check their outcomes. By comparing three census methods (Chapter 2), I found that they return consistent estimations of roe deer densities, but the precision of the results is markedly different. A higher precision may be useful to better identify the annual –or seasonal- fluctuation in population density, clarifying some aspects of population dynamics or helping evaluating the effects of management actions. The method used by the Fish and Wildlife Service of Arezzo Province resulted to be the one with the lowest precision, resulting in a wide 95% confidence interval that in its lower limit reaches 0. The other two methods tested reported a higher precision, especially the modified version of the pellet-group count estimation (Fattorini et al., 2011). But when dealing with management issues, the applicability of the methods is even more important, especially if they must be used by volunteers or hunters rather than by professional wildlife managers. A technique that returns optimal results but is very difficult to apply may be discarded in favor to a simpler one., less performing but yet less demanding. I found that drive censuses return a higher estimation than pellet-group count, which confirms the findings of Bongi et al. (2009). The cause for this may rely in the difficulty for the operators to individuate the pellet-groups on the sampling plots. Ground vegetation, herbs or bushes, and the fallen leaves layer may have lowered operators performance in locating the pellet-groups. A study on the effect of ground visibility on the operators’ ability to locate pellet groups may help to mitigate those biases in estimation, and return more accurate results. One of the factors that contributed to the high precision of the method was the elevated number of sampling areas, paired with a small range in counting results. In fact, in all our 294 sampling points the number of pellet groups found was between 0 and 7, which in turn resulted in a low variance of the estimate. But the high sampling activity required for this results may not be practically feasible in wide areas unless if performed by numerous operators. The R.E.M. method resulted to have an intermediate precision between the two other methods, and returned an estimate slightly higher than the one obtained by drive censuses for the same year. It must be noted, thou, that not all the possible sources of uncertainties have been included in the variance calculation for this method, as detection area parameters and average daily distance were assumed to have no variation. The applicability of this method in our study area was generally good, with the only exception of some very dense vegetation patches where cameras had very small open areas in front of them, limiting the efficiency of trapping. As I stratified the sampling effort across vegetation categories, this issue arose mostly in the categories with denser vegetation, such as bushes and coppice, that may have resulted in a underestimation of the densities for those two strata. This problem could be avoided using the approach described in Rowcliffe et al. (2011), where he suggests the calculation of the detection area parameters with a data-based procedure that is an adaptation of distance sampling approach, to calculate the species- and site-specific parameters. The application of this approach, however, markedly increase the work required, as for every picture taken by each camera the animal position relative to the camera has to be determined. This requires the presence of two operators and increases the time spent at each camera trap site.. Another factor that could increase the accuracy of the technique is a proper estimation of the average daily speed. This should ideally be estimated in the same area and season during which the sampling is performed. However this would require a parallel study, increasing the commitments, both as economic investment and manpower. It seems that the R.E.M. has the potential to be the most situation-specific method, amongst the ones I applied, allowing the calibration of all its parameters on collected-on-site data. Nonetheless, further studies on its accuracy in different context are needed, to confirm the first promising results. Even if the R.E.M. application seemed to be a good compromise between the underestimation of the pellet-group count results and the large uncertainty of the drive census ones, the pellet-group count method might outperform the R.E.M. if a valid approach towards differential ground visibility is found, or if the local conditions are more suited to the method compared to ours, e.g. plain topography. Once the estimated number of deer is known, their impact on forest should be assess, as the relation between densities and impact are often not linear, and site-specific. Our findings shows that the browsing incidence on coppice areas is quite high –almost one-third of sprouts are browsed – even at low densities, and it increases as densities increase. It is interesting to note that the difference of browsing incidence between areas with medium and high densities is not significant, as if over a certain threshold the severity of the incidence would reach an asymptote. This could be linked to alternative food sources, or other food-independent factors, in the area with the highest densities. However, it shows how impact is not linearly correlated to densities, and that monitoring the former is as important as estimating the latter. For this reason I proposed the method I applied in our study as a compendium to density estimation for wildlife and forest managers, on account of its fast, simple and cost-effective procedures that make it suitable for large scale monitoring. Considering both these factors while preparing a management plan would help managers to better address the issues and optimize their efforts. Once the early stage browsing impact is assessed, the question arises what are the long-term consequences of it. Some studies show that after some years, due to compensational growth, the effects of early stage browsing become negligible (Gill, Webber & Peace 2000, Pellerin *et al.* 2010). Our study found that this is not the case in our context, as even 6 or 11 years after the clear cutting, the effects of browsing impact are still found as a significant difference in basal area and volume between browsed and untouched stems . However, those differences where less severe 11 years after coppicing than they were 6 years after coppicing. This suggests that, in the long run, those differences will be lower and lower to finally vanish.,. Such hypothesis, anyway, is not interesting from an economical point of view, as the rotation period for coppice stands is quite short, having its minimum at 18 years (Tuscany regional laws). This time lag in forest response to disturbances is well known to foresters, and is a problem because their effects will be visible only in the long run. Researchers face the same problem when trying to understand the dynamics that drive the ecosystem, as some of the effects or relationships between actors need years - or even decades - to be clearly visible. Moreover, the complexity of the ecological network and its interactions, makes it difficult to understand which of the several factors involved participated in the outcomes and to what extent. This difficulty led to the development of tools that would allow the simulation of ecological dynamics and, considering the interactions between factors, show a plausible outcome of the scenario considered: the ecological models. I decided to apply a landscape development model, LANDIS-II (Scheller *et al.* 2007), to simulate the development of our study area considering two disturbances: forest management and roe deer impact. Our results show how both disturbances, applied as singleton or combined, influence several aspects of the ecology of the forest. Species richness, age structure, species abundance and distribution, and even forested area extent, are affected by disturbances. The direction and magnitude of the effects vary between disturbances, and interact when those are considered combined. The forest types abundance distribution resulted very different between the scenarios considering either harvest of deer disturbance as forest management aimed at maximize the economically interesting species, while roe deer caused a shift in species abundance due to its feeding preferences. This in turn influenced the ability of other tree species – not directly involved in selection by the disturbances – to establish, due to species-specific shade tolerance limitations, and at the end of this process, species richness was affected too. It’s interesting to see how, when considered together, the effects of the two disturbances are additive, causing a strong decline/increase or a mediated effect, depending on the forest type considered. A similar interaction can be seen in the resulting age structure of the forest, where the age distribution is affected by the cohorts targeted by harvesting prescriptions on one hand, while on the other hand, roe deer impact targets only very young trees. The LANDIS-II ability to model ecological processes, such that their interactions are emergent proprieties of the simulation, may help researchers to identify dynamics and interactions between factors that were not apparent. Moreover, it can help simulate scenarios under different conditions, and help managers to understand the effects of their interventions. The simulation outputs, however, should not be taken as certain predictions. The model is able to provide a realistic simulation of the ecological development of a landscape, but the outcomes are limited by its constrains and simplifications, and while it is able to show us ecological trends and interactions, our knowledge on landscape development dynamics and the complexity of the interactions involved, prevent it to returns outputs that could be taken as prediction. Ecological models are still be refined, and empirical evidences of their modeling capabilities is needed. When a model simulation resulted to be false, it is an indication that a variable or an interaction has been excluded from the modeling process, giving us a hint on what I am missing in the ecological framework. As mentioned before, this will take time, as forest time span are long, but in the last decades the advanced in model studies and ecological networks makes for good premises.

Changing the prospective from where I am looking at ungulate and forest interaction, helps us to properly understand the ecological network. The ability to estimate ungulate numbers, and to evaluate their impact, are very important for a proper evaluation of the issue and for the preparation of a site-specific management plan, that ideally should consider both the active components involved as part of an interaction. The complexity of those relationships and the time needed to see the outcomes of the action taken are hindering this process, but the use of ecological models may help to increase our knowledge and understanding of the interactions between factors. The advanced in research suggests that the more efficient solution to the ungulate-forest issue is a shift towards a close-to-nature management, and a restoration of the natural functionality of the ecosystem. This would allow the stakeholders – foresters, hunters, tourists. – to exploit the resources of the environment in a sustainable and profitable way, and at the same time to restore a complete and self-managing ecosystem.

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Appendix

Appendix A

Use of refuge areas by wild boar in a multi predator area

Manuscritp

Use of refuge areas by wild boar in a multi predator area

Stefano Grignolio; Elisa Bertolotto; Andrea Marcon; Paolo Bongi; Siriano Luccarini; Marco Apollonio

1 Department of Science for Nature and Environmental Resources, University of Sassari, Sassari, Italy

ABSTRACT

Spatial behaviour and resource selection of wild animals are affected, inter alia, by predation sensitivity and human harassment. We studied the behavioural patterns of wild boar (Sus scrofa) in a forest region in the Arezzo province, which included a protected area where two natural predators (Canis lupus and Vulpes vulpes) were present. The protected area was surrounded by hunting districts. From 2002 to 2010, we collected radio-tracking information for 81 wild boars, and calculated home range sizes and animal distances from safe areas. We assessed anti-predator behavior by analyzing i) home ranges size and area covered by shrubs ii) the proximity of wild boar locations to shrubs refuge areas, in different parts of the day and in different seasons. Results showed that males had larger home range sizes than females. Twilight home ranges were smaller during the hunting season (i.e., autumn) than in the other seasons. Subadult and adult females stayed closer to shrub patches than males. Female and piglets behaved similarly with respect to the distance from shrubs and kept close to refuge areas, especially during the resting phase. These findings point out the importance of micro-scale habitat selection for this species, suggesting that a different use of resources by males and females may induce fine scale sexual segregation.

Keywords: antipredator behavior, Canis lupus, radio tracking, Sus scrofa

INTRODUCTION

It is generally accepted that natural selection favours the optimal individual trade-off between the benefits and the costs of predation risk reduction (Lima, 1998; Lima, 2002). Several authors analysed the spatial behaviour of ungulates so as to define anti-predator behavioural patterns considering both environmental and human factors (Ciuti *et al.*, 2012b; Grignolio *et al.*, 2007a; St. Clair and Forrest, 2009; Winnie *et al.*, 2008). Anti-predator patterns are shaped by habitat characteristics (Hollén *et al.*, 2011; Kauffman *et al.*, 2007), as well as by the presence of predators (Morrison, 2011) and by human disturbance (Wang *et al.*, 2011). In multipredator environments, preys may be forced to diversify their anti-predator strategies. In fact, defences may be subject to additional selection pressures which are not likely to occur in single-predator systems. Anti-predator behaviours designed to avoid a particular predator could be useless against another, or may even make the prey more vulnerable to other predators (Caro, 2005).

In the case of wild ungulates, large and meso carnivores and human hunters act as predators. Human activities cause significant harassment to some species, to such extent that an encounter with humans can provoke reactions similar to those triggered by natural predators, and consequently modify their behaviour and spatial distribution (Apollonio *et al.*, 2005; Ciuti *et al.*, 2012a; Ciuti *et al.*, 2012b; Frid and Dill, 2002). In order to avoid predation and human harassment, wild ungulates may increase movement (Kilpatrick and Lima, 1999; Root *et al.*, 1988), enlarge their resting range (Jeppesen, 1987), shift their centre of activity (Kilpatrick and Lima, 1999), and differentiate habitat selection (Kufeld *et al.*, 1988). In addition, the risk perception doesn’t apply to all individuals in the same way: Neumann *et al.* (2009), for instance, suggested that moose may perceive the human predation risk to be similar to other predation risks and that some individuals are more sensitive to hunting disturbance than others. In fact, ungulates’ responses to human harassment usually depend on sex and, for females, on their reproductive status (Stankowich, 2008). Age class can have a role too: Grignolio *et al.* (2011), for example, showed that human harassment induced different responses in roe deer (Capreolus capreolus) of different ages, which consequently used refuge areas to different extents.

In polygynous ungulates, males and females use different strategies to maximize reproductive success. Males tend to maximize their body mass in order to positively affect their chances to gain access to females and ultimately increase their fitness, whereas females try to maximize offspring survival. These different tactics affect predation risk perception and, as a consequence, anti-predator strategies. In those species, for example, home range size, habitat selection and group size differ between males and females, as well as between females with and without juveniles (Barten *et al.*, 2001; Bongi *et al.*, 2008; Ciuti *et al.*, 2006; Grignolio *et al.*, 2007b; Winnie Jr and Creel, 2007).

Habitat use by wild boar (Sus scrofa) is difficult to investigate. Authors have used indirect methods (Abaigar *et al.*, 1994; Meriggi and Sacchi, 2000), and only recently radio-tracking techniques (Saïd *et al.*, 2012; Tolon *et al.*, 2009), to try and understand the way in which individuals select their habitat. Meriggi and Sacchi (2000) showed that wild boars are more likely to prefer denser vegetation as a cover against predators and a shelter from adverse microclimatic conditions. Wild boar spatial behaviour has been investigated in many studies that showed heterogeneous patterns also in response to hunting activities (Keuling *et al.*, 2008a; Scillitani *et al.*, 2010; Sodeikat and Pohlmeyer, 2007; Tolon *et al.*, 2009). Human harassment was shown to affect wild boars habitat selection (Saïd *et al.*, 2012) causing, among other things, an increased use of refuge areas (Tolon *et al.*, 2009), or a widening of their resting range by moving to safer areas outside their usual resting ranges (Calenge *et al.*, 2002; Sodeikat and Pohlmeyer, 2003). Unlike hunting, which is only allowed in a well-defined season, natural predation and other human disturbances occur all year long. It is therefore difficult to disentangle the causes of these behavioral patterns, also because seasonal environmental changes might mask the effects of both predation risk perception and human disturbance (Keuling *et al.*, 2008b).

We investigated the spatial behaviour and habitat use of wild boar in a heterogeneous landscape, characterised by the presence of a small protected area surrounded by hunting districts and with high-density populations of wolves (Canis lupus) and foxes (Vulpes vulpes). We analysed the spatial behaviour and the use of refuge areas (i.e., high vegetation cover sites) searching for different patterns in relation to sex and age class. Moreover, we checked whether wild boar modified their behaviour in relation to daily period and season, also considering that predation risk perception for boars of different sex/age varies according to their biological status.

We expect to find a different spatial behaviour between the two sexes, with females generally closer to refuge areas to protect the newborns. In addition, for the same reason we expect an age effect, which will cause that difference to be at its maximum between adults individuals, and at its minimum between piglets. We also expect females to have smaller home ranges, with a higher percentage of shrubs inside it, because their movements and habitat selection can be affected by the presence of piglets. The part of the day should affect the boars behaviour, as they are generally biphasic and more active during the night (Mauget *et al.*, 1984), and we suppose this effect would be stronger during autumn and winter twilight, when hunting is allowed. For the same reason we predict to find smaller home ranges during twilight in those seasons. The climate effect is expected to have an influence on spatial behaviour, hindering movements during winter because of snow cover and causing wider roaming during summer while searching for water. At last, we predict subadults boars to have a bigger home range than the other classes, being inexperienced and showing dispersal/exploratory behavior.

METHODS

Study area - The study was performed in the Tuscan Apennine (Arezzo Province, Italy) in an area of about 13400 ha, which includes a protected area (Oasi Alpe di Catenaia, OAC) of 2700 ha surrounded by wild boar hunting districts. The altitude range varies from 400m to more than 1400m a.s.l.. The climate is continental, characterized by hot and dry summers and cold and rainy winters, with a high humidity rate. Snow falls from October to April above 1000m a.s.l.. Forest cover exceeds 80% of the study area, while 6% is covered by shrubs. Seven wild boar hunting districts were located all around the OAC, and wild boar hunting season ranged from September to January, three days per week. Drive hunts were carried out with 25-50 hunters and many hounds. Hunting bags were on average 9.6 boars/100 ha. Wild boars constantly roam inside and outside the OAC. Roe deer was the only other ungulate present in the study area. Two predators are present in the area, wolf (with one pack permanently settled, Davis *et al.*, 2012) and red fox (with a density of 1 fox /100 ha, Battocchio *et al.*, Unpublished data), and both use wild boar as a food item. Wolves annual diet is constituted by wild boar for the 58.71%, with a positive selection of 6-12 months old wild boar piglets, which are 33.76% of the annual diet (Bassi *et al.*, 2012). Red fox is homogenously distributed in the area, and 10.65% of its annual diet is wild boar (90.8% of which are piglets; Bassi *et al.*, 2012).

Data collection - Wild boars were captured using both vertical drop nets and traps baited with maize. Captured animals were fitted with Televilt radio collars and transmitting ear tags (Televilt, Sweden, 150-151 MHz wavebands), weighed, measured and aged by teeth eruption and wear according to Briedermann (1990), and released. Only adult wild boars were treated with sedative Zoletil®. During the capture sessions, animals were categorized in 3 age classes: piglets (less than 1 year old), subadults (1-2 years old) and adults (more than 2 years old). We used Wildlife Materials TRX-1000S receivers and a three-element hand-held Yagi antenna to locate radio-collared individuals. From June 2002 to February 2010, all individuals have been located by triangulation of three bearings (White and Garrott, 1990) by the “loudest signal” method. Telemetry data were uniformly distributed over the 24 hours (Swihart and Slade, 1985) with 8-12 locations for each boar per month. We considered 12 hours as the minimum time interval between consecutive locations for the same individual, to exclude data autocorrelation (van Winkle, 1975). From April 2007 to July 2007, we mapped dense shrub areas (DSA) in the OAC, consisting of Rubus spp., Erica spp., Crataegus spp., Prunus spinosa, Spartium junceum and Cystus scoparius, using a GPS receiver (GPS Garmin 60CSX), in order to develop a fine-scale analysis of the influence of shrub areas on wild boar spatial behaviour.

Data analysis - Diurnal, nocturnal and twilight home range sizes were evaluated on a seasonal scale by means of Ranges VI software (Kenward *et al.*, 2003). We used the Kernel method (Worton, 1989) considering 90% of available locations for each animal (Börger *et al.*, 2006). By means of Linear Mixed Models (LMM) we tested the influence of the categorical variables - i.e., sex, age class (piglet, subadult, adult), part of the day (daylight, night, twilight) and season - on: i. percentage of home range area covered by shrubs; ii. distance of boar locations from shrub areas (Corine IV); and iii. distance of boar locations from DSA. The periods included between 1.5 hours before and after sunrise and 1.5 hours before and after sunset were considered as twilight for our analysis. We considered seasons as follows: spring = March-May; summer = June-August; autumn = September-November; winter = December-February. For the home ranges analysis we used telemetry data from 37 wild boars (subadults, 1-2 y.o.; N = 13; adults, ≥ 2 y.o.; N = 24; home ranges N = 117). Piglets (< 1 y.o.) were not considered in this analysis because mothers affected the piglets’ home range size for the first months of life.

In a broad scale analysis we assessed the use of shrubs patches by overlapping the seasonal home ranges on a Corine Land Cover (IV) map using a GIS software (Arcview 3.2, ESRI). We also evaluated the distance of each wild boar location from the nearest shrub area on the Corine Land Cover (IV) map (broad-scale analysis). The dataset for this analysis consisted in 2902 locations of 81 boars (piglets N = 53, subadults N = 14, adults N = 14).

Moreover we performed a fine scale analysis evaluating the distance of each wild boar location from DSA. For this analysis we considered 2279 locations of 56 wild boars (piglets N = 32, subadults N = 10, adults N = 14) collected from 2006 to 2008. We chose to consider only the data recorded one year before and one year after the data collection on DSA, because the perimeter of this habitat changed dynamically. In these analyses piglets' locations were also considered. We assumed that piglets captured simultaneously in the trap were likely to belong to the same group and therefore considered them as a single individual in the statistical analysis so as to avoid the pseudoreplication effect.

In all models, boar identity was considered as a random factor to control for repeated measurements of the same individual. We included all the main effects and all two-way interactions in the LMMs and subsequently excluded the interaction terms that were found not to be significant (P=0.05, for all analyses). Where necessary, dependent variables have been log-transformed to obtain a normal distribution in the model residuals. LMM pairwise comparisons, with adjustment for multiple comparisons, were performed in order to show differences among values of significant variables. All analyses were run using the SPSS 13.0 program (SPSS inc. 1989-2004), and all means have been reported with standard errors.

RESULTS

Home range analyses - Wild boar home range sizes (see Table 1) were affected by sex (F1,116 = 7.44, P = 0.010): males were found to have larger home ranges than females (LMM pairwise adjusted comparisons: P = 0.010; Figure 1). Age had no influence on home range size (LMM: F1,116= 2.24, P = 0.144). Adult males and females showed similar spatial behaviour, whereas subadults males were found to cover broader areas with respect to subadult females (LMM: F1,116 = 3.63, P = 0.065; Figure 1). Boars home range size did not vary significantly among seasons (LMM: F3,114 = 62.72, P = 0.541) and among the different parts of the day (daylight, twilight, night; LMM: F2,115 = 1.99, P = 0.153). The only significant interaction effect between season and part of the day (LMM: F6,111 = 2.93, P = 0.014) occurred in autumn, when boars used smaller home ranges at twilight (Figure 2).

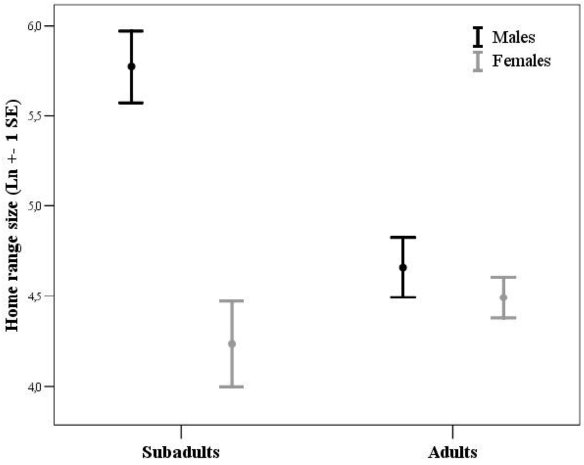

Figure 7 Home range size of female and male wild boars of different age classes in Oasi Alpe Catenaia, Arezzo province, Italy.

Broad scale analysis of the use of refuge areas - The percentage of shrubs in the seasonal home ranges was influenced by sex (LMM: F1,27.895 = 8.442, P = 0.007): females used refuge areas more often than males (mean ± SE: females: 35.128% ± 4.698; males: 16.091% ± 5.371). Boar age, season, and part of the day had no effects on the use of refuge areas.

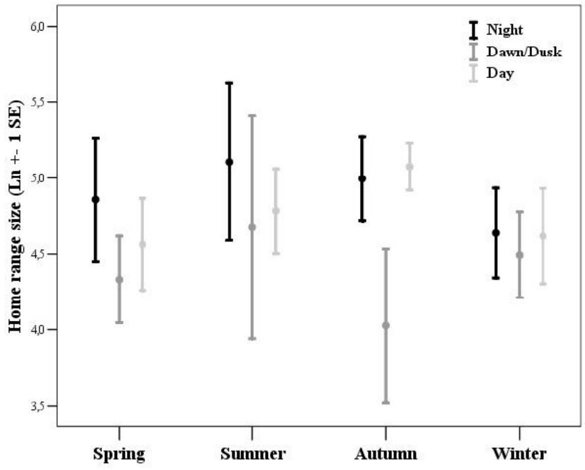

Figure 2 Seasonal home range size of wild boars during different parts of the day in Oasi Alpe Catenaia, Arezzo province, Italy.

Distance of wild boar from shrubs was affected by sex (LME: F1,2260 = 38.35, P < 0.001), season (LME: F3,2258 = 10.56, P < 0.001) and age (LME: F2,2259 = 70.01, P < 0.001). Females stayed, on average, closer to shrubs than males (133.22 ± 10.10 m vs. 204.30 ± 7.92 m; P < 0.001). In winter all boars stayed closer to refuge areas with respect to the other seasons, whereas in summer they used areas further from shrubs (Figure 3a). Throughout the year, females selected shrubs areas differently from males (LME: F3,2258 = 3.02, P = 0.020), showing a less heterogeneous behavior (Figure 3a).

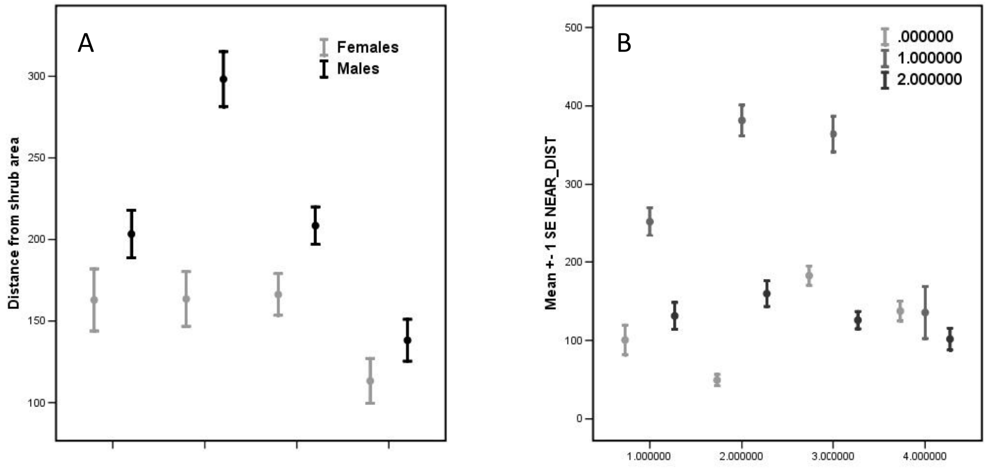

Figure 3 Seasonal distance from shrub areas of wild boars of different sex (A) and age (B) in Oasi Alpe Catenaia, Arezzo province, Italy.

During the year, boars of different ages used the refuge areas differently (LME: F3,2255 = 9.01, P < 0.001): adults showed a more homogeneous behaviour (Figure 3b), whereas subadult individuals could be found significantly further (276.91 ± 12.30) from refuge areas than both piglets (124.55 ± 10.23; P < 0.001) and adults (104.82 ± 11.31; P < 0.001). The part of the day seemed to have no effect on the wild boars' distance from shrub areas (LMM: F2,2259 = 0.33, P = 0.716).

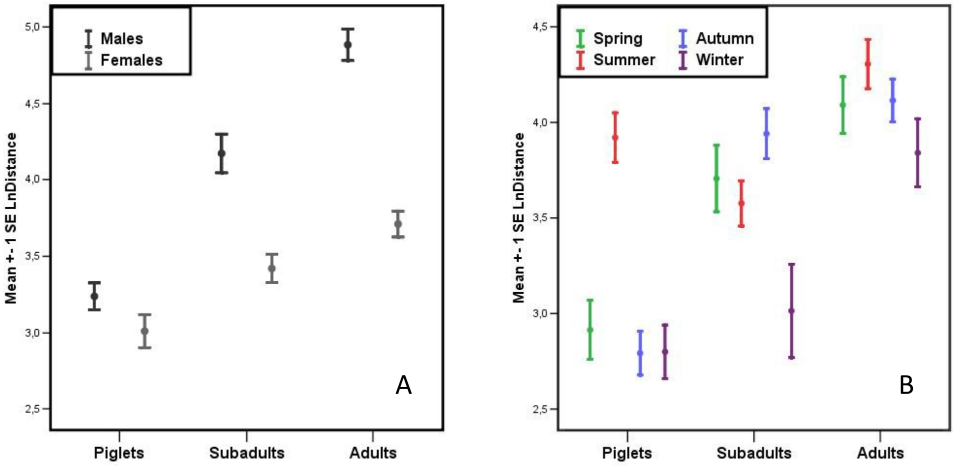

Figure 4 Distance from dense shrub areas of wild boars of different sex (A) and age (B) in Oasi Alpe Catenaia,Arezzo province, Italy

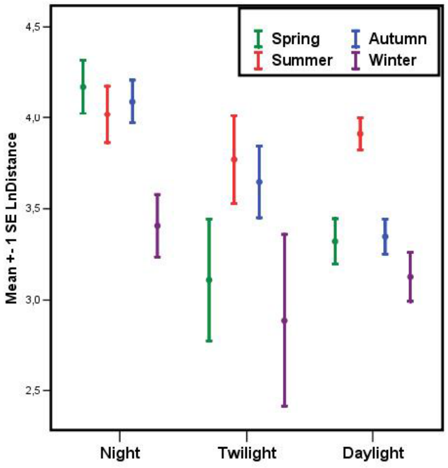

Figure 58 Seasonal distance from dense shrub areas of wild boars during different parts of the day in Oasi Alpe Catenaia, Arezzo province, Italy.

Fine scale analysis of the use of refuge areas - In the finer scale analysis, we found the distance of locations from DSA being affected by sex (LMM:

$F1,2260 = 47.77$, $P < 0.001$) and age class (LMM: $F2, 2259 = 43.79$, $P < 0.001$). Males were generally further from DSA than females (Figure 4a). The LMM pairwise adjusted comparisons showed a significantly different behaviour between piglets and the other age classes (piglets vs. subadults and adults $P < 0.001$), as well as between subadults and adults (subadults vs. adults $P = 0.001$). The combined effect of age class and sex accounted for adult and subadult males being further than females from DSA (LMM: $F2,2259 = 9.81$, $P = 0.007$; Figure 4a).

A)	Female		Both Age Classes
	Adult	Subadult	
Autumn	112.78 (77.27)	151.56 (48.94)	116.3 (75.96)
Spring	105.67 (78.72)	86.62 (49.94)	100.23 (72.11)
Summer	194.55 (257.75)	73.39 (46.33)	156.69 (222.48)
Winter	108.53 (67.64)	97.79 (105.28)	106.63 (75.77)
Total	126.76 (137.5)	93.57 (69.48)	120.02 (75.77)

B)	Male		Both Age Classes
	Adult	Subadult	
Autumn	201.61 (135.17)	425.48 (260.39)	293.79 (225.4)
Spring	183.37 (114.71)	283.52 (215.29)	233.45 (179.61)
Summer	107.31 (103.38)	630.06 (371.98)	392.45 (384.82)
Winter	85.19 (58.5)	379.57 (251.91)	211.35 (224.44)
Total	145.55 (120.13)	449.4 (311.61)	284.81 (274.3)

Table 7 Home range dimensions (mean with standard deviation between brackets) for females (A) and males (B) wild boars. Data are shown by season and age classes, and are expressed as hectares.

Boars used DSA differently throughout the year (LMM: $F3,2258 = 4.06$, $P < 0.001$): in winter they lived closer to refuge areas, while summer is when they stay the furthest. Wild boars of different age showed different behavioural patterns in different seasons (LMM $F6,2255 = 7.55$, $P < 0.001$). In particular, piglets were found to stay further from refuge areas in summer than in the other seasons, and subadults increased the use of areas closer to shrub lands in winter (Figure 4b). The distance from DSA differed significantly according to the part of the day ($F3,2258 = 14.98$, $p < 0.001$). The night was the period in which wild boars were more distant from shrubs (LMM pairwise adjusted comparisons: $P < 0.001$), whereas no difference was found between daylight and twilight. The combined effect of part of the day and season influenced the distance from refuge areas (F6,2255 = 3.60, P = 0.001), as during the day and at twilight, wild boars were closer to shrubs in winter and spring (Figure 5).

DISCUSSION

Home range size and seasonal variations showed a quite pronounced variability with high variance among individuals, however clear patterns emerged, mainly related to sex and to potential predation risk. Broad and fine scale analyses on the use of shrubs areas gave consistent results, coherent with their role as refuge areas and with different sensitivity of sex and age classes to predation risk.

The use of shrubs areas for resting is a typical wild boar behaviour, as reported by several authors (Meriggi and Sacchi, 2000; Saïd *et al.*, 2012; Scillitani *et al.*, 2010; Spitz and Janeau, 1995). Shrubs also provide opportunities to hide from predators and shelter from adverse climatic conditions. Hence, boars use this habitat all year round, in spite of its scarce food availability, making a trade-off between the need to minimize the predation risk and their foraging necessities. Wild boars respond to different environmental stresses (presence and distribution of resources, predation risk and climatic conditions) with heterogeneous behavioral patterns (Fernanda Cuevas *et al.*, 2013; Keuling *et al.*, 2008b). Due to this plasticity, researchers found diversified results as regards the spatial behaviour and habitat selection of wild boar (Keuling *et al.*, 2009).

Hunting and carnivores predation can both exert a considerable pressure on an ungulate population, defining their spatial behaviour and habitat selection, especially refuge areas use (Bongi *et al.*, 2008; Ciuti *et al.*, 2006). Defense strategies of preys often result from a trade-off between predation pressure of different predators and use of resources (Lawton and McNeill, 1979; Sinclair and Arcese, 1995).

In our study area, predators were represented by high-density populations of wolves and foxes, and the area was characterised by a considerable hunting pressure. Wolves preyed on all age classes, but piglets represented up to 34% of their diet (Bassi *et al.*, 2012), and about 10% of the foxes' annual diet. At the same time, hunting can subtract up to 1200 boars per year to the population, generating mortalities that can be as high as 43 to 60% of all marked individuals from different age and sex classes per year. Several authors argued that ungulates' response to hunting is similar to their response to natural predation (Ciuti *et al.*, 2004; Frid, 2003). Neumann *et al.* (2009) suggested that some individuals and some age/sex classes were more sensitive to hunting disturbance, and that they may perceive the human predation risk to be similar to other predation risks. Stankowich (2008) also reported that ungulate responses to human harassment were dependent on sex and on the reproductive status of females. In the same study area, Grignolio *et al.* (2011) showed that human harassment induced different responses in roe deer of different ages, which consequently used refuge areas, represented in that case by protected areas, to different extents.

It is generally accepted that anti-predator behaviour constitutes a major constraint on ungulate behaviour, and that happens especially when small, vulnerable offspring are present (Berger, 1991; Festa-Bianchet, 1988).

Wild boar mothers in our study area, to minimize this risk choose safe places where to give birth and to nurse piglets till they became bigger and more independent. In accordance with this theory, our data show a difference in home range size between sexes: females had smaller home range sizes, with a higher percentage of refuge areas. Moreover, both subadult and adult females were closer to shrubs than males, whereas piglets of both sexes showed similar distances from shrubs. Age was also found to affect home range size: subadult individuals (both males and females) covered larger home ranges than adults, likely on account of their scarcer knowledge of resources and predation risk distribution. Theuerkauf *et al.* (2003) argued that dim light provides the best hunting conditions for wolves, and twilight hours (i.e. dawn and dusk) also coincided with the peak of hunting pressure in our study area. Accordingly, the use of refuge areas by wild boars reaches its highest at this time of day in autumn and winter, presumably due to the combined effect, during those seasons, of natural predation and human hunting.

Wild boar is generally biphasic with a nocturnal active phase (Mauget *et al.*, 1984). Our results showed that wild boars ventured further from shrubs patches during night, while during the day and twilight they used refuge areas more frequently. In our study area, where the forest is highly used by humans almost all year long (forest workers, hunters, hikers, etc.), this behavioural pattern could also be related to human harassment level, which is lowest – if not absent – during the night.

As the differences between sexes and parts of the day seem to be mostly related to predation risk and disturbances, the differences between seasons showed by our analyses are most probably related to climatic conditions too. Wild boar are clearly closer to refuge areas during winter, in face of hunting pressure and harsh climate, and further away during summer (Figure 5). During winter, the climatic conditions are quite difficult, sometimes with as much as 1m of snow on the ground, which probably works as a mechanical impediment for the animals, that in turn stay closer to refuge areas. Supporting this idea is the fact that adults, the taller and bigger individuals, are less affected by the winter season compared to the other age classes (Figure 4B). Conversely, summer results to be the season where wild boar stays further from shrubs areas. In our opinion, this is due to the scarcity of water that affects the area during the warm season, forcing animals to roam further to find it. In conclusion, our results pointed out the importance of small-scale habitat selection in wild boar, suggesting that a different use of resources between sexes may induce a fine scale sexual segregation. Further studies should aim at clarifying whether males and females of wild boar live segregated, at least during the weaning period, and if this segregation could be explained by the predation risk-reproductive success hypothesis (Main *et al.*, 1996; Mooring *et al.*, 2003; Ruckstuhl and Neuhaus, 2000).

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Appendix B

Wild boar under fire: how to survive?

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Wild boar under fire: how to survive?

Merli E.[1], Grignolio S.[1], Marcon A.[1], Apollonio M.[1]

1 Department of Science for Nature and Environmental Resources, University of Sassari, Sassari, Italy

ABSTRACT

Wild boar (*Sus scrofa*) is an ungulate of major management concern, often controlled only by indiscriminate recreational hunting which represents its main cause of death. Several studies have dealt with the effects of hunting on wild boar populations, pointing out controversial changes in spatial behaviour and habitat use related to it. Conversely, little information on the relationship between spatial behaviour, habitat use and hunting mortality is available. In this study, 105 wild boars were monitored by means of radio-tracking and their cause of death was assessed, thus confirming the major role of hunting. For 89 of them, spatial behaviour and habitat use as well as social class were related to hunting mortality by means of Generalized Linear Mixed Models. Spatial behaviour, expressed as home range size, average daily distance among fixes and familiarity with the hunting area, resulted to have no significant effect on hunting mortality. Conversely, habitat use, expressed as the proportion of forests in the home range, landscape complexity and habitat diversity, had a major role in predicting hunting mortality. In particular, the best model including social class and refuges pointed out a positive effect of landscape complexity. Forests had a negative effect on the animals which were not close to refuges and a positive one on the others. Adult males and subadults of both sexes were more liable to be hunted than family groups. On the whole, behavioural and ecological differences in hunting vulnerability should be taken into account in management plans in order to optimise population management.

Keywords: wild boar, mortality, habitat, movement, hunting, management,

INTRODUCTION

Among mammals, ungulates are one of the most directly human-impacted and managed animal taxa (Apollonio, Andersen & Putman 2010). The fate of many ungulate species depends on the interaction with humans whose survival and culture, on the other hand, often depended on the interaction with ungulates (Jarman 1972). Hunting and poaching are often the activities by which humans directly affect ungulate populations (Darimont *et al.* 2009). Nowadays major attention has been devoted to the possibility to properly manage ungulates by developing hunting plans, though their effectiveness is still debated (Brown *et al.* 2000, Riley *et al.* 2003, Stedman *et al.* 2004, Lebel *et al.* 2012). Researchers have recently increased their interest in the evolutionary effects of harvesting on life history and morphological traits (Ciuti *et al.* 2012, Allendorf & Hard 2009, Coltman *et al.* 2003), as humans can cause more rapid phenotypic changes than many natural agents (Darimont *et al.* 2009). Population size reduction is often accompanied by bias in the balance of sex and age classes, thus causing knock-on consequences that negatively affect populations and lead to a severe perturbation and decline of ecosystems (Festa-Bianchet & Apollonio 2003, Milner, Nilsen & Andreassen 2007, Hengeveld & Festa-Bianchet 2011, Coltman *et al.* 2003). Biased hunting plans are more frequent in areas where a species is considered a pest and therefore their aim is to reduce the population size without adopting any qualitative approach (Apollonio *et al.* 2011).

In Europe, among ungulates, wild boar is one of the most serious agricultural pests (Calenge *et al.* 2004, Schley *et al.* 2008, Schley & Roper 2003), causing problems also to livestock farmers by destroying pastures and acting as a vector for disease transmission and zoonosis (Artois *et al.* 2002, Costard *et al.* 2009). This species is also a threat to natural habitats because of its ground rooting habit, which affects plant species richness and, consequently, biodiversity (Bruinderink & Hazebroek 1996, Motta 1996, Hone 2002). Moreover wild boar is a species of major management concern because of its massive increase in demographics and distribution all over Europe and North America ((Saez-Royuela & Telleria 1986, Vetter *et al.* 2015). Moreover, in many European countries, wild boar is considered one of the most attractive game species by hunters, who continuously attempt to maximise their number (Apollonio, Andersen & Putman 2010). Wild boar hunting plans rarely imply a well-balanced harvest among sex and age classes and take advantage of long hunting seasons regardless of biological periods (Apollonio *et al.* 2011). As recently reported by Massei et al .(2015), recreational hunting represents an ineffective method to reducewild boar populations. However, in Europe, this species is recognised to have a high economic value especially in the light of such intensive harvest regime (Toigo *et al.* 2008, Tsachalidis & Hadjisterkotis 2008, Massei *et al.* 2015).

If compared to other European ungulates, this species is also characterised by uncommon life history traits and behavioural responses to environmental stress and hunting pressure, modifying reproduction phenology and social class contribution to reproduction (Gamelon *et al.* 2011, Servanty *et al.* 2011, Servanty *et al.* 2009), altering habitat selection (Said *et al.* 2012, Theuerkauf & Rouys 2008) and spatial behaviour (Calenge *et al.* 2002, Keuling *et al.* 2010, Scillitani, Monaco & Toso 2010, Sodeikat & Pohlmeyer 2002). Even though hunting does not appear to be effective in controlling populations, it is often the main cause of death in wild boar (Keuling *et al.* 2013). However, as indiscriminate hunting is an established practice, the chances of wild boar individuals being killed are related to behavioural rather than morphological cues. Behavioural characteristics are seldom specifically addressed in management plans, even though they can lead to important variations in population dynamics (Gamelon *et al.* 2011), especially in the case of wild boar. Several studies have dealt with spatial behaviour of this species in relation to hunting, though their results are controversial, varying according to intensity of hunting (Morelle *et al.* 2015). A number of authors found that hunting had a strong influence on the distance between consecutive resting sites and home range size (Calenge *et al.* 2002, Maillard & Fournier 1995). Conversely, in other studies hunting is associated to weak (Keuling, Stier & Roth 2008) or heterogeneous effects, highly related to the degree of hunting pressure and refuge position (Scillitani, Monaco & Toso 2010, Tolon *et al.* 2008). Studies on the habitat use of wild boar tend to focus on the sex-biased use of habitat and refuge areas (Said *et al.* 2012) and on human disturbance, pointing out how this species avoids open habitats and prefers forest areas, particularly when facing intense hunting pressure (Boitani *et al.* 1994, Merli & Meriggi 2006, Scillitani, Monaco & Toso 2010, Theuerkauf & Rouys 2008, Tolon *et al.* 2009). On the other hand, wild boars adopting different behavioural patterns can run heterogeneous culling risks. In general, little is known about the actual culling success in case of ungulates adopting different behavioural patterns and thus of a human-mediated selection of behavioural traits (Ciuti *et al.* 2012). In wild boar, as yet, no study has dealt with the individual consequences of adopting different behavioural patterns on account of hunting. In this paper, we stressed the importance of understanding the consequences for wild boar survival chances to adopt different ecological choices in face of hunting. This study was conducted in an area of Central Italy where wild boar hunting is intensively practiced and very popular among hunters in order to define: i) the importance of hunting as a cause of death among wild boar populations; ii) the role of different individual behavioural traits in influencing hunting mortality.

MATERIALS AND METHODS

Study area

Data were collected in an area of the Tuscan Apennines (Provinceof Arezzo, Central Italy). The borders of the study site (8,612 ha) were determined by using the 100% Minimum Convex Polygon, computed with all wild boar locations (see below for more details on spatial behaviour data collection). The study area partially overlapped a protected area, the 'Oasi Alpe di Catenaia' (OAC), which covers 28 km^2 (15.1% of the study area). Elevation ranges from 330 to 1,414 m a.s.l., with main peaks within the OAC. The area has a continental climate, with hot and dry summers, cold and rainy winters, high humidity rate and occasional snow from October to April above 1,000 m a.s.l.. The area is mainly covered with deciduous forests (67%), consisting of beech (*Fagus sylvatica*) at higher altitudes, and Turkey oak (*Quercus cerris*) and chestnut (*Castanea sativa*) at lower altitudes. Conifer forests of black pine (*Pinusnigra*) and Douglas-fir (*Pseudotsuga menziesii*) represent 7% of the study area, while shrubs and pastures cover around 7% and cultivated areas 16%. Deciduous coppice forests with a harvest rotation of 20 years (mainly oak, *Quercus* spp, and chestnut) are prevalent outside the OAC. These forests are characterised by a high density of stems and, as a consequence, by a rich undergrowth vegetation. Conversely, high deciduous forests (mainly beech, *Fagus sylvatica*) and conifer forests (*Pinus nigra*, *Abies alba*, *Pseudotsuga menziesii*) with scarce undergrowth vegetation prevail inside the OAC. Red fox (*Vulpes vulpes*) and wolf (*Canis lupus*) inhabit the study area and wild boar resulted to be the most important prey for the latter (Bassi *et al.* 2012). Roe deer (*Capreolus capreolus*) is homogeneously distributed throughout the study area, while the presence of red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) is limited.

Hunting was forbidden inside the OAC and regulated outside of it. In particular, wild boar hunting began on the third Sunday of September and ended on 31 January. Wild boar hunting was permitted on Wednesdays, Saturdays and Sundays and included battues (i.e., dog drives) with 6-7 teams, each composed by 30-50 hunters (no less than 25 hunters allowed by law) and many hounds.

During the study period, the yearly hunting days averaged 58.3 (min= 47, max = 68, ES= 2.528) and the wild boars killed averaged 687.1 (min= 300; max= 1066; SE= 85.907).

Data collection

To capture wild boars, we used both vertical drop nets and traps baited with maize. We manipulated piglets and subadult wild boars without chemical immobilisation, while adults were treated with sedative ZoletilR. Each individual was weighted, measured and aged on the basis of teeth eruption and wear (Briedermann 1990). During the capture sessions, animals were categorised into 3 age classes: piglets (less than 1 year old), subadults (1-2 years old) and adults (more than 2 years old). All animals were tagged with radio-collars or ear-tag transmitters (Televilt, Sweden, 150-151 MHz wavebands) equipped with mortality sensor.

From June 2002 to February 2010, we located all marked wild boars by means of triangulation of three bearings (White & Garrott 1990) by using the “loudest signal” method. Telemetry data were uniformly distributed over the 24 hours (Swihart & Slade 1985). In order to better distribute fixes in the monitoring period, we considered 12 hours as the minimum time interval between consecutive locations for the same individual.

In order to assess mortality factors, whenever we received a mortality signal from a tag, we searched for the animal and identified the cause of death whenever possible. Causes of death were classified as: culling, poaching, predation, disease and unknown. Culled animals with a tag were usually reported directly by the hunters.

Data analysis

To assess for the possibility of a non-random distribution of the causes of death (Allendorf & Hard 2009), we resampled them via bootstrapping by using the Boot package (Canty & Ripley 2014) of R version 3.1.1 (R Core Team 2014). In so doing, we preliminarily ranked the causes of death by frequency and visually assessed the importance of the differences among them. Hunting harvest proved to be the first cause of death (see the result section) and therefore we performed our analyses to investigate which behavioural and ecological patterns, among wild boar individuals, accounted for survival likelihood during the hunting season. As a first step, we determined the variables of spatial behaviour, habitat use and social class affecting wild boar fate by means of 3 sets of models. Then, we built a new set of models by using only the variables selected during the first step of our analyses. To explore the potential effects of our predictor variables on wild boar fate, we fitted Generalised Linear Mixed Models (GLMM) by using the R library lme4, glmer procedure. Wild boar fate was considered as a binary response variable (death= 1). All the models included two random effects: i) wild boar identity, to account for individual differences; ii) the hunting season, to account for differences among years in environmental conditions potentially affecting hunting efficiency. Fully saturated models were obtained by combining uncorrelated fixed effects ($r < 0.2$). We used a model simplification approach by using backward selection, thus removing the least significant variable to reach the lowest value of AIC (Burnham & Anderson 2002). In all models, we considered the effect of the refuge area (Tolon *et al.* 2009) by using two alternative measures: i) the proportion of the summer home range overlapping the protected area (pREFUGE); ii) whenever collinearity problems with other fixed factors arose, we used a binary variable which took the value 1 when summer home ranges were mainly in the OAC and 0 in any other cases (REFUGE).

To determine which spatial behaviour factors affected hunting mortality, we considered the following predictor variables:

- Summer home range size (HRANGE): we estimated this variable by means of the 90% Kernel method (Borger *et al.* 2006)by using ARCMAP v. 9.3 (ESRI Inc., Redlands, CA) with the Hawth's Tools extension (http://www.spatialecology.com/htools/). Home ranges were computed for boars located at least 12 times during the season (n° fix per individual: mean ± SD 23.7 ± 9.87). In accordance with Borger *et al.* (2006), the Kernel method gives accurate home range estimates with at least 10 fixes, while larger per–animal sampling is necessary to address the high home range inter-individual variation. We chose to use summer home ranges to take into account the same season for all individuals, since the seasonal scale was important to evaluate behaviour (Said *et al.* 2009) in the time span immediately preceding the hunting season, i.e., when individual home range differences were often due to the death of culled individual.

In the models, this variable was log-transformed (LogHRANGE) in order to have a better residual distribution.

- Wild boar mobility (MOB): it was estimated by means of the average minimum summer daily distance between consecutive fixes by using ARCMAP v. 9.3 (ESRI Inc., Redlands, CA) with the Hawth's Tools extension. In the model, the log-transformed values (LogMOB) were analysed to increase the quality of the residual distribution.
- Site familiarity: wild boars were classified into two groups to discriminate the individuals which spent at least the previous three months in the same area used during the hunting season from those which did not. The classification was conducted on the basis of the net-squared displacement (NSD), that measures the straight-line distance between the starting location and the subsequent locations from the movement path of a given individual (Bunnefeld *et al.* 2011). The visual inspection of the pattern discriminated the animals living in the same area in summer and autumn (site familiar) from those which arrived in the area just before the start of the hunting season (site unfamiliar).

Spatial models were computed by using alternatively LogHRANGE and LogMOB because of their strong collinearity (Pearson correlation coefficient $r=0.724$; d.f. = 104; $p<0.001$).

In the second set of models, the aim of the analyses was to assess the influence of habitat use on wild boar fate. Accordingly, we fitted models by using the following independent variables:

- Habitat composition: the proportion of habitat types in the home range was computed by using ArcGis 9.3 and the Corine Land Cover dataset (EEA & ETC/LC, 1999). The Corine Land Cover categories were grouped into 3 larger and homogeneous categories (see Appendix 1 for details): i) open habitats (OPEN); ii) shrubs (SHRUB) and iii) forests (FOREST).
- Shannon-Wiener diversity index (SHANNON): as suggested by Krebs (1999), for each summer home range, we computed the modified Shannon-Wiener index.
- Patches (PATCH): the number of habitat patches (as provided by the Corine Land Cover) overlapped by each summer home range was counted as a proxy of landscape complexity.

Exploratory analysis showed a high correlation among proportions of habitat types in the home range. Hence, in the models we only used the proportion of forests since it was the most strongly related to the others (Pearson correlation coefficients with OPEN and SHRUBS were: r=-0.921 and r=-0.769) and forests were always present in wild boar home ranges, while shrubs and open habitats were sometimes missing. Given the clear collinearity between SHANNON and PATCH, two distinct fully saturated models were constructed by using one of the two variables, alternatively.

The third set was composed of models considering different combinations of sex and age classes, fitted to assess the influence of social class on culling likelihood. Indeed, as reported by several studies (Bieber & Ruf 2005, Massei *et al.* 1997, Morelle *et al.* 2015, Said *et al.* 2012, Spitz & Janeau 1995), social behaviour has been shown to affect spatial behaviour.

- Classification A (CLASS A) provided 2 groups: i) adults: including adult wild boars and piglets of both sexes; ii) subadults: including subadult wild boars of both sexes;
- Classification B (CLASS B) provided 3 groups: i) families: including adult females and piglets, ii) adult males, iii) subadults: including subadult wild boars of both sexes;
- Classification C (CLASS C): provided 3 groups: i) families: including adult females and piglets, ii) males: including both adult and subadults, iii) subadult females.

Finally, the predictors retained by the best GLMMs for spatial behaviour, habitat use and social class were considered for a global synthetic GLMM which included all relevant factors to predict wild boar hunting mortality.

Inspection of variograms enabled us to exclude spatial autocorrelation of residuals in the models. To test for a possible bias due to spatial segregation between harvested and survived wild boars, the distribution of the home ranges was visually tested by means of the Standard Distance tool in ArcGIS. From the geometric mean centre of home-range centroids of survived wild boars we drew a circle with the double of standard deviation of their mean distance as radius. We then compared it with the circle drawn for culled wild boars and did not find spatial patterns.

RESULTS

From 2002 to 2010, 164 wild boars were radio-tagged and 107 (65.2%) died during the monitoring period. The causes were ascertained for 105 animals: 2 boars (1.9% of the sample) were predated, 35 (33.3%) were poached, 67 (63.8%) were hunted and 1 died of starvation (other causes). Variability assessed by bootstrap resampling pointed out hunting as the main mortality factor for the species (mean= 0.638; SE=0.048), and poaching as the second (mean=0.334; SE=0.044). The other factors appeared to be negligible (Fig. 1). From 2004 to 2010, the annual hunting mortality rate of the sample averaged 0.320 (SE=0.0474; min=0.167; max=0.545) and was always the first cause of death, followed by poaching (average = 0.136; SE=0.0294; min=0.000; max=0.250). Once verified the role of hunting, our three sets of mortality models were computed by means of the summer home ranges of 89 wild boars, which had to cope with the hunting season 106 times, surviving in 81 occasions and dying (hunted) in 25. On average, HRANGE was 265.6 ha (SE=22.91; min= 28.85; max= 1530.32), while the average daily distance between fixes of the animals (Mobility) was 257.4 m/day (SE=12.50; min=91.91; max=934.88). 82 wild boars were familiar with the area (77.3%), while the others were not. In 83 occasions (78.3%) homeranges overlapped the refuge area on more than 50% of their extension, with a death rate of 0.17 (14 wildboars shot). In the residual 23 occasions death rate was 0.48.

The best model, among those computed to investigate the role of spatial behaviour on hunting mortality, included LogHRANGE (with a weak positive effect on the likelihoodof being killed) and the variable pREFUGE (with a negative effect) as predictors, while the second-ranked model included only pREFUGE (Table 1). Mobility was included in the third-ranked model, while neither site familiarity nor interaction among variables entered the best-ranked models.

Model	Predictors	Coefficient (SE)	Z	p	AIC	ΔAIC
SP1	LogHRANGE	0.453 (0.310)	1.462	0.144	112.7	-
	pREFUGE	-2.432 (0.803)	-3.029	0.002		
Control	pREFUGE	-2.518 (0.787)	-3.2	0.001	112.9	0.2
SP2	LogMOB	0.663 (0.572)	1.158	0.247	113.5	0.8
	pREFUGE	-2.661(0.812)	-3.279	0.001		
HA1	FOREST	-10.530 (4.476)	-2.352	0.019	103.7	-
	PATCH	2.293 (0.812)	2.824	0.005		
	REFUGE (in)	-22.225 (13.679)	-1.625	0.104		
	FOREST*REFUGE (in)	24.231 (14.454)	1.677	0.094		
HA2	FOREST	-5.429 (1.853)	-2.929	0.003	104.5	0.8
	PATCH	1.682 (0.628)	2.678	0.007		
HA3	FOREST	-9.515 (4.385)	-2.17	0.03	105.1	1.4
	PATCH	1.724 (1.060)	1.626	0.104		
	REFUGE (in)	-28.008 (16.956)	-1.652	0.099		
	FOREST*REFUGE (in)	27.901 (16.344)	1.707	0.088		
	PATCH*REFUGE (in)	1.178 (1.604)	0.735	0.463		
DE1	CLASS A (subadult)	0.878 (0.528)	1.661	0.097	112.1	-
	pREFUGE	-2.421(0.896)	-2.703	0.007		
DE2	CLASS B (adult male)	1.042 (0.809)	1.289	0.197	112.4	0.3
	CLASS B (subadult)	1.186 (0.587)	2.019	0.043		
	pREFUGE	-2.177 (0.906)	-2.404	0.016		
DE3	CLASS C (subadult female)	1.064 (0.661)	1.609	0.107	112.4	0.3
	CLASS C (male)	1.243 (0.661)	1.88	0.06		
	pREFUGE	-2.157 (0.902)	-2.392	0.017		

Table 1 Best-ranked GLMMs of wild boar hunting mortality predicted by spatial behaviour, habitat use and social class, Province of Arezzo (Italy). See text for details.

The best-ranked model describing the influence of habitat use on wild boar fate included FOREST, PATCH, REFUGE and the interaction FOREST*REFUGE (Table 1). The increase in proportion of FORESTS, particularly in home ranges widely not overlapping the OAC, reduced the likelihood of being killed. Landscape complexity had the opposite effect. The other two models selected did not provide any new variable or information. SHANNON was not included in the best models.

Social class	Animals in the sample	Hunted (N)	Hunted (%)
Piglets	38	6	15.8
Subadult females	20	7	35
Subadult males	12	5	41.7
Adult females	23	2	8.7
Adult males	13	5	38.5
TOTAL	106	25	23.6%

Table 2 Wild boar sample size for each social class considered and fate of the animals in the hunting season

As regards the age class and sex of the 106 wild boars (89 individuals) at the beginning of the hunting seasons, we monitored 43 females, 25 males and 38 piglets, whose fate is shown in Table 2. The best model accounting for the role of sex and age of the animals in culling susceptibility pointed out that CLASS A was the most effective to predict mortality (DE1, Table 1). In the model, subadult wild boars, no matter their sex, had a slightly significant higher likelihoodof being killed than adults and piglets. Small differences in AIC were found in the other two models selected. In the first case (model DE 2 considering CLASS B), the likelihood of being culled was higher for subadults than for family groups (adult females and piglets). In the last model selected (model DE3) we found a weak difference between males (adults and subadults) and females with piglets, the former havinga lower likelihood of surviving hunting.

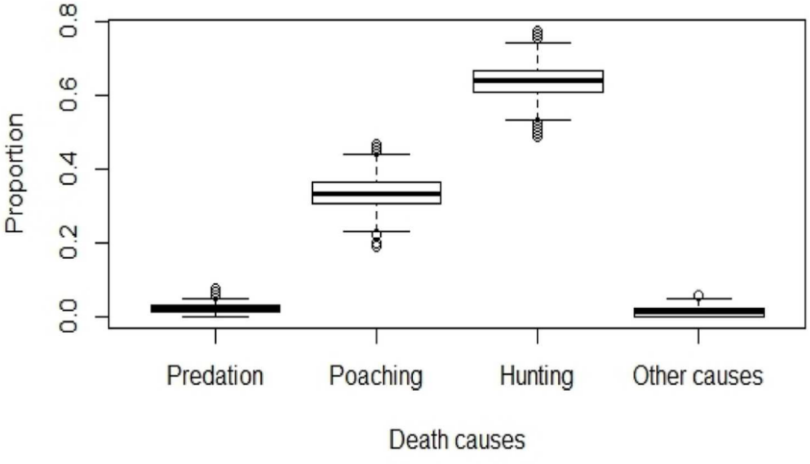

Figure 1 Relative importance (proportion) of mortality causes for 105 wild boars radio-tagged (booted) in the Tuscan Apennines (Italy)

To have a synthetic picture of the role of wild boar behavioural ecology on the likelihoodof being killed during the hunting season, we fitted 6 fully saturated GLMMs taking into account the collinearity between LogHRANGE and PATCHES (Pearson correlation coefficient $r = 0.782$; d.f. = 104; $p < 0.001$) and including, alternatively, the three social classifications pointed out in the models in Table 1. Table 3 shows the results of each model selection process.

Model	Variables	Final predictors	Coefficient (SE)	Z	p	AIC	ΔAIC
SINT1	FOREST PATCH REFUGE CLASS B	FOREST	-9.649 (4.979)	-1.938	0.053	103.4	-
		REFUGE (in)	-21.890 (12.780)	-1.713	0.087		
		CLASS B (Adult male)	1.625 (0.981)	1.656	0.098		
		CLASS B (Subadult)	1.041 (0.620)	1.679	0.093		
		PATCH	2.426 (0.841)	2.883	0.004		
		FOREST*REFUGE (in)	24.261 (13.682)	1.773	0.076		
SINT2	FOREST PATCH REFUGE CLASS C	FOREST	-9.219 (4.624)	-1.994	0.046	103.7	0.3
		REFUGE (in)	-21.05 (12.504)	-1.684	0.092		
		PATCH	2.352 (0.821)	2.866	0.004		
		CLASS C (Subadult female)	1.009 (0.714)	1.414	0.157		
		CLASS C (Male)	1.281 (0.694)	1.845	0.065		
		FOREST*REFUGE (in)	23.194 (13.291)	1.745	0.081		
SINT3	FOREST PATCH REFUGE CLASS A	FOREST	-9.495 (4.261)	-2.228	0.026	104.1	0.7
		REFUGE (in)	-20.152 (12.799)	-1.574	0.115		
		PATCH	2.242 (0.796)	2.815	0.005		
		CLASS A (Subadult)	0.734 (0.570)	1.288	0.198		
		FOREST*REFUGE (in)	21.984 (13.559)	1.621	0.105		
SINT4	FOREST LogHRANGE REFUGE CLASS B	FOREST LogHRANGE	-5.697 (1.763)	-3.231	0.001	109	5.6
		LogHRANGE	0.603 (0.317)	1.904	0.057		
SINT5	FOREST LogHRANGE REFUGE CLASS C	FOREST LogHRANGE	-5.697 (1.763)	-3.231	0.001	109	5.6
		LogHRANGE	0.603 (0.317)	1.904	0.057		
SINT6	FOREST LogHRANGE REFUGE CLASS A	FOREST LogHRANGE	-5.697 (1.763)	-3.231	0.001	109	5.6
		LogHRANGE	0.603 (0.317)	1.904	0.057		

Table 3 GLMMs on wild boar hunting mortality. The independent variables were selected by previous models on spatial behaviour, habitat use and social class, Province of Arezzo (Italy). See the text for more details

When ranking the final models by means of AIC, LogHRANGE provided models with a poorer predictive power of hunting mortality than PATCH. The three best-ranked models showed higher survival chances for wild boars using refuges or having a higher proportion of forests in their home range. The percentage of forests played a negative key-role in individual mortality outside the protected area, while landscape complexity (PATCH) had a positive effect (Figg. 3a and b).

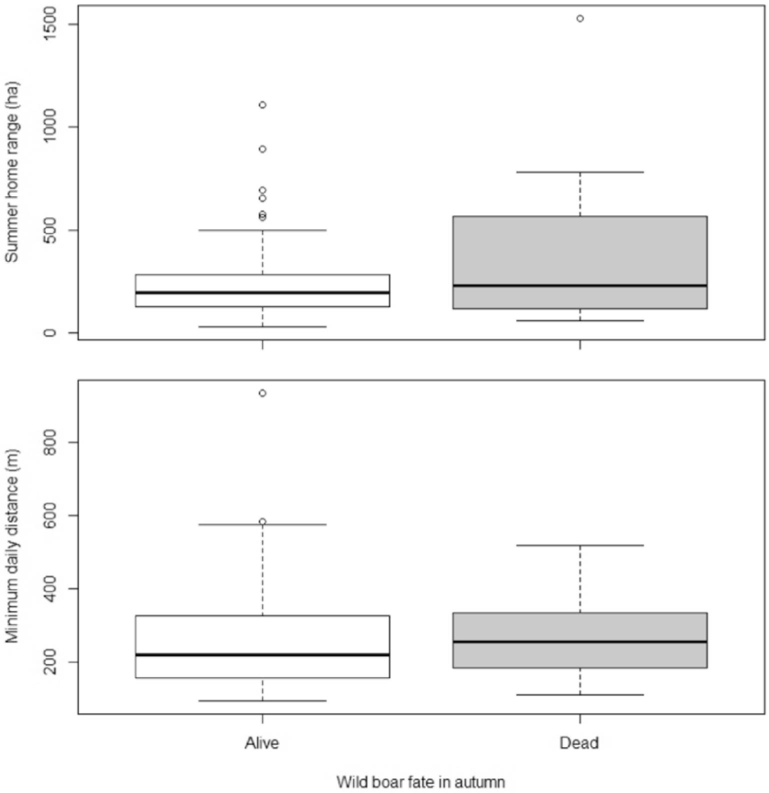

Figure 2 Size (ha) of summer home ranges observed and mobility of wild boars monitored with respect to their fate in the Tuscan Apennines, Italy.

DISCUSSION

Wild boar has been reintroduced in our study area in the 1970s for hunting purposes and nowadays hunting results to be the major cause of death for this species, as reported also in other studies on different locations (Keuling *et al.* 2013, Nores, Llaneza & Alvarez 2008, Toigo *et al.* 2008). In the review by Keuling *et al.* (2013) referring to Europe, 85% of adult mortality was due to culling, while, in our study, hunting accounted for 63.8% of deaths of marked wild boars. By adding poaching (33.3% of death), we obtained a likelihood of 97.1% for wild boar of dying due to direct human persecution, in our study area. The annual hunting kill rate of 0.32 accounted for about one third of the population each year, slightly less than the 40% rate observed in an intensively hunted population in North-Eastern France by Toigo *et al.* (2008). In the latter, no mortality rate due to poaching was reported (while it was 0.14 in our study).

By analysing the effect of spatial behaviour on hunting mortality, we found only a weak positive effect of the size of summer home ranges, while other spatial behavioural patterns did not enter in the predictive models. The choice of the wild boar to enlarge its usual range, to improve mobility and to shift to unfamiliar sites had a negligible impact on survival to hunting. This is consistent with the heterogeneous results found in the studies on the effects of hunting on wild boar spatial behaviour. Indeed, findings reporting an increase in the home range and distance between consecutive resting sites (Baubet 1998, Calenge *et al.* 2002, Maillard & Fournier 1995, Scillitani, Monaco & Toso 2010) contrast with the results of other research in which smaller home ranges and reduced movements to secure places were observed (Singer *et al.* 1981, Sodeikat & Pohlmeyer 2002). In the light of these findings, Keuling, Stier and Roth (2008) argued that modifications of wild boar spatial behaviour due to hunting are rarely significant and often reversible.

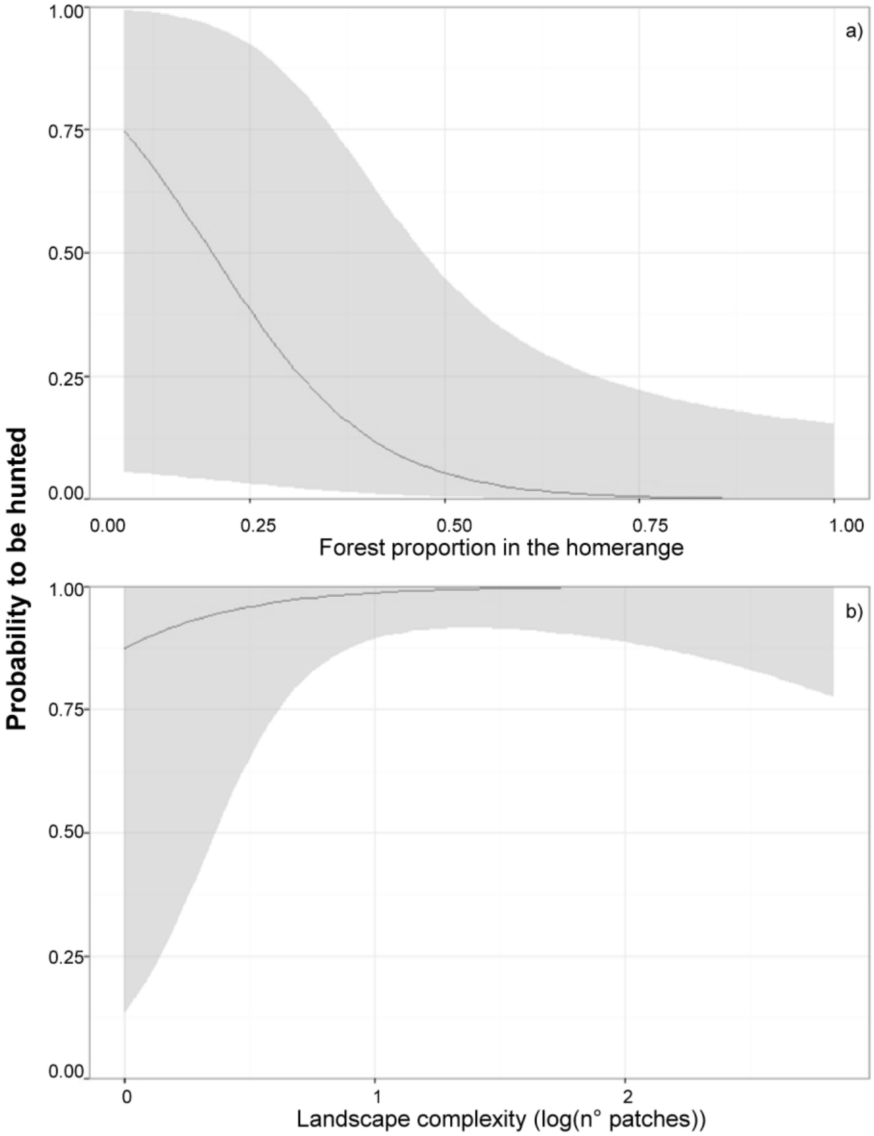

Figure 3 Predicted probabilities of wild boars to be hunted in relation to forest habitat (a) and landscape complexity (b) in the homerange. Predicted probabilities are based on the fixed effects intercept's estimate and each specific fixed term's estimate(Ludeke 2015) . All other fixed effects are set to zero.

Morelle *et al.* (2015) assessed an effect varying according to intensity of hunting pressure. Our results support the hypothesis that, at least in the case of drive hunts with hounds, movements response to hunting does not considerably affect the likelihood of being harvested. Conversely, the hunting risk may be due to differences in the habitat composition of the home range, which can determine the failure or success of the same spatial response to hunting. As reported by Scillitani, Monaco and Toso (2010), family groups reacted to drive hunts by increasing mobility if directly chased by dogs and beaters, while they rested hidden if not found. Habitats offering more shelters can favour resting animals, while habitats with poorer refuge opportunity may disfavour them. In our study, this was confirmed by the importance of the presence of forests in the home range to enhance survival chances.

Given their suitability for feeding and sheltering, forest habitats, particularly deciduous forests, are known to be often selected by wild boars both in Southern and North-Eastern Europe (Boitani *et al.* 1994, Fonseca 2008, Meriggi & Sacchi 2000, Thurfjell *et al.* 2009). In our study area, the choice of forest clearly seemed to reduce the hunting risk, together with the use of protected areas. Tolon *et al.* (2009) showed that wild boars with home ranges close to a protected area shifted toward the refuge site during the hunting season.

Habitat categories	CORINE LAND COVER Classes within the home ranges (Code and Legend)
OPEN	112 Discontinuous urban fabric (residual) 211 Non-irrigated arable land 231 Pastures 241 Annual crops associated with permanent crops 242 Complex cultivation patterns 243 Land principally occupied by agriculture, with significant areas of natural vegetation 321 Natural grasslands
FOREST	311 Broad-leaved forest 312 Coniferous forest 313 Mixed forest 322 Moors and heathland 324 Transitional woodland-shrub
SHRUB	311 Broad-leaved forest 312 Coniferous forest

Table 4 CORINE LAND COVER classes and habitat categories they have been grouped in.

Our results highlighted the importance of the protected area for survival and thus supported the conclusion that, when the risk was higher, the ability to locate safe places increased the likelihood of surviving. These findings on the role of landscape characteristics on hunting mortality demonstrate that environmental management (e.g., forest management, establishment and management of protected areas) is a key factor for wild boar population dynamics. Our results pointed out that subadult and adult males were more susceptible to hunting mortality than females and piglets, with the former using forests less frequently than the latter, though the difference in forest use was not wide enough to fully explain the variation observed. A relationship between habitat use and social class in ungulates does exist: animals of different sex and age classes are more sensitive to predation (including hunting) and use habitats and refuge areas differently (Ciuti *et al.* 2004, Main, Weckerly & Bleich 1996). Accordingly, Spitz and Janeau (1995) observed how sows with piglets preferred dense habitats, while subadult males often used open habitats. During the hunting season, females react differently from males and tend to increase the selection of coppice habitats rather than bush-lands, while males do not (Said *et al.* 2012).This may explain the higher likelihood of males and subadults being hunted. Moreover juveniles show poorer movement abilities, possibly leading family leaders to "evaluate" (in the movement ecology framework developed by Nathan *et al.*, 2008) too expensive and dangerous those strategies which imply increasing mobility.

These results pointed out the unnatural population dynamics of this species, which are strictly affected by human activities. Although wild boar is one of the most relevant pests in Europe (Calenge *et al.* 2004, Schley *et al.* 2008, Schley & Roper 2003), the information provided by much research as well as by the results of our study on Central Italy showed that human harvest (i.e., hunting and poaching) cannot be the only answer to this problem (Massei *et al.* 2015). Even though human harassment is virtually the only cause of death for wild boars, no significant signs of a reduction in the population size or in damages caused by wild boars were found in Tuscany. In this framework, it seems clear that a part of the wild boar population is more affected by culling, while the other is able to survive and reproduce.

The goal of wild boar management should be the maintenance of well-structured populations with the lowest density, compatible with the survival of the populations, in order to reduce the impact of the species while preserving its ecological role. Since recreational hunting is the main tool to control wild boar populations, it is of primary importance to be aware of the ecological effects of this practice and to take them into account in hunting programs. As demonstrated by this research, drive with hounds is selective with respect to social class and habitat use of wild boars. This, combined with the actual inadequacy of the present hunting practices in controlling population levels, can promote perturbations in the socio-ecology of the species which may potentially lead to undesired scenarios.

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Conflict of interest: the authors declare that they have no conflict of interest.

Ethical standards: this study complies with all national and regional laws dealing with ethics and animal welfare. The research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

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