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REVIEW

Lack of natural control mechanisms increases wildlife–forestry conflict in managed temperate European forest systems

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Abstract Across Europe, ungulate numbers have greatly increased over the past decades, leading to increasing concerns about the ecological and economical impacts and pleas for stronger population control. However, focussing on population control only ignores other underlying factors which may enhance the wildlife–forestry conflict. I reviewed factors which shape herbivore top-down effects in natural temperate forest systems aiming at understanding how these interactions are altered in managed forests. Carnivores are important in modifying ungulate–plant interactions. They can directly influence the numbers of ungulates, but this effect is dependent on productivity and predicted to be smallest in highly productive temperate forest. Indirectly, they modify herbivore top-down effects by creating a landscape of fear. Despite the abundance of knowledge from American systems, there is a lack of knowledge on how this process might work in European systems. Next to carnivores, abiotic conditions interact with herbivory by influencing forage quality and availability. Forest gaps lead to concentration of ungulates and their effects, due to increased forage supply. Abiotic conditions also influence the response of plants following herbivory, which can be tolerated by showing increased regrowth or resistance due to chemical or physical defence. In typical managed forest systems, carnivores and abiotic conditions which shape ungulate top-down effects in natural forests are altered or absent. Human hunting might replace the direct effects of carnivores, but does not replace their indirect effects. Forestry practices also have modified herbivore–plant interactions in several ways, creating a forest with lower ungulate carrying capacity and higher sensitivity for ungulate browsing. These changes logically increase the strength of herbivore top-down effects in managed forests and increase the wildlife–forestry conflict. To reduce this conflict, aiming only at reducing wildlife numbers is predicted to have little effects when they do not coincide with habitat ameliorations. Forestry practices may therefore greatly enhance the conflict that exists between wildlife and forestry but can also be an important tool to reduce this conflict by adapting management practices that allow more natural functioning of forests systems.

Keywords Ungulates · Browsing · Damage · Red deer · Roe deer · Carnivores · Top-down effects

Introduction

Across Europe, ungulate numbers, especially different deer species, have greatly increased over the past decades (Apollonio et al. 2010). This phenomenon is not unique to Europe as in many areas within the temperate zone there has been much attention on the overabundance of deer, for example in North America (McShea et al. 1997; Côté et al. 2004) and New Zealand (Tanentzap et al. 2009). Different factors have been indicated in driving this increase: increasing frequency of mild winters (Mysterud et al. 2001), changes in management rules (Milner et al., 2006), changes in forestry practices (Bobek et al. 1984) and changes in the agricultural landscape (Mysterud et al. 2002).

The growing numbers of deer have resulted in increased herbivore pressure which affected ecosystems in many

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ways. Several studies reported a negative impact on tree regeneration (Ammer 1996; Van Hees et al. 1996; Kriebitzsch et al. 2000; Scott et al. 2000) or decreasing abundance of preferred forage species (Horsley et al. 2003; Modry et al. 2004; Long et al. 2007). As a result, tree species diversity (Ammer 1996; Kriebitzsch et al. 2000) and herbaceous vegetation diversity (Augustine and Frelich 1998) tend to decrease in many areas in the presence of deer. Next to effects on plant communities, other trophic levels have also been affected such as decreasing songbird diversity (McShea and Rappole 2000; deCalesta 1994) and small mammal communities (Healy and Brooks 1988; Smit et al. 2001). Finally, increasing deer numbers cause economical damage to forest plantations enhancing the conflict between forestry and wildlife (Ammer 1996; Putman and Moore 1998; Senn and Suter 2003). These growing ungulate populations have led to growing concerns about both the ecological and economical consequences (Fuller and Gill 2001; Côté et al. 2004; Gordon et al. 2004) and pleas for stronger population control (Côté et al. 2004; Gordon et al. 2004). However, focussing only on population control ignores other underlying factors which may enhance the conflict with wildlife. As in practice, population control seems unable to counteract the strong increases in ungulate populations (Milner et al. 2006), a better understanding of the factors that shape the effects that ungulates have in forest systems could help to mitigate problems in alternative ways.

Most of our knowledge concerning the effects of ungulates on forest communities in the temperate zone originates from managed or in other ways strongly human-impacted forest systems. This is not surprising given that temperate biomes are globally most affected by humans. In relatively densely populated areas, such as in Europe, only small remnants of forests with a pristine or primeval character can be found (Hannah et al. 1995; Bengtsson et al. 2000). This bias towards managed forest systems may strongly influence the observed effects of ungulates, as in complete or natural forest systems their top-down effects are likely to be shaped by several factors which are often absent in managed forests. The presence of large carnivores is often first pointed out as a likely control mechanism preventing increasing ungulate numbers and overutilisation of food resources by herbivores. However, next to carnivores, the importance of environmental conditions in shaping herbivore top-down effects is often neglected. They may directly influence patterns in tree recruitment but also indirectly alter foraging habitat quality for herbivores and hence influence foraging behaviour. As in human-impacted landscapes, both carnivore abundances and environmental conditions have often been altered, and herbivore top-down effects are likely to be different from those in more primeval or natural environments.

In this article, I will address how both factors (carnivores and environmental conditions) shape herbivore top-down effects, aiming at understanding how these effects can change when environmental changes occur as a result of management practices or disappearance of top-carnivores. I will discuss why top-down effects of ungulates are likely to differ greatly between natural and managed forest systems with a primary focus on European temperate forest systems. The ungulate species I am focusing on are the ones which naturally occur inside contemporary European temperate forest systems; Red deer (*Cervus elaphus*), Roe deer (*Capreolus capreolus*), moose (*Alces alces*), European bison (*Bison bonassus*) and wild boar (*Sus scrofa*), but will refer to studies on other ungulate species from temperate forest systems across the globe.

In natural systems carnivores shape herbivore top-down effects

Large carnivores can play an important role in structuring ungulate communities with cascading effects on other trophic levels (Fortin et al. 2005; Beyer et al. 2007; Beschta and Ripple 2009; Terborgh and Estes 2010). They modify plant–herbivore relationships both directly and indirectly. The classical view is that carnivores directly modify these relationships by top-down regulating herbivore populations and releasing plants from herbivore control (Oksanen et al. 1981; Fretwell 1987; DeAngelis 1992). For several temperate forest systems, these top-down effects of carnivores on the ungulate community have been illustrated both inside (f.e. Jędrzejewski et al. 2002; Jędrzejewska and Jędrzejewski 2005) and outside Europe (f.e. Messier 1994; Ripple and Beschta 2005). The strength of these direct effects of carnivores on the ungulate community is dependent on the productivity of the system. Melis et al. (2009) illustrated this for Roe deer, *Capreolus capreolus*. They showed that on a geographical scale, large carnivores regulate their prey population strongly in low productive habitats, whereas carnivores had smaller effects on prey population in productive habitats. Similarly, Jędrzejewska and Jędrzejewski (2005) showed for one area on a long timescale that top-down effects were most pronounced during periods with colder climatic conditions and hence lower plant productivity.

Next to these direct density-mediated effects, recent studies suggest that indirect, nonlethal effects of carnivores may be as important (Schmitz et al. 1997) or even more important in influencing herbivore–plant interactions than their direct lethal effects on population density (Creel and Christianson 2008). The presence of carnivores influences behaviour, habitat choice and spatial distribution of ungulates that are preyed upon (Creel et al. 2005; Fortin et al.

2005; Frair et al. 2005). A well-known example of indirect effects of carnivores on ungulate-plant interactions originates from studies carried out in the Yellowstone National Park, USA. These studies showed that after reintroduction of wolf (*Canus lupus*), their main prey species elk (*Cervus elaphus*) changes its habitat choice by avoiding high-risk areas. Carnivores thus created a 'landscape of fear' in which some habitats with high predation risk were avoided by ungulates (Creel et al. 2005; Fortin et al. 2005; Mao et al. 2005). Elk avoided encounters with wolves on a large landscape scale by moving to areas less frequently used by wolves (Mao et al. 2005) in areas further away from hard edges, such as streams and forest edges that increase vulnerability of elk to wolf predation (Bergman et al. 2006). On the other hand, they avoided on a small scale the high predation risk habitats. Avoided habitats were characterised by a higher amount of escape impediments, structural objects that could affect speed, manoeuverability and escape potential (Halofsky and Ripple 2008). Escape impediments affect elk vigilance levels at a very fine scale (1–187 m). Other studies indicated that habitat visibility also plays a role as visual obstructions can reduce detectability of predators (Ripple and Beschta 2006). In areas which were preferred by elk as foraging habitat during the wolf-free period, the numbers decreased after the reintroduction of wolves. As a result of these shifts, the spatial patterns of herbivore top-down effects were also altered. In avoided areas, such as river valleys, increased tree recruitment occurred as trees were released from herbivore top-down control (see review by Beschta and Ripple 2009). This resulted in a change of these areas with cascading effects on other trophic levels, as the increased tree regeneration created suitable habitats for other species which depended on them, such as fish and bird communities.

Our knowledge of the indirect effects of large carnivores in shaping herbivore–plant interactions mainly stems from American ecosystems (see review by Beschta and Ripple 2009). The role large carnivores play or can play in shaping these interactions in European forest systems is still poorly studied (Manning et al. 2009). This is mainly due to the fact that carnivores have been exterminated and are absent in most forest systems in the temperate region in Europe. Recently, there has been an increasing debate on the reintroduction of large carnivores, such as wolves and lynx, in areas in Western Europe, as they may play an important role in nature management by directly and indirectly affecting ungulate numbers and behaviour (Manning et al. 2009). However, the question arises whether they will actually meet these expectations. Firstly, the effects of predators on ungulate populations in highly productive environments, such as temperate forests, are expected to be low (Melis et al. 2009). This is in line with studies from the Białowieża Primeval Forest, one of the few European temperate forest systems where both wolves and lynx are present (Jędrzejewski et al. 2002; Jędrzejewska and Jędrzejewski 2005). These studies showed that predation rate by both carnivores for the ungulate species they preyed upon (Red deer, Roe deer and wild boar) is inversely density-dependent or did not change with prey density. This indicates that carnivores did not regulate ungulate abundance but did limit the population under the level set by the carrying capacity at a given moment (Jędrzejewski et al. 2002; Jędrzejewska and Jędrzejewski 2005). These findings correspond to studies from Isle Royal, USA, which showed that inter-annual variation in moose population growth rate was more explained by bottom-up factors (food availability) and abiotic factors (climate) than by predation (top-down factors, Vucetich and Peterson 2004). Secondly, the indirect effects of carnivores have been illustrated to work in large national parks in America (Beschta and Ripple 2009) which show large landscape heterogeneity including dense forest, open plains, large rivers and mountain ridges. It is the question whether similar effects of carnivores, via the creation of a landscape of fear, will operate in much smaller nature reserves present in Europe containing more finely grained landscape heterogeneity. This difference in scale is, for example, illustrated by the size of the Yellowstone National Park (8,980 km^2) where much of the existing knowledge originates from, which is more than 15× as large as the entire Polish part of the Białowieża Primeval Forest (600 km^2) or 85× the Bialowieza National Park (105 km^2) Europe's best preserved lowland forest system.

In summary, carnivores can be an important agent in modifying ungulate–plant interactions (Fig 1a). They can directly influence the numbers of ungulates, but this effect depends on productivity. In highly productive temperate forest systems in Europe, the direct effect in regulating ungulate numbers is relatively small. Next to their direct effects, carnivores may indirectly modify the (spatial distribution of) herbivore top-down effects by creating a landscape of fear. Despite the abundance of knowledge from American systems, there is a lack of knowledge from European systems. Whether indirect effects of carnivores on ungulate behaviour will occur on rather small scale, more finely grained European systems is the question. Hence, reintroduction of large carnivores, ignoring the fact that this may not be feasible at all in many areas due to ecological or socio-economical constraints (Wilson 2004), is not a straightforward solution to prevent the wildlife–forestry conflict.

In natural systems environmental conditions shape herbivore top-down effects

Environmental conditions largely determine the quantity and quality of forage available for ungulates. Both are

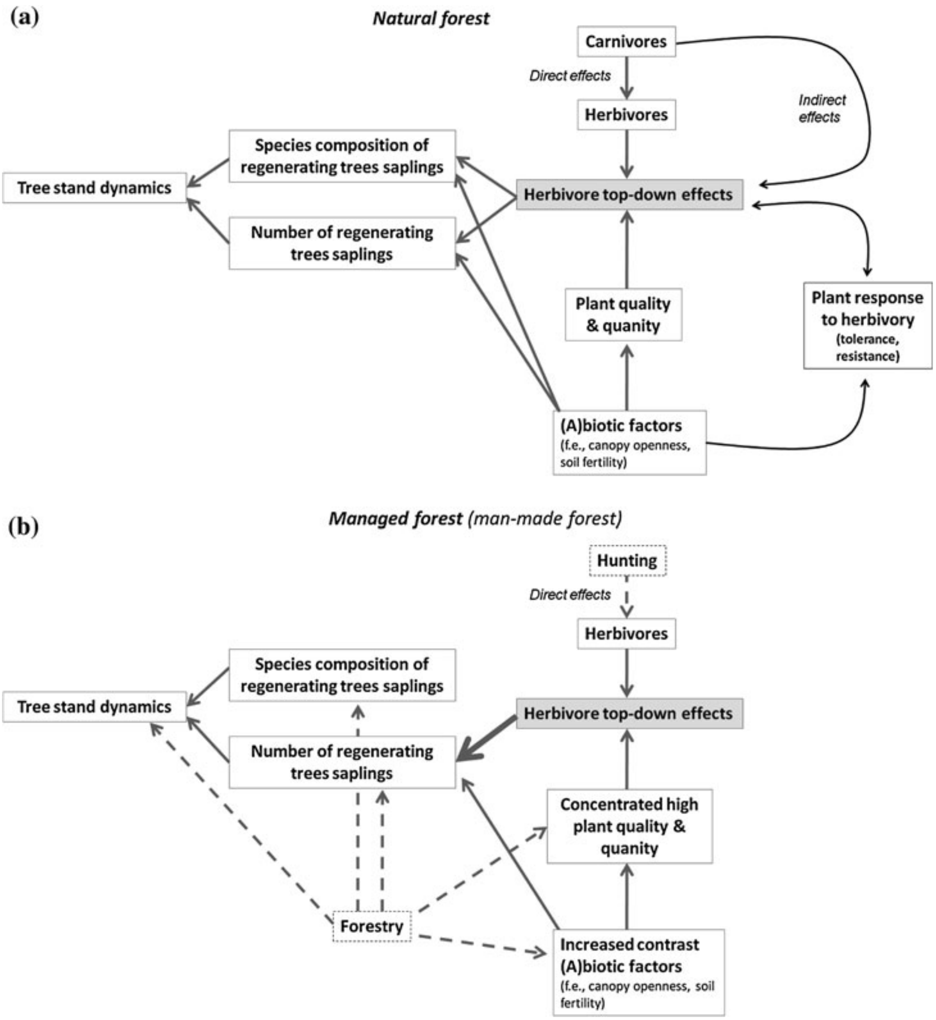

Fig. 1 Differences in herbivore top-down effects between natural forest systems and managed systems. Note that these two extremes are shown and combinations of both may occur, i.e., hunting and natural predators present. In a natural forest, carnivores shape herbivore top-down effects both directly and indirectly. Besides, herbivore top-down effects are shaped via effects of abiotic conditions on plant (forage) quality and indirectly via affecting plant response to herbivory. In managed forest, hunters at best replace the direct role of carnivores not indirectly change foraging behaviour. Forestry practices affect abiotic conditions to larger extent than natural processes and prevent plant response following herbivory by determining species composition and number of trees in the regeneration pool. Due to the change in interactions, herbivore top-down effects on tree growth are stronger in a managed forest systems

relevant factors for ungulates as their foraging decisions are based on the selection of those patches that will result in highest protein and energy intake rates (Langvatn and Hanley 1993; Wilmshurst and Fryxell 1995). Most European forest-dwelling herbivorous ungulates (Red deer, Roe deer, moose and European bison) have a high proportion of woody plant species in their diet throughout the year (Dzięciołowski 1967; Morow 1976; Gębczyńska 1980; Gębczyńska et al. 1991; Kowalczyk et al. 2011). Hence, environmental factors which determine tree recruitment are likely to affect foraging behaviour of ungulates. In mature temperate forests, recruitment of trees typically depends on the formation of gaps (natural or human induced) in the tree canopy (e.g. Runkle 1981; Bobiec 2007) associated with increased light availability. On the one hand, this increases forage availability for ungulates by enhanced regeneration of trees (Runkle 1981; Bobiec 2007) and growth of tree saplings (Latham 1992; Modry et al. 2004). Additionally, the higher abundance of herbaceous vegetation inside forest gaps (Modry et al. 2004) can increase food availability for ungulates with a mixed feeding strategy (browser/grazer). On the other hand, forage quality is affected by increased light levels. Due to higher photosynthetic activity, trees growing in full light tend to have higher C/N ratios in their leaves and twigs (Bryant et al. 1983), resulting in lower digestible forage for herbivores (Molvar et al. 1993; Hartley et al. 1997).

Hence, ungulates selecting for high biomass should select for forest gaps, but ungulates selecting for high quality should rather select for tree saplings in closed forest. Kuijper et al. (2009) showed, in an experimental set-up for an assemblage of ungulate species, that forest gaps were preferentially being visited compared with adjacent closed forest but the effect depended on the species. The main browsers in the system, Red deer and Roe deer, showed respectively 3× and 2× higher visitation frequency inside forest gaps. Wild boar was the only species which tended to occur more in closed forest. As a result of the higher visitation frequency, trees planted in forest gaps had a higher chance of being browsed (70%) compared with trees growing under a more closed canopy (47%, Kuijper et al. 2009). Despite the more favourable growing conditions inside forest gaps, comparison with fenced off trees at the same location illustrated that the reduction in growth by browsing after three growing seasons was larger inside forest gaps compared with closed forest (D.P.J. Kuijper unpubl. results). This illustrates that herbivores more strongly regulate tree growth inside forest gaps. As increased light levels increase productivity of trees but decrease tree chemical quality, the higher visitation in forest gaps and the higher proportion of browsed trees as observed in Kuijper et al. (2009) suggest that ungulates were selected for higher food availability rather than nutritional quality. This is in line with the findings of Edenius (1993) and Hartley et al. (1997) who showed that ungulates preferentially foraged on trees cultivated at high light levels and suggested that the more favourable growth form of trees growing in light conditions may be overruling their reduced nutritional quality. Trees growing in full light had a higher twig biomass and produced more lateral branches resulting in broader and bushier trees which can explain the preference by ungulates (Edenius 1993). However, other studies, all from boreal forest systems, illustrated the importance of plant chemical quality in determining foraging behaviour of ungulates and smaller herbivores such as snow shoe hare (Crawley 1983; Ball et al. 2000; Bryant 2003) suggesting that in lower productive habitats, plant chemical quality may be more important in shaping plant–herbivore interactions. Preferential foraging of deer inside tree canopy gaps (clear-cuts) has also been found in several other studies inside temperate forest systems (Reimoser and Gossow 1996; Welch et al. 1990; Campbell et al. 2006), which illustrates that foraging behaviour and consequently ungulate top-down effects can to a large extent be shaped by an abiotic factor, such as light.

Next to the effects of abiotic conditions on forage quality and quantity, they can indirectly shape herbivore top-down effects by influencing the response of plants following herbivory (Fig. 1a). Plants can respond to herbivory in three different ways; tolerance, resistance or phenological escape (Agrawal 1998). Plants can tolerate browsing by showing compensatory growth following herbivore foraging, whereas resistance means that plants prevent browsing by the production of secondary plant components or physical barriers. Secondary plant components consist of chemical compounds, such as terpenoids or alkanoids which are toxic. They can also consist of tannins, fibres or lignine, which are not toxic but decrease the digestibility of the plant material (see Verheyden-Tixier et al. 2008; Stolter et al. 2009). Finally, trees can escape from browsing by growing in periods when herbivores are not present. This will only be possible in systems with migratory herbivores and with a long growing season, such as in African systems, and is not likely to occur in temperate systems. Abiotic conditions determine to a large extent which of these responses is shown by plants. It determines on the one hand the regrowth ability following herbivory. In a more productive environment, plants can more easily regrow their lost tissue than in a low productive one (Coley et al. 1985) and hence can be more tolerant. On the other hand, abiotic conditions determine resistance to browsing (Bryant et al. 1983; Coley et al. 1985; Herms and Mattson 1992). The amount and type of chemical defence produced by a plant depend on the resource that most limits plant growth (Bryant et al. 1983). For example, in full light conditions, plants produce carbohydrates due to high photosynthetic activity and are more likely to invest in carbon-based defences. In contrast, in nutrient-rich, low-light conditions, plants have abundant access to nutrients, and nitrogen-based defence is predicted to occur. Physical defence mechanisms are predicted to occur mainly under nutrient poor and dry conditions (Ritchie and Olff 1997), such as deserts and sand dunes. In productive temperate forests, this mechanism is less likely to occur, indicated by the low abundance of spiny bushes or thorny trees in these systems. Hence, tolerance and resistance are two likely mechanisms by which the response of trees to herbivory in temperate forest can be influenced by environmental conditions. For example, inside forest gaps regenerating trees may be able to tolerate higher levels of browsing and/or may show higher defence with carbon-based compounds. Consequently, herbivore top-down effects may differ between forest gaps and closed forest.

A large body of literature exists that illustrates the importance of abiotic conditions in determining the recruitment of trees, such as canopy openness (Runkle 1981; Faliński 1986; Bobiec 2007) and soil fertility (Sipe and Bazzaz 1995; Lusk and Matus 2000; Kuijper et al. 2010a, b). Besides, many studies show the importance of ungulate top-down effects in affecting numbers and species composition of recruiting trees (Ammer 1996; Van Hees et al. 1996; Kriebitzsch et al. 2000; Scott et al. 2000). However, surprisingly, little empirical data are available that show how biotic and abiotic conditions may interact and how this can modify the importance of top-down and bottom-up forces (Hunter and Price 1992). Using long-term exclosures in one of the most natural and complete temperate forest systems of Europe, the Białowieża Primeval forest, Kuijper et al. (2010b) tested how these interactions may shape the recruitment process. In contrast to their predictions, they observed that abiotic factors (soil fertility and light conditions) dominated at the early stages of tree recruitment, whereas herbivore top-down effects shaped the later stages (starting from saplings >50 cm). Other studies, without using exclosures, indicated that the effects of deer foraging on the forest floor herbaceous vegetation may interact with productivity (Randall and Walters 2011). Strongest reduction in forest floor vegetation diversity was observed at high soil productivity. Both studies illustrated the context-dependence of herbivore top-down effects as abiotic conditions that can shape herbivore top-down effects.

In summary, abiotic factors interact in several ways with herbivory by influencing forage quality and availability, so influencing foraging behaviour of ungulates (Fig 1a). Next to the effects of predators on ungulate population or behaviour, interacting effects of herbivory with abiotic factors, therefore, shape herbivore top-down effects (Alberti et al. 2009; Hopcraft et al. 2010). Consequently, heterogeneity in abiotic and biotic conditions may have an important influence on the strength of top-down effects and the role that herbivores play in ecosystems (Hopcraft et al. 2010).

In managed systems lack of carnivores prevents direct and indirect effects on ungulates

I have described earlier how in natural forest systems herbivore top-down effects are shaped by the presence of large carnivores and environmental conditions. In managed forest systems, both these factors are typically (and often strongly) altered by management practices. As a consequence, herbivore top-down effects may greatly differ between managed forests compared with natural complete forest ecosystems. Below, I will discuss how the alteration of both factors strengthens the top-down effects of ungulates and how this increases ungulate–forestry conflict (Fig 1b).

Carnivores have shown long-term declining trends across the globe (Laliberte and Ripple 2004), especially in densely populated areas such as in Europe (Morrison et al. 2007) coinciding with increasing human pressure on the landscape. In recent decades, especially wolves are recovering in several places in Europe both in numbers and in geographic range. For example, following a long period of absence, small populations of wolves live in Germany, Austria, Swiss, France, Sweden and Western Poland (see f.e. Breitenmoser 1998). This trend most probably will continue. However, in the larger part of their former range, large predators are still absent. Also in recently colonised areas, their numbers might currently be too low to have any significant impact on ungulate populations in areas across Europe. The lack of carnivores or the lack of ecologically functional population may have large consequences for the functioning of lower trophic layers such as ungulate-forest relationships. This has been illustrated by American studies attributing the high ungulate numbers and lack of tree regeneration to the disappearance of large carnivores (Beschta and Ripple 2009).

Instead of regulation by carnivores, ungulates in most temperate forest systems are regulated by hunting. Although hunting may well be a way to control numbers at a local scale or at larger scale with a coordinated effort (Hothorn and Müller 2010), there is limited empirical evidence that current (and past) wildlife management is able to control ungulate at larger scales (Milner et al. 2006; McShea et al. 1997). This is illustrated by the strongly increasing deer populations observed throughout Europe (Apollonio et al. 2010) and the USA (McShea et al. 1997, Côté et al. 2004). Therefore, a one-sided focus on hunting to solve the problems between forestry is ineffective. Besides, hunting may for several other reasons be a poor substitute for natural predators as it cannot replace the role of carnivores in an ecologically functional way (Berger 2005). In the context of this paper, the most relevant issue is the difference in the landscape of fear that is produced by human hunting which differs both spatially and temporally from that produced by natural predators. These indirect effects, which result in behavioural changes of ungulates, are determined principally by the hunting method used as well as by the times when hunting occurs. Spatially, the landscape of fear differs between hunting and natural predation because natural predation operates via habitat characteristics in which some habitats have a higher predation risk and are avoided by ungulates. As large carnivores occupy large home ranges, for example on average 200 km^2 for wolves in Białowieża forest (Okarma et al. 1998), these effects operate at a large scale. However, habitat characteristics also have an impact at a very fine scale of only a few metres, such as the number of escape impediments which determines that some locations are more risky than others and avoided by ungulates (Halofsky and Ripple 2008). In contrast, human hunting effort is normally concentrated in a small part of the area and in certain habitats, which provide profitable conditions for hunting (Proffitt et al. 2009). As a result, habitat selection of human hunters differs greatly from that of natural predators which result in different effects on ungulate behaviour. This has been illustrated by Proffitt et al. (2009) who showed that differences in habitat choice between large carnivores and human hunters resulted in a largely different spatial landscape of fear. Whereas human hunters in the Greater Yellowstone Area, USA, mainly shot elk (*Cervus canadensis*) in grassland flats, the chances of being killed by wolves was 23 times higher in sagebrush steppe and 4.5 times higher in grassland hills. The areas used by human hunters were mainly related to factors facilitating access to them, such as the vicinity of infrastructure or hunting towers. In this way, human hunting activity was more predictable and deer reacted stronger to human hunters, and their behaviour (grouping size and movement rates) was affected differentially depending on habitat type when under human hunting pressure compared with when only natural predators were present. Also Jędrzejewski et al. (2006) observed that Red deer group size increased in relation to an increase in human hunting pressure in the presence of natural predators, indicating that human hunting can largely affect deer behaviour in a different way than large predators do. As there is a lack of connection between human hunting effort and habitat characteristics on a large scale, ungulates do not avoid certain habitat types across the entire area but learn quickly to avoid those locations with highest hunting pressure (Proffitt et al. 2009; Tolon et al. 2009).

Regarding the temporal patterns of hunting, specifically defined hunting seasons are common practice. In most areas in Europe, hunting takes place after the reproductive season, generally in late summer to winter (Milner et al. 2006). In several countries in Europe, there are differences in hunting season between males and females, the open season for females being usually somewhat later and shorter (Milner et al. 2006). These open seasons with concentrated hunting activity result in temporally highly discontinuous landscape of fear. Predation risk (by human hunting) only exists for several months or shorter during the year. The frequency depends on the type of hunting, whereas hunting types carried out by single hunters may occur frequently (by different hunters) hunting types including large organised hunts such as drive counts generally occur in low frequency or often only once per year for a certain area. Besides, as hunting activity in most areas tends to be concentrated during weekends (Proffitt et al. 2009) and mainly takes place during dusk and dawn also within the open hunting season, there is not an equal risk effect during the day or on a day-to-day basis. This contrasts largely with natural predations which occurs 24 hr a day during 365 days of the year (Jędrzejewski et al. 2002). Both the spatial and temporal differences between human hunters and natural carnivores result in landscapes of fear created by natural carnivores are more continuous, cover larger areas and exist at a finer scale than those created by human hunting (Manning et al. 2009). As a result, hunting does not mimic the way in which carnivores shape plant–herbivore interactions.

This leads to the conclusion that the lack of predators usually leads to increasing herbivore numbers. Whereas, at a local scale, hunting may control numbers, it does not replace the indirect effects that result from the presence of carnivores. As a result, in carnivore-free environment, ungulates will concentrate more in the most profitable foraging habitats and exert stronger top-down effects on regenerating trees at these sites (Fig 1b).

In managed systems lack of natural environmental heterogeneity

The presence of carnivores as a control mechanism on herbivore top-down effects is only one factor. In the present review, I have illustrated that abiotic, environmental conditions largely modify herbivore foraging behaviour and plant response and hence can shape herbivore top-down effects as well. As carnivores are absent in many temperate forest systems or may even in their presence have a minor role in regulating their ungulate prey populations in these productive environments (Melis et al. 2009), environmental conditions are of prime importance in shaping herbivore–plant interactions in temperate forest systems (Fig 1a).

Despite the growing interest in nature-based silviculture, large parts of the (central) European forests are managed according to strict forestry management techniques to improve timber production but largely ruling out natural processes (Kenderes et al. 2008). In the eastern part of the temperate-lowland zone, clear-cutting prevails, especially in pine-dominated stands (Angelstam et al. 1997). In the western part, for example in Germany, clear-cutting is strongly restricted and target diameter cutting is preferred (Matthews 1991; Angelstam et al. 1997). Cutting of canopy trees is often followed by removal of coarse woody debris and stumps followed by planting tree saplings (Matthews 1991; Angelstam et al. 1997). Also in areas where natural regeneration is preferred, management of vegetation competition is an integral part of silvicultural practices and regarded as critical silvicultural to achieve forest establishment (Ammer et al. 2011; McCarthy et al. 2011). On the one hand, tending measures to control woody competitors are common in European even-aged stands. On the other hand, herbaceous vegetation control is widespread. In European forest, this is mainly done by mechanical methods, whereas the use of herbicides is less common than in forests in North America, South Africa, Australia and New Zealand (Ammer et al. 2011; McCarthy et al. 2011). All of these management activities interfere with natural processes and do not allow complete natural regeneration. Even management activities that have similarities with natural processes such as gap formation following selective cutting change abiotic and biotic conditions to a greater extent than natural gap formation. Although several environmental factors will be affected by forestry management, three are relevant from an ungulate point of view to explain why herbivore top-down effects are likely to be larger in managed forest compared with natural old-growth forest.

The first factor, the size of the clear-cuts or gaps created in the tree canopy, affects the foraging behaviour and the amount of concentration of ungulates inside these areas. Sizes of clear-cuts or gaps created differ between countries or regions and depend heavily on the silvicultural methods. For example, in Germany, forests clear-cut areas are commonly maximally 0.3 ha (M. Adam personal communication), whereas mean gap size in the United Kingdom amounts 3.2 ha (Eycott et al. 2006), in Belgium 0.02–12 ha (Pontégnie et al. 2005) and Poland 0.1 ha–4 ha (Rozwałka 2003). Forests managed under this silvicultural system are characterised by a coarse-grained mosaic of more or less homogeneous management units. In contrast, fine-scale, gap-phase dynamics is a characteristic feature in old-growth temperate forest (Faliński 1986; Bobiec et al. 2000; Kenderes et al. 2008). Gap formation typically occurs of one single tree falling down and creating relatively small gaps, with mean gap sizes ranging between 40 to 190 m^2 for temperate deciduous forest (Tanaka and Nakashizuka 1997; Henbo et al. 2004; Kenderes et al. 2008, 2009). The majority of gaps belong to the smallest size categories of 20–50 m^2 (Kenderes et al. 2009). This type of gap formation is a continuous process resulting in a mosaic of forest in different developmental stages (Bobiec et al. 2000). In addition to these small gaps, sporadic catastrophic events, such as fires, spruce bark beetle attacks or windfall areas, may create large-scale gaps up to 2.5 ha (Castelli et al. 1999), hence similar or even larger in size than clear-cuts. However, the typical natural gap (excluding such sporadic events) is at the lower end of the range in gaps created by clear-cutting. As a result, the gaps in tree canopy created by forest management practices resemble more the uncommon catastrophic events occurring in natural unmanaged forests. The larger gaps created by forestry result in larger changes in micro-climatic conditions, such as air and soil temperature, soil humidity, solar radiation which all increase in relation to increasing gap size (Latif and Blackburn 2010). Besides, there exists a linear relationship between gap size and number of ungulates visiting the gap, and the larger gaps created in managed forest will result in a higher concentration of ungulates and more intense browsing (Kuijper et al. 2009), hence increasing the effects of ungulates on reducing growth of regenerating or planted trees.

The second factor is the change in tree species composition towards more browsing-intolerant species, meaning they are more reduced in growth following browsing compared with tolerant species. As forestry is aimed at the production of wood, commercially attractive, often fast-growing species are planted or promoted after clear-cutting. In many temperate areas, the most profitable are coniferous species, such as *Picea abies, Pinus sylvestris* or exotic species as *Pseudotsuga menziesii*, *Abies grandis, Picea sitchensis, Larix kaempferi.* This borealisation, the increasing amount of coniferous species, is a well-documented phenomenon throughout the European temperate region (Spencer and Kirby 1992; Jedrzejewska et al. 1994). It has resulted in the dominance of coniferous species in forest stands which naturally should be dominated by broadleaved species. In Europe, many forests have been converted to Norway Spruce-dominated stands in the past which, outside its natural range can only be maintained by silvicultural interventions to control interspecific competition and pests (Ammer et al. 2008). The plantation forests that are created or maintained under this system are among others characterised by large homogeneous (often even-aged and dominated by single species) stands. One of the major objectives of many forestry management units throughout central Europe nowadays is the conversion of these pure stands into mixed stands with broadleaved species (Ammer et al. 2008). In Germany, this has resulted in a large conversion of Norway spruce (*Picea abies*)-dominated stands by mixed stands with European beech (*Fagus sylvaticus*) and other broadleaved species in state forests (Ammer et al. 2008; Knoke et al. 2008). However, there is an ongoing debate, whether mixed stands are economically more attractive than monocultures, causing that many, mainly, private forests have not been converted and coniferous species still cover large areal extent outside their natural range (Knoke et al. 2008). Tree species which are economically the most attractive are nutritionally often not the most attractive species for herbivores and are often secondary choice food plants. Dietary studies in natural mixed tree stands in the Białowieża Primeval Forest showed that Red deer and Roe deer in spring and summer prefer to forage on deciduous species, whereas coniferous species (*Picea abies* and *Pinus sylvestris*) comprise less than 9% and 11% of the volume of all woody species in Roe deer and Red deer, respectively. Only their winter diet coniferous species increase and constitute, 32% in Roe deer and 47% in Red deer form the volume of all woody species consumed (Gębczyńska 1980). Due to strong apical dominance, conifers in general are expected to be less tolerant towards browsing (i.e. are more reduced in growth). However, I am aware of no studies that have systematically compared regrowth capacity following browsing to determine which species is more browsing tolerant than the other for a range of temperate forest species. Kuijper et al. (2010a) showed for old-growth stands with natural regeneration that species composition of regenerating trees changes in relation to fluctuating ungulate densities. Periods with low ungulate density were characterised by highest regeneration of unpreferred and intolerant, coniferous species (*Picea abies* and *Pinus sylvestris*), whereas the proportion of preferred and tolerant, deciduous species (especially *Carpinus betulus* and *Tilia cordata*) increased with increasing ungulate numbers (Figs. 2, 3). This finding contrast to that studied from several others from temperate forest systems (Wardle et al. 2002; Horsley et al., 2003; Long et al., 2007; Mason et al., 2010) and the general idea

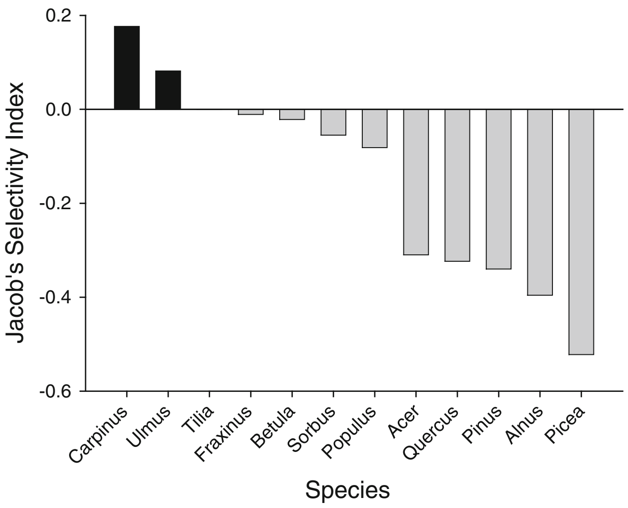

Fig. 2 Selection of tree species saplings in the height class of 0.3–1.3 m by the ungulate community (European bison, moose, Red deer and Roe deer) of natural old-growth stands of the Białowieża Primeval Forest, Poland. Species are ranked according to their Jacob's selectivity index. Positive values indicate species which are more intensively browsed than are expected based on their occurrence and hence are positively selected by the ungulates in the system. Calculations are based on the proportion of trees which had their last-year leader shoot browsed. Tree species are *Carpinus betulus, Ulmus glabra, Tilia cordata, Fraxinus excelsior, Betula pubescens and B. pendula, Sorbus aucuparia, Populus tremula, Acer platanoides, Quercus robur, Pinus sylvestris, Alnus glutinosa* and *Picea abies* (Data from Kuijper et al. 2010a)

that browsing reduces the abundance of preferred tree species. The reason why our study area contrasts to several others may mainly be related to the natural regeneration without forestry practices and presence of carnivores (see Cromsigt and Kuijper (2011) for a detailed discussion on this topic). Studies from the Białowieża Primeval Forest show that the most preferred tree species may also be the most browsing tolerant. Hence, relative to intolerant tree species, tolerant and preferred species profit and increase in abundance during periods of high ungulate density (Kuijper et al. 2010a). In this respect, tree regeneration in a managed forest is fundamentally different from that in a natural forest. In the latter, ungulate browsing selects for browse-tolerant deciduous tree species during the regeneration process and changes the species composition towards a higher proportion of tolerant and more preferred, palatable tree species (Kuijper et al. 2010a, b; Fig. 3). Hence, on longer timescales, the tree stand will be composed of a higher proportion of browsing-tolerant species in a natural forest (Bernadzki et al. 1998; Kuijper et al. 2010a). In contrast, economically attractive species (mainly coniferous) are being promoted during regeneration in managed forest resulting in an increased proportion of more browsing-sensitive tree species in managed tree stands (Jedrzejewska et al. 1994). This makes managed forests in general more prone to browsing by ungulates and likely results in stronger growth depression following browsing in managed forest compared with natural forest.

The third factor is related to and strengthens the former two. The planting or promoting of commercially attractive species creates habitats with lower attractivity for wildlife and lower carrying capacity because of lower variation in age class structure and more monotonous tree species composition (Jedrzejewska et al. 1994). When a clear-cut is created, the increased tree regeneration and higher cover of herbaceous vegetation (Modry et al. 2004) result in patches with higher forage availability, contrasting strongly with the low-quality surrounding (even-aged) tree stands. These patches provide favourable foraging sites for ungulates but only for a short interval (Alaback 1982). The first 10 years following the creation of the clear-cut are characterised by increasing food supplies in terms of high herbaceous vegetation cover and high amounts of regenerating trees; however, when trees increase in size most biomass will be out of reach of the herbivores and shading reduces ground vegetation cover resulting in reducing quality as wildlife habitat. In contrast, natural tree stands are composed of a mosaic of stands in different developmental stages (Bobiec et al. 2000), creating many alternative, attractive foraging sites for ungulates. Ungulates are then predicted to be less concentrated in only a few available attractive locations but more evenly spread over the entire forest system (Kuijper et al. 2010a, b).

Finally, the perceived effects of ungulates in managed forest versus natural stands are an important factor explaining that the different effects ungulates may have in each habitat. When management is aimed at creating natural tree stands, which means tree stands that develop without forestry practices and allow natural dynamics, ungulates should be seen as an integral part of the system in which they do not damage but shape tree recruitment as part of the natural processes (see Kuijper et al. 2010a). In managed forest systems, there can be several reasons to depart from this do not allow ungulate densities to grow beyond certain levels. As management is often in the first place aimed at wood production, any reduction in this caused by ungulates is perceived as damage (Gill 1992). In these systems, the question is often not what we regard as being natural dynamics but how much impact of deer do we accept.

Although several studies have indicated that management practices interact with foraging behaviour and consequently with top-down effects of herbivores (Jędrzejewska et al. 1994; Reimoser and Gossow 1996), few studies have actually tested directly how they interact. An exception is the study from Tremblay et al. (2007) which used an elegant controlled experimental approach in which they both manipulated deer densities and forest cover (simulating

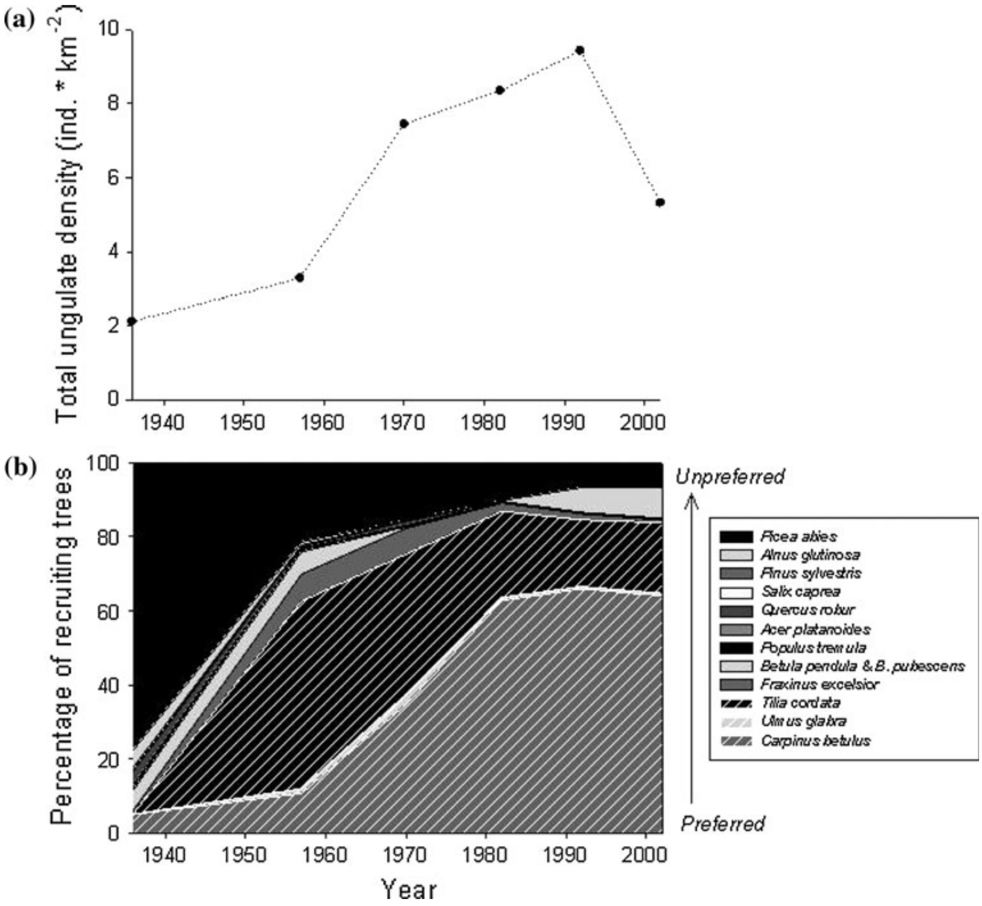

Fig. 3 **a** Fluctuations in total density of all browsing ungulates (European bison, moose, Red deer and Roe deer) occurring in the period 1936–2002 in the Białowieża Primeval Forest, Poland. Data from Jędrzejewska et al. (1997), Jędrzejewski et al. (2002) and unpubl. data. Proportion of each tree species within the pool of recruiting trees (Kuijper et al. 2010a), measured on 15-ha permanent transects (see Bernadzki et al. 1998 for detailed description of method), is indicated in the corresponding period (**b**). Tree species are ranked according to the Jacob's selectivity index from positively to negatively selected species. The figure indicates that preferred tree species are also the most browsing tolerant and increase together with increasing ungulate density. Total recruitment rate of trees declined from 16.7 trees * year^{-1} * ha^{-1} in 1936 to 10.4 trees * year^{-1} * ha^{-1} in 2002

timber harvesting) in a boreal forest on Anticosti Island, Canada. They observed that inside clear-cuts, the mortality of tree seedlings increased exponentially with increasing deer density, whereas mortality only moderately increased under a closed canopy. Their experiment provided evidence for nonlinear relationships between deer density and regeneration dynamics of forest in interaction with timber harvesting. Also the study of Horsley et al. (2003) showed that forestry practices interact with deer impact. Whereas, in general, tree recruitment was reduced with increasing deer density, the reduction was more pronounced in clear-cut areas followed by thinned stands and the longest time before an effect was visible was required in uncut stands. This indicated that the top-down effects were most pronounced in the least affected stands. Moreover, the study found that the trajectory of vegetation development was different between treatments. Clear-cuts and thinned stands in the presence of high deer density developed into a high cover of ferns. As ferns may inhibit tree regeneration, the effects of deer may be lasting long after deer densities have decreased. These effects in relation to deer densities were not observed in uncut stands. These results are in line with those of Reyes and Vasseur (2003) who showed for spruce-balsam fir stands in Nova Scotia that most intensive deer browsing and strongest depression in tree sapling growth occurred in the first 4 years after harvesting with negligible browsing impact in mature stands.

Still little is known about the long-term consequences of these interacting effects. Does the role of ungulates in shaping forest systems differ between managed and unmanaged forest systems as a result of these management practices? There are several studies from temperate forest systems which experimentally exclude ungulates from sample plots to test how they influence tree regeneration or vegetation but they are either carried out in managed forest (f.e. Ammer 1996; Van Hees et al. 1996; Kriebitzsch et al. 2000) or old-growth tree stands (Scott et al. 2000; Long et al. 2007; Kuijper et al. 2010a, b). As these study areas greatly differ in ungulate management, ungulate community, presence of carnivores, forestry practices, etc., they do not allow for separating the effect of forestry management only. However, studies carried out in the Białowieża Primeval Forest, Poland, where the managed part of the forest (c. 500 km^2) borders the strictly protected old-growth (100 km^2), suggest that the effects greatly differ. As both areas are close to each other, the existing differences in stand age-structure and species composition are mainly related to differences in forest management regimes. In studies carried out in the managed part of the forest, strong interacting effects of canopy openness (by clear-cutting) with the visitation and browsing of ungulates occurred. Both the number of ungulate visits and the proportion of browsed trees were higher inside clear-cuts compared with those of adjacent uncut stands (Kuijper et al. 2009). As a result, ungulates exerted stronger top-down effects inside clear-cuts. Whereas experimentally excluding ungulates from these plots resulted in a 1–6 times higher tree growth (tested for 5 species) in uncut stands, it increased tree growth by 3–40 times inside small clear-cuts (D.P.J. Kuijper, unpublished data). In contrast to these studies, experimental exclusion of ungulates in the natural old-growth forest showed no interactions between the effects of herbivores and canopy openness (Kuijper et al. 2010a, b). This indicates that effects of herbivores are context-dependent and increase in strength once the forest systems lose its natural heterogeneity as a result of management. In Białowieża Primeval Forest, these differences in effects of herbivores cannot be explained by differences in ungulate density, as overall ungulate densities are highest inside the old-growth forest where no hunting takes place (Jedrzejewska et al. 1994). There are also no differences in the presence of carnivores (wolf and lynx) which are present in the managed part as in the old-growth forest. Hence, these studies indicate that the change of forest structure as a result of forestry is a major driving factor in causing differences in effects of ungulates. In comparison with other systems, ungulate densities have to be taken into account. The observed differences between managed and old-growth forest occur with ungulate densities which may be low compared with other systems. In other words, a threshold ungulate density is likely to exist, below which forestry practices are playing a main role, above which ungulates are the main driver of the system (see for example Horsley et al. 2003).

In summary, the lack of environmental heterogeneity (fewer and larger gaps, lower tree species composition and lower structural diversity) is a factor which influences the quality of wildlife habitat. As such, forestry practices can strongly influence ungulate foraging behaviour (Alaback 1982; Bobek et al. 1984; Reimoser and Gossow 1996) and the effects that ungulates have on tree regeneration. As a result of these changes in environment, the effects of ungulate browsing on tree regeneration in managed forest are predicted to be higher than in natural forest (Fig. 1b). Forestry practices in itself may therefore greatly enhance the conflict that exists between wildlife and forestry (see also Bobek et al. 1984; Reimoser and Gossow 1996).

How to implement knowledge from natural systems into forestry?

In managed forest systems that occur throughout temperate Europe and United States, two factors which shape ungulate top-down effects in natural forest systems are altered or absent. Firstly, the absence of carnivores may prevent direct effects on ungulate numbers or evenly important their indirect effects on ungulate foraging behaviour. Secondly, the changes in environment that result from forestry management increase the strength of herbivore top-down effects. In the present paper, I discussed the interacting effects of carnivores and environmental conditions that shape herbivore top-down effects in complete temperate forest systems. As carnivores are absent and/or environmental heterogeneity is limited in managed forest systems, the strength of herbivore top-down effects at a given density of ungulates are expected to be higher in managed forests compared with those in complete systems. Hence, next to increasing deer numbers which have been observed in many areas, the way how we modify forest ecosystems is an important additional factor leading to the increasing wildlife–forestry conflict. The change of natural tree species composition towards species which are economically profitable creates a forest which has lower carrying capacity and lower tolerance for ungulates. In other words, ungulates may play a different role in a *‘human-made’* forest compared with a natural forest (Fig 1).

But what should be the way forward to solve or ameliorate this problem? When thinking about solutions to prevent or reduce wildlife–forestry conflicts, it is crucial to realise the changes that occured in herbivore–plant interactions as a result of the changed environment. Often, there is a one-sided focus on trying to reduce wildlife numbers by either increasing hunting bags (Hothorn and Müller 2010) or reintroducing top-predators (Manning et al. 2009). However, environmental conditions are at least equally important in shaping herbivore behaviour and hence their effects on forest systems. As a result, aiming only at reducing wildlife numbers is predicted to have little effects when they do not coincide with habitat ameliorations to allow for more natural processes that shape herbivore foraging and that resemble those from natural old-growth forest. As described in this review, forestry practices interact in several ways with herbivory and play an important role in enlarging the wildlife–forestry conflict. These interactions also show that they can play an important role in reversing the problem and reduce the conflict by adopting close-to-nature forestry principles, which allow part of the natural control mechanisms to operate. In areas where large carnivores are absent and not likely to return, forestry management is likely the main factor to shape herbivore top-down effects at a given ungulate density. There has already been a recent trend in

Europe and North America towards a more ecosystem-orientated management in forestry (Gamborg and Larsen 2003). This entails a shift from focus solely on timber production towards enhancing other ecosystem services of forest complexes, such as providing wildlife habitat, conserving biodiversity or nutrient and water cycling (Puettmann and Ammer 2007). A transformation of typical managed forest systems towards forests with semi-natural woody species composition that allow for more natural processes to occur may be hampered by too intense herbivore browsing (Kamler et al. 2010). This is caused by the lack of several control mechanisms, i.e., factors which interact with herbivore top-down effects, which are still absent in a 'human-made' system. These mechanisms need time to get established as they operate in systems which have already a close to natural structure tree stands and tree species composition. Studies that have tested forestry management based on close-to-nature principles, for example by mimicking the gap dynamics of semi-natural forests, showed that impact of herbivores may be low in affecting tree regeneration despite high deer densities (Madsen and Hahn 2008). This illustrates that forestry management can be an important tool to reduce wildlife–forestry conflict by adapting management practices that allow more natural functioning of forests systems.

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