Research

Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland

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Large carnivores can either directly influence ungulate populations or indirectly affect their behaviour. Knowledge from European systems, in contrast to North American systems, on how this might lead to cascading effects on lower trophic levels is virtually absent. We studied whether wolves *Canis lupus* via density-mediated and behaviorally-mediated effects on their ungulate prey species influence patterns of browsing and tree regeneration inside the Białowieża National Park, Poland. Browsing intensity of tree saplings (height class < 150 cm), irrespective of tree species or forest type, was lower inside a wolf core area (50.5%) where predator presence is highest, than in the remainder of the wolf pack's home range (58.3%). Additionally, browsing intensity was reduced when the amount of coarse woody debris (CWD), which can act as a 'ungulate escape impediment', increased (within 5-m radius) inside the wolf core area. No relationship existed outside the core area. As a result, the proportion of trees growing out of herbivore control increased more strongly with increasing amount of CWD inside compared to outside the wolf core area. This suggests that next to direct effects of wolves on ungulate density caused by a higher predation pressure inside the core area, risk effects are important and are enhanced by habitat characteristics. These results indicate that behaviorally-mediated effects of predators on prey can become more important than density-mediated effects in affecting lower trophic levels. This is the first study we are aware of, that shows CWD can create fine-scale risk effects on ungulates with the potential for cascading effects of large predators on patterns of tree regeneration for a European forest system. This knowledge broadens the discussion on how the impact of large predators on ecosystem functioning depends on the physical landscape, by illustrating these effects for a system which largely contrasts in this respect to the North American systems.

Large carnivores can play an important role in structuring ungulate communities with cascading effects on lower trophic levels (Terborgh and Estes 2010). In the classical view 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 density-mediated effects of carnivores on the ungulate community have been illustrated both inside (Jędrzejewski et al. 2002, Jędrzejewska and Jędrzejewski 2005) and outside Europe (McLaren and Peterson 1994, Messier 1994, Ripple and Beschta 2005). Recently, there is an increasing recognition that indirect, non-lethal predator effects are also important or even more important than their direct lethal effects (Schmitz et al. 1997, Creel and Christianson 2008).

Predators may indirectly influence ungulates by changing their distribution towards less risky habitat types (Lima and Dill 1990, Kie 1999, Creel et al. 2005, Mao et al. 2005, Thaker et al. 2011), change their movement patterns (Fortin et al. 2005, Fischhoff et al. 2007), or shift their activity towards less risky times (Creel et al. 2008, Valeix et al. 2009). Besides or instead of changing their spatio-temporal distribution, animals can reduce predation risk by changing their behaviour. A common tactic for ungulates is to increase vigilance levels while foraging (Pulliam 1973, Hunter and Skinner 1998, Brown et al. 1999). Alternatively, group size may increase to reduce individual predation risk due to the dilution and confusion effect (Bertram 1978, Dehn 1990). An increase in group size may on its turn decrease individual vigilance time (Pulliam 1973, Bertram 1978, Pulliam et al. 1982, McNamara and Houston 1992), and may increase individual foraging efficiency (Lipetz and Bekoff 1982, LaGory 1986, Lima and Dill 1990). Both avoidance of high risk areas and behavioral changes can mediate browsing pressure on plants growing in these areas (Ripple et al. 2001). Browsing should be reduced when ungulates avoid high risk areas or increase their vigilance levels at the expense of foraging. Alternatively, in case group size increases in response to predation pressure, coinciding with a reduction of individual vigilance level, browsing pressure may potentially increase in high risk areas.

Predation risk effects have played an important role in explaining patterns of tree recruitment in Yellowstone

National Park (YNP) after the reintroduction of wolves *Canis lupus*. Feeding behavior of elk *Cervus elaphus canadensis* changed when wolves reappeared in the system (Laundré et al. 2001, Ripple and Beschta 2003, Beyer et al. 2007). Habitats with a high amount of escape impediments (objects which obstruct deer escape from a predator) or low visibility are regarded to have higher perceived predation risk and tend to be avoided by elk (Ripple and Beschta 2006, Halofsky and Ripple 2008). Trees growing in these high risk areas may experience lower herbivore top-down effects. Ripple et al. (2001) found evidence for that by showing that sapling height of quaking aspen *Populus tremuloides* was higher and elk dropping density lower inside high wolf-use areas, suggesting an avoidance of deer of these areas. Later studies, including other tree species, found similar indirect evidence for behaviorally-induced changes in foraging patterns, with lower browsing and taller tree height inside habitats with low visibility and/or the presence of escape impediments (Ripple and Beschta 2003, 2006). However, there is still an ongoing debate on how important these indirect risk (non-lethal) effects are relative to direct (lethal) effects of predators on their prey in explaining patterns of tree regeneration (Creel and Christianson 2009, Kauffman et al. 2010, Beschta and Ripple 2011). Moreover, Winnie (2012) recently argued that there is currently little undisputed evidence for the occurrence of fine-scale risk effects created by escape impediments leading to cascading effects on tree recruitment inside YNP.

In contrast to the large body of literature from North American systems, knowledge on whether large carnivores (in)directly influence vegetation via effects on ungulate prey are virtually absent from other systems, and particularly European systems. Obvious reasons for this gap of knowledge is the lack of natural predators in many areas and the scarcity of areas with undisturbed forest development. The strictly protected parts of the Białowieża Primeval Forest (BPF) in Poland offer one of the rare examples in Europe where these tri-trophic interactions can be studied (Jędrzejewska and Jędrzejewski 2005). This area is unique as it harbours the natural European assemblage of ungulate species (European bison *Bison bonasus*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*) which co-occur with their natural predators (wolf, lynx *Lynx lynx*). An additional unique feature is that it belongs to one of the last remaining natural, temperate, lowland forest systems in Europe where in part of the area (Białowieża National Park, BNP) human intervention (hunting, forestry) has been excluded. The question is whether knowledge from North American systems is directly applicable to other systems which have largely contrasting landscapes. The landscape of fear in YNP is strongly determined by the physical landscape with strongest risk effects occurring in, for example, large river valleys and mountain ridges (Kauffman et al. 2007). The physical landscape of Białowieża Primeval forest differs largely from the well-studied North American systems in at least two factors that might affect predator–prey interactions. Firstly, the area lacks large river valleys, mountains and is mainly composed of lowland forest as only 5% of the land consists of open grassland. Secondly, the area is small (Polish part of Białowieża Primeval Forest: 600 km^2, Białowieża National

Park: 105 km^2) compared to YNP (8980 km^2). As a result, there are virtually no parts of this area where wolves and lynxes are absent, simply because their home ranges cover the entire forest complex (Schmidt et al. 2009). Therefore, ungulate prey cannot reduce predation risk by moving to predator-free areas as has been illustrated for the YNP (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005, Kauffman et al. 2007). However, there are gradients in risk related to the frequency of large carnivore presence and ungulate prey may shift from high-risk habitats towards low-risk habitats. For wolves, core areas of their pack territories can be defined where on a yearly basis 50% or more of all observations of radio-collared individuals occurred (Jędrzejewski et al. 2007, Schmidt et al. 2009). During the reproductive season (spring–summer) their spatial distribution is restricted within this core area whereas outside this period they regularly return to the core area (Jędrzejewski et al. 2001). The average size of a wolf pack territory in BPF is 201 km^2 with a core area of 35 km^2 (Jędrzejewski et al. 2007). Taken into account the average kill rate of their main prey species, on a yearly basis one wolf pack kills 118 red deer per year within its territory (Jędrzejewski et al. 2002), of which half would be predated inside the core area based on the amount of time spent by the wolf pack there. This would result in 1.7 red deer km^{-2} (59 deer in 35 km^2) taken per year inside the core, versus 0.36 red deer km^{-2} (59 deer in 166 km^2) taken in the rest of their territory. Due to this 5-fold higher predation pressure, wolves are predicted to directly affect red deer density leading to a lower density inside compared to outside the wolf core area. Moreover, because of more frequent predator presence and cues that result from this, ungulates may perceive these areas as risky and avoid them or change their behavior. Core areas of wolf territories are most intensively scent-marked by means of urination, scats and territorial scratchings (Zub et al. 2003) and also howling activity is concentrated inside core areas (Nowak et al. 2007). These olfactory and acoustic cues, next to visual cues, could be used by ungulates. Perceived predation risk for red deer is predicted to be higher inside wolf core areas resulting in higher vigilance levels at the cost of time spent foraging. These predator-mediated direct and indirect changes may affect spatial patterns in herbivore top-down effects by creating areas with reduced browsing intensity of trees.

The present study was aimed at testing whether these direct and indirect effects of wolves on deer are visible in browsing intensity of tree saplings and affect patterns of tree regeneration. We compared browsing intensity on tree saplings growing inside a wolf core area with the area in the remainder of the wolf pack's territory. Due to a higher predation pressure inside versus outside the wolf core area, we predict that wolves via density-mediated effects reduce browsing intensity inside the wolf core area. To test whether additionally behaviorally-mediated effects of wolves occurred, we related habitat characteristics associated with perceived predation risk to browsing intensity. For this we measured the amount of 'escape impediments' for deer (sensu Halofsky and Ripple 2008) in the vicinity of each tree sapling; coarse woody debris is the only physical barrier which could act as such in our system (Fig. 2). When (perceived) predation risk is additionally affecting foraging

behavior of deer, the amount of escape impediments should strengthen the density-mediated effects and result in a stronger reduction in browsing intensity especially inside the wolf core area.

Methods

Study site

The Białowieża Primeval Forest (BPF, 52°45′N, 23°50′E) situated in eastern Poland (600 km^2) and western Belarus (850 km^2) is a large continuous forest composed of multi-species tree stands. Since 1921, the best preserved central part of the BPF (47 km^2) have been strictly protected and no human intervention (including forestry activities and hunting) has been allowed. Human impact before this period is considered as minimal (Jędrzejewska et al. 1997, Samojlik et al. 2007). In 1996, the Białowieża National Park (BNP), including the strictly protected area, was enlarged to 105.2 km^2 (Fig. 1). In this enlarged area (acting as a buffer zone of the strictly protected part), forestry activities are minimized to sanitary cutting of diseased Norway spruce *Picea abies*, and tree regeneration occurs naturally without human intervention (Theuerkauf and Rouys 2008). Inside the entire BNP hunting and access by motorized vehicles have been prohibited and tourist access is only permitted with a guide. The area outside BNP is managed by the state forestry service, including wood exploitation and regulation of ungulate numbers.

The present study was carried out inside the BNP, where old-growth forest stands (81–120 yr) prevail and cover 42% of the area. Very old stands, dominated by trees aged over 120 yr, account for 39%. Only 0.8% of the BNP consists of open grassland (Michalczuk 2001). A mosaic of different forest types exists dominated by deciduous forest (54% of the area) with *Quercus robur*, *Tilia cordata* and *Carpinus betulus* as dominant species) and mixed deciduous forest (23% with *Picea abies*, *Quercus robur*, *Tilia cordata* and *Carpinus betulus*).

Along the small streams alder ash forest (dominated by *Alnus glutinosa* and *Fraxinus excelsior*) occurs, whereas mixed coniferous forest (*Pinus sylvestris*, *Picea abies* and *Quercus robur*) and coniferous forest (*Pinus sylvestris* and *Picea abies*) are found in the drier, more nutrient-poor parts (see for more details Faliński 1986). The mean altitude of the BNP is 158 m a.s.l. and the total altitudinal range is 23 m. Mean annual air temperature is 6.8°C with the coldest month in January with on average −4.7°C and the warmest month is July with 17.8°C. Mean annual precipitation is 641 mm and snow cover lasts for an average of 92 d.

A unique feature of the BPF is that it is one of the few areas in Europe, where the complete native assemblage of forest ungulates still occurs (five species) together with
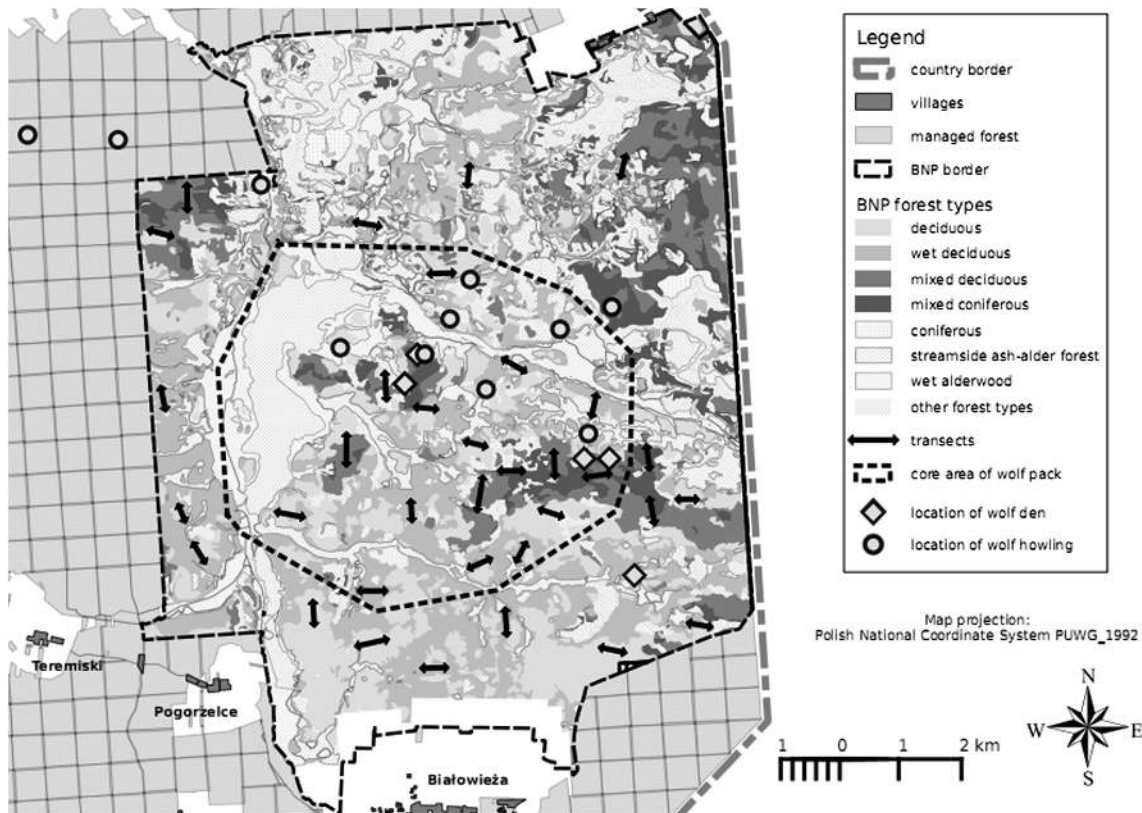

Figure 1. Map of the study area, the Białowieża National Park, showing the forest types (based on Michalczuk 2001) utilized most by ungulates. Under 'other forest types', very wet forest types (such as swamps and bog forest) are included which have in general lower ungulate numbers. Locations of 34 transects, 17 inside and 17 outside the wolf core area, on which saplings were measured are indicated. The location of the core area of the annual territory of the wolf pack present is based on Jędrzejewski et al. (2007). Locations of wolf dens and observations of wolf natural howling in the period 2000–2012 indicates continuous use of the core area.

their natural predators. The most abundant species, both in numbers and crude biomass (Jędrzejewska et al. 1997), is red deer with a winter density evaluated at about 12 individuals km^{-2} during the most recent survey based on drive counts in January 2010 inside the BNP (T. Borowik pers. comm.). The second-most numerous ungulate is wild boar with a density evaluated at about 10 individuals km^{-2} in 2010. Roe deer were present at a density evaluated at about 2 individuals km^{-2}, whereas the larger species European bison and moose occur in the lowest densities, evaluated at about 0.8 individuals km^{-2} and 0.4 individuals km^{-2} respectively in the winter of 2010 (T. Borowik pers. comm.). These relative densities of ungulate species based on drive counts are confirmed by other census techniques carried out during the last decades (Jędrzejewska et al. 1997). Natural predators, wolf and lynx, are strictly protected in BPF since 1989 and are not hunted throughout Poland. In BPF, they occur with average densities around 1–5 individuals 100 km^{-2} (wolf) and 1–3 individuals 100 km^{-2} (lynx) (Schmidt et al. 2008).

Location of the wolf core area

Accurate estimates of size and core areas of wolf pack territories originate from earlier studies on collared wolves (Jędrzejewski et al. 2007, Schmidt et al. 2009) which are continuously being updated by new surveys. The present four wolf pack territories inside the entire BPF cover the entire forested area leaving no vacant areas (Jędrzejewski et al. 2007, Schmidt et al. 2009). Likely as a result of this, the location and size of wolf pack territories and core areas in the BPF has been very stable (Jędrzejewski et al. 2007, Schmidt et al. 2009) with dens located throughout the years inside the same core areas (Theuerkauf et al. 2003a, Zub et al. 2003, Schmidt et al. 2008).

As the location of only one territory of a wolf pack overlaps with the BNP, which excludes forestry activities and prohibits hunting, this was the only one that allowed us to study patterns of tree regeneration undisturbed by humans. Location of the core area of this wolf pack (containing 3–8 wolves) was based on Jędrzejewski et al. (2007). In the present study we compared the wolf core area with the area outside it (Fig. 1), but still within the boundaries of the annual territory of the wolf pack (95% MCP, Jędrzejewski et al. 2007). Previous studies showed that wolves inside the BPF howled from the central parts of their territories where the den for breeding was also located and not from the peripheries (Nowak et al. 2007). As an indication for the continuous use of the core area, we selected all wolf howling observations and known den sites from the period 2000–2012 inside the BNP collected by park rangers or scientists working in the area (Fig. 1).

Measuring browsing intensity inside and outside the wolf core area

In April–May 2012 we established transects 150–300 m long and 2 m wide and recorded all tree saplings between 10–200 cm height. The exact length of the transects depended on the density of saplings, the aim was to measure

at least 200 saplings per transect to get a proper estimate of browsing intensity. For each tree sapling we measured its height and estimated browsing intensity by measuring the number of browsed branches (both old and new browsing marks) of the 10 top branches. We measured the top branches as they have highest chance to be browsed, and it is likely the main factor slowing down tree growth. As we cannot distinguish browsing marks by the different ungulate species, we studied the browsing intensity on trees resulting from the entire ungulate community. We recorded only tree saplings between 10–200 cm as these are within reach of the ungulates in the system and overlap with the preferred height classes (50–150 cm) of red deer (Renaud et al. 2003). As red deer is the dominant browser in the system (79% of the total number of browsing ungulate species excluding wild boar), browsing intensity is largely influenced by this species (see also Kuijper et al. 2010a).

The location of transects (n = 34) was assigned randomly, but stratified within forest types. We selected four forest types which together cover 90% of the study area (Michalczuk 2001): deciduous forest (n = 12), wet deciduous forest (n = 10), mixed deciduous forest (n = 6), mixed coniferous forest (n = 6). We divided the 34 transects equally over the area inside and outside the wolf core area, resulting in total in 17 transects inside and 17 outside the wolf core area with equal numbers within each forest type (Fig. 1). The number of transects within each forest type is related to the areal extent of each type, with most transects in the most common forest type. These forest types compose the prime habitat for ungulates (especially red deer) in the forest (Jędrzejewska et al. 1994, Kamler et al. 2008). We used the existing division into forest compartments inside the BNP to randomly assign transects per forest type inside and outside the wolf core area. Forest compartments are equal-sized compartment blocks of 1.15 km^2 (based on former Russian system). In every forest compartment one transect per forest type was assigned. In some cases two transects occurred within one forest compartment, but within different forest types and a minimum distance of 300 m between transects.

This set-up allowed us to study the effect of the wolf core area on tree browsing level within each forest type and hence taking into account differences in forest structure and environmental circumstances. As both wolf and deer activity are affected by human presence (Theuerkauf et al. 2003b, Theuerkauf and Rouys 2008) we established the transects only inside the borders of the National Park which prohibits hunting and access by motorized vehicles and has only restricted access for public. Besides, transects were established in all cardinal directions from the core area to exclude any gradients in human activity present in the study area (Fig. 1).

Trees growing out of reach of ungulate browsing inside and outside wolf core area

Within every transect, the number of trees per species that had grown out of reach of browsing ungulates were counted, measuring between 200 and 400 cm in height. Trees above 200 cm are not browsed on the leader shoot

(Renaud et al. 2003) and hence potentially can recruit into the tree stand. We used a maximum of 400 cm, to exclude regenerating trees from before the 1990s when no information on the location of the wolf core area is available.

Browsing intensity in relation to escape impediments

We followed the definition by Halofsky and Ripple (2008) and regarded large pieces of downed woody debris as possible escape impediments which might block view or escape routes for ungulates (Fig. 2). To study how browsing intensity interacted with small-scale habitat characteristics, we counted the presence of escape impediments in four (wind) directions for each encountered tree sapling. We measured this at two spatial scales; within a radius of 1 m and 5 m around each tree sapling. We considered CWD as a possible escape impediment when its size measured minimally 0.5 m in height above the ground and 0.5 m in length for escape impediments within a radius of 1 m, and 0.5 m in height and 1 m in length for escape impediments between 1 and 5 m radius. A minimum height of 0.5 m was used (similar to the height used by Halofsky and Ripple 2008) because this blocks the view of a head-down foraging

Figure 2. Large pieces of coarse woody debris may act as escape impediments by obstructing escape routes of ungulates or increase their perceived predation risk by blocking view on potential predators (top, photo by Hidde Zemel). An example of a tree sapling (*Tilia cordata*) growing in between two escape impediment (bottom).

ungulate, and forms an obstacle that a deer should step or jump over while escaping. The minimum length for escape impediments of 1 m within the 1–5 m radius was chosen as we assumed that an object of 0.5 m in length cannot be considered as a relevant obstacle when it was located further away. A red deer could easily run around it and it blocks only a small fraction of the view of a foraging ungulate.

Possible confounding factors affecting browsing inside and outside wolf core area

As tree canopy gap formation is a main driving factor in tree regeneration inside old-growth forest (Runkle 1981) and ungulate browsing is more intense in forest gaps (Kuijper et al. 2009) we additionally measured canopy openness as a potential confounding factor. Canopy cover was recorded in June (leaves fully developed) with a spherical densiometer with a convex mirror as described by Lemmon (1956). For this we established additional transects in June 2012 during peak leaf cover of trees, one in each of the four forest types. We estimated canopy cover into the four wind directions and calculated an average percentage of canopy cover at regular locations (n = 50 inside and n = 75 outside the wolf core area) with an interval of 15 m along these transects with a minimum of 10 measurements per transect.

As tree species composition or diversity potentially differs between inside and outside wolf core area because of (micro)habitat preferences of wolves (Theuerkauf et al. 2003a) we calculated Shannon diversity indices (Pielou 1975) per transect for all tree saplings available for ungulates (10–200 cm), and averaged them for inside and outside wolf core area, according to:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where S is the number of species and p the proportion of species i among all tree individuals within the height class. The minimum value of the Shannon index is 0 when there is only one species present and the index is highest when each species is present in equal proportions. Low values indicate a high dominance of a single species, either due to low number of species or relatively high abundance of one species.

Statistical analysis

Tree sapling height were log-transformed and all percentage browsing intensity data were arcsinus transformed before testing to meet requirements for parametric testing (Zar 1984).

We used Chi-square test to test whether tree sapling species composition differed between inside and outside the wolf core area. We used the percentages of each species in the entire sample of recorded tree saplings, and combined all species which accounted less than 5% in a rest group. Subsequently, we carried out a multivariate GLM in which inside and outside wolf core area and forest type were entered as fixed factors, and the number of saplings of each species recorded per transect as dependent

variable. We applied a univariate GLM to test for the effects of sapling height on browsing intensity inside and outside the wolf core area. We entered both sapling height and whether the sapling grew inside or outside the wolf core area as fixed factors. To test for differences in average tree sapling height and browsing intensity between core and non-core area an independent t-test was used.

A Kruskall–Wallis test was used to test for group differences in browsing intensity between different amounts of escape impediments inside and outside the core area, while the differences within groups with a given number of escape impediments was tested using Mann–Whitney U test (with Bonferroni correction of significance level for the number of tests performed). We used non-parametric tests here because the sometimes small and unequal sample size per group violated assumptions for parametric testing (Kolmogorov–Smirnov test $p < 0.05$). For a reasonable estimate of the average browsing intensity considering the existing variation, we calculated browsing intensity on a minimum of 10 trees and when the number of trees per impediment was lower than 10 in core or non-core it was taken out of the analysis. A Jonckheere–Terpstra test was used to test for a possible ordered pattern (trend) in browsing intensity with increasing amounts of escape impediments inside and outside the wolf core area. This test is a nonparametric test and has more statistical power than a Kruskall–Wallis test when ordered differences among classes occur (Field 2009). The difference in Shannon diversity index between wolf core and non-core area was tested with a Mann–Whitney U test. To test for differences in number of trees growing out of reach of ungulates between inside and outside the wolf core area a Chi-square test was used, whereas, we used Spearman correlation to test whether the percentage of these trees which escaped ungulate control increased was related to the number of escape impediments for inside and outside the wolf core area separately. Subsequently, we used Spearman correlation to test whether the differences between percentage of trees which escaped ungulate control inside and outside the core area was related to the number of escape impediments, indicating that the difference between these two areas is increasing or decreasing. All statistical analyses were performed using SPSS 19.0. All maps were created using QGIS software (Quantum GIS Development Team 2012)

Results

Browsing inside and outside wolf core area

We measured in total 7414 tree saplings (10–200 cm in height) equally divided over the area inside and outside the wolf core area (Table 1). Species composition based on proportion of each species in the samples tree sapling was similar inside and outside the wolf core area ($\chi^2 = 2.137$, DF = 4, p = 0.711) and dominated by *Carpinus betulus* (>50%), followed by *Acer platanoides*, *Tilia cordata* and *Picea abies* (Table 1). Other tree species accounted less than 5% of the sampled trees (with the exception of *Sorbus aucuparia* outside the wolf core area). Number of recorded individuals per species obviously varied between forest types,

Table 1. Characteristics of sampled area inside and outside the wolf core area in Białowieża National Park, Poland. Number of recorded tree saplings, transect length, description of tree sapling species composition (percentage of saplings, number of saplings) in which only saplings which are available for ungulate browsing are included (<200 cm). Canopy cover refers to canopy closure of tree stands inside and outside the wolf core area.

Description	Inside wolf core area	Outside wolf core area
Number of trees saplings (10–200 cm)	3689	3725
Number of transects	17	17
Total transect lenght (m)	3570	3540
Tree sapling density (no. m^{-2} ± SE)	0.52 (± 0.06)	0.53 (± 0.04)
Tree sapling height (in cm ± SE)	52.9 (± 0.59)	59.8 (± 0.61)
Carpinus betulus (%, no.)	58 (2135)	52 (1931)
Acer platanoides	12 (458)	14 (510)
Tilia cordata	8 (293)	9 (323)
Picea abies	5 (199)	7 (250)
Ulmus glabra	4 (134)	1 (45)
Betulus spp.	3 (123)	2 (87)
Sorbus aucuparia	3 (93)	8 (294)
Corylus avellana	2 (90)	3 (98)
Quercus robur	2 (82)	2 (62)
Fraxinus excelsior	2 (59)	2 (61)
Euonymus europaeus	<1 (10)	<1 (15)
Populus tremula	<1 (6)	<1 (26)
Pinus sylvestris	<1 (5)	<1 (5)
Salix spp.	<1 (1)	<1 (8)
Sambucus nigra	<1 (1)	0 (0)
Malus sylvestris	0 (0)	<1 (10)
Shannon diversity index (± SE)	0.51 (± 0.03)	0.54 (± 0.04)
Canopy cover (% ± SE)	78.1 (± 3.3)	77.4 (± 2.8)

but were highly similar between inside and outside wolf core area (Table 1). Only some less abundant tree species (< 5% of sampled trees) showed a higher number of records inside compared with outside the wolf core area; *Sorbus aucuparia* (93 vs 294 saplings, $F_{1, 68} = 4.65$, p = 0.035), *Populus tremulus* (6 vs 26, $F_{1, 68} = 5.70$, p = 0.020), *Malus sylvestris* (0 vs 10, $F_{1, 68} = 6.46$, p = 0.013). Tree sapling density (0.52 ± 0.06 vs 0.53 ± 0.04 saplings m^{-2}, $t = 0.380$, DF = 32, p = 0.706) and Shannon diversity index (0.51 ± 0.03 vs 0.54 ± 0.04, $t = 0.474$, DF = 32, p = 0.639) were not different between the transects respectively inside and outside the wolf core area. Besides, canopy cover did not differ between both areas (inside 78.1 ± 3.3 vs outside 77.4 ± 2.8, $t = -0.48$, DF = 6.259, p = 0.963). All this combined indicates that available forage for ungulates was comparable between inside and outside the wolf core area. Only the average height of tree sapling was slightly, but statistically significantly higher outside (59.8 cm ± 0.61) than inside (52.9 cm ± 0.59) the wolf core area (Table 1, $t = -9.491$, DF = 7412, p < 0.001).

Browsing intensity, measured as the proportion of branches browsed for all tree species combined, showed an optimum between 50 and 150 cm of sapling height both inside and outside the wolf core area (effect of sapling height: $F_{10,7819} = 221.33$, p < 0.001, Fig. 3). Browsing intensity for all height classes combined was lower on tree saplings growing inside ($44.7\% \pm 4.6$) than outside ($51.4\% \pm 5.2$) the wolf core area ($F_{1,7819} = 45.64$, p < 0.001), but this difference became smaller with increasing sapling height (interaction between sapling height and core area:
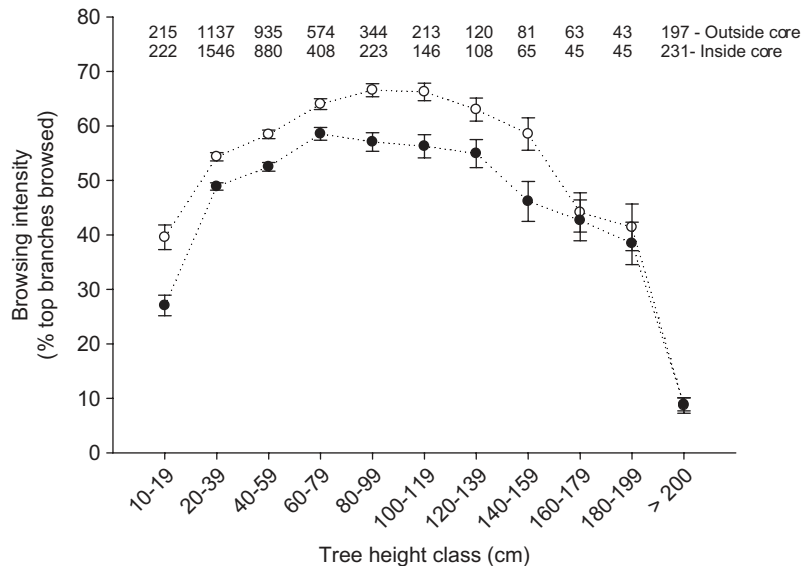
Figure 3. Browsing intensity of tree sapling per height class outside (○) and inside (●) the wolf core area measured as the proportion of browsed top 10 branches at different classes of tree sapling height. Averages (± SE) are based on 17 transects inside and outside the wolf core area. Sample sizes are indicated at the top of the graph.

$F_{10,7819} = 2.62$, $p < 0.003$). Above 160 cm there was no difference. When all trees within preferred foraging height of red deer are combined (all trees < 150 cm, Renaud et al. 2003), overall browsing intensity was 8% lower inside (50.5%) than outside (58.3%) the wolf core area ($t = -11.95$, DF = 7156, $p < 0.001$).

This overall pattern of lower browsing intensity (for all species combined) was also observed when comparing the transects inside and outside the wolf core area within forest types (Fig. 4A). Browsing intensity of tree saplings (height 10–200 cm) was lower inside than outside the wolf core area for wet deciduous ($t = -3.131$, DF = 2379, $p < 0.01$), deciduous forest ($t = -8.207$, DF = 2867.50 (equal variances not assumed), $p < 0.001$), mixed deciduous forest ($t = -11.355$, DF = 909.83, $p < 0.001$), mixed coniferous forest ($t = -3.082$, DF = 1090, $p < 0.01$). In addition, browsing intensity was lower inside wolf core areas than outside when comparing within the four most common tree species (Fig. 4B); *Acer platanoides* ($t = -2.308$, DF = 922.95, $p = 0.021$), *Tilia cordata* ($t = -2.565$, DF = 614, $p = 0.011$), *Carpinus betulus* ($t = -12.800$, DF = 4064, $p < 0.001$), *Picea abies* ($t = -2.224$, DF = 447, $p = 0.027$).

Browsing intensity and escape impediments

We tested the effect of the presence of escape impediments separately for the saplings inside and outside the wolf core area at two spatial scales; within 1 m radius, and within 5 m radius (Fig. 5). When the number of escape impediments within 1 m radius of a sapling increased, the percentage of browsing on tree saplings (10–200 cm) decreased both inside (Jonckheere test J = 1039546.00, z = –4.870, $p < 0.001$) and outside the wolf core area (Jonckheere test J = 934532.50, z = –2.769, $p < 0.01$, Fig. 5A). However, browsing intensity decreased more strongly with the number of escape impediments inside (from 51 to 27%)

than outside (from 59 to 52%) and was always lower inside the wolf core area at each number of escape impediments present (at $p < 0.0125$ following Bonferroni correction). Within a 5 m radius, the percentage of browsing on tree saplings decreased with increasing number of escape impediments, however this effect only occurred inside the wolf core area (Jonckheere test J = 2363964.00, z = 4.731, $p < 0.001$, Fig. 5B). Outside the wolf core area the browsing intensity was not related to the number of escape impediments present (Kruskal–Wallis test, H (6) = 7.725, DF = 1, $p = 0.259$).

Trees growing out of reach of ungulate browsing

We explored the possible long term effects of wolves on forest regeneration by comparing the proportion of trees that escaped browsing by ungulates (all trees 200–400 cm in height). Overall we observed a higher number of escaped trees (200–400 cm) inside (n = 230) than outside (n = 197) the wolf core area. Inside the wolf core area, trees that grew out of reach of browsing ungulate occurred more on locations where escape impediments where present than on locations lacking escape impediments (194 with escape impediments vs 36 without impediments, ($\chi^2 = 108.54$, DF = 1, $p < 0.0001$). Outside the wolf core area there was no difference in the numbers of trees above browsing height that were growing near escape impediments (105) compared to the number of trees (92) that did not ($\chi^2 = 0.858$, DF = 1, $p = 0.354$). Although the absolute number of trees above browsing height was low (Fig. 6), the percentage they made up of the total recorded trees within each class increased with the number of escape impediments both inside (Spearman correlation coefficient, $\rho = 0.90$, n = 9, $p = 0.001$) and outside ($\rho = 0.667$, n = 9, $p = 0.05$) the wolf core area. However, the percentage of trees above browsing height increased more strongly with increasing number of escape impediments
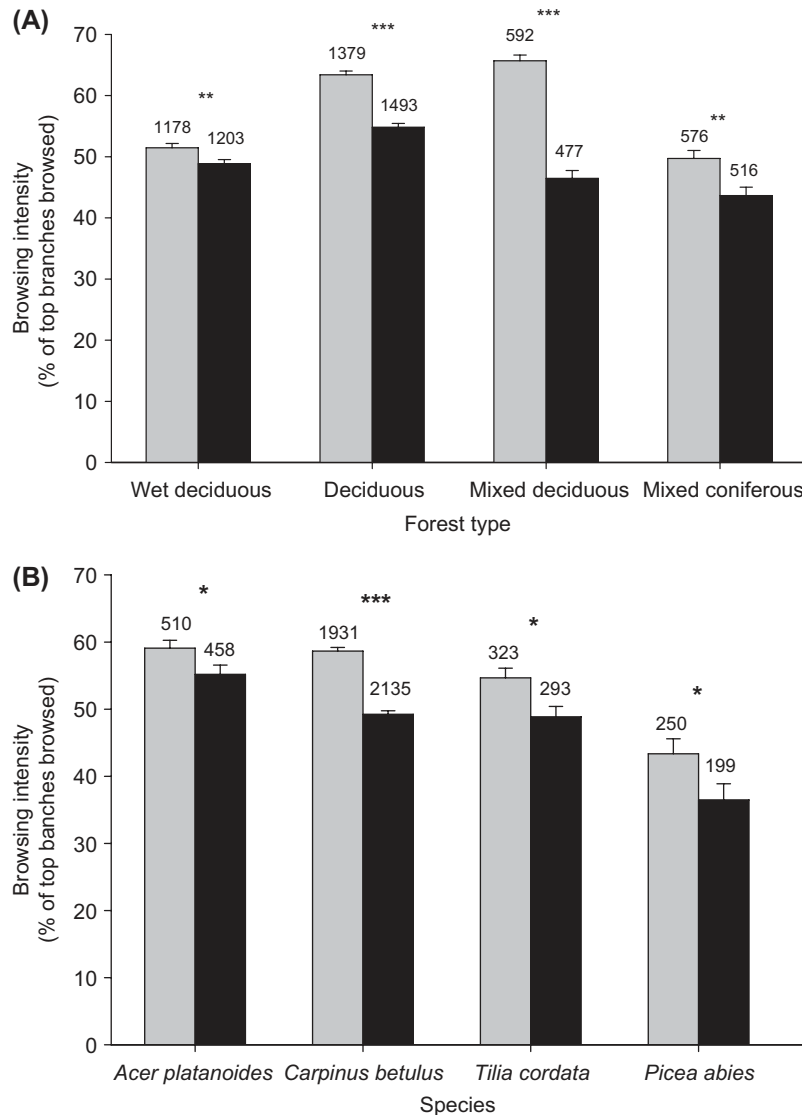
Figure 4. (A) Browsing intensity of tree saplings (10–200 cm in height) per forest type outside (grey bars) and inside (black bars) the wolf core area. (B) Browsing intensity of the four most common tree saplings (10–200 cm) per tree species with more than 150 saplings outside (grey bars) and inside (black bars) the wolf core area. Only the four most common tree species in the sample are presented with at least 150 saplings in both inside and outside the wolf core area (sample sizes are indicated above the bars). Significant differences in browsing intensity within forest types and within tree species are indicated with an asterisk (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

inside the wolf core (correlation on differences inside and outside core area $\rho = 0.883$, n = 9, p = 0.002). With a high number of escape impediments, up to 75% of tree saplings grew above browsing height inside the wolf core area versus 16% outside.

Discussion

Our study showed that ungulate browsing intensity of tree saplings, irrespective of tree species, was reduced by 8% inside a wolf pack core area compared to the rest of their territory. This difference in browsing intensity between inside and outside the core area strongly increased with the amount of coarse woody debris (CWD) in direct vicinity of tree saplings. As a result, more trees can grow above browsing height with increasing amount of CWD inside compared to outside

the wolf core area. Whereas higher predation pressure can explain the overall lower browsing intensity inside the core area, behavioral changes of ungulates lead to a stronger reduction in browsing than density-mediated effects alone. These patterns strongly indicate that CWD can create fine-scale risk effects for ungulate browsers. This is the first study we are aware of, that shows the potential for cascading effects of large predators on tree regeneration for a European forest system. As the physical landscape of our study area contrasts largely with already studied American systems, this study increases our understanding of indirect predator effects on ecosystem functioning in different landscapes.

Ungulate browsing inside and outside wolf core area

We observed lower browsing levels on trees growing inside the core area of the territory of a wolf pack. Different tree
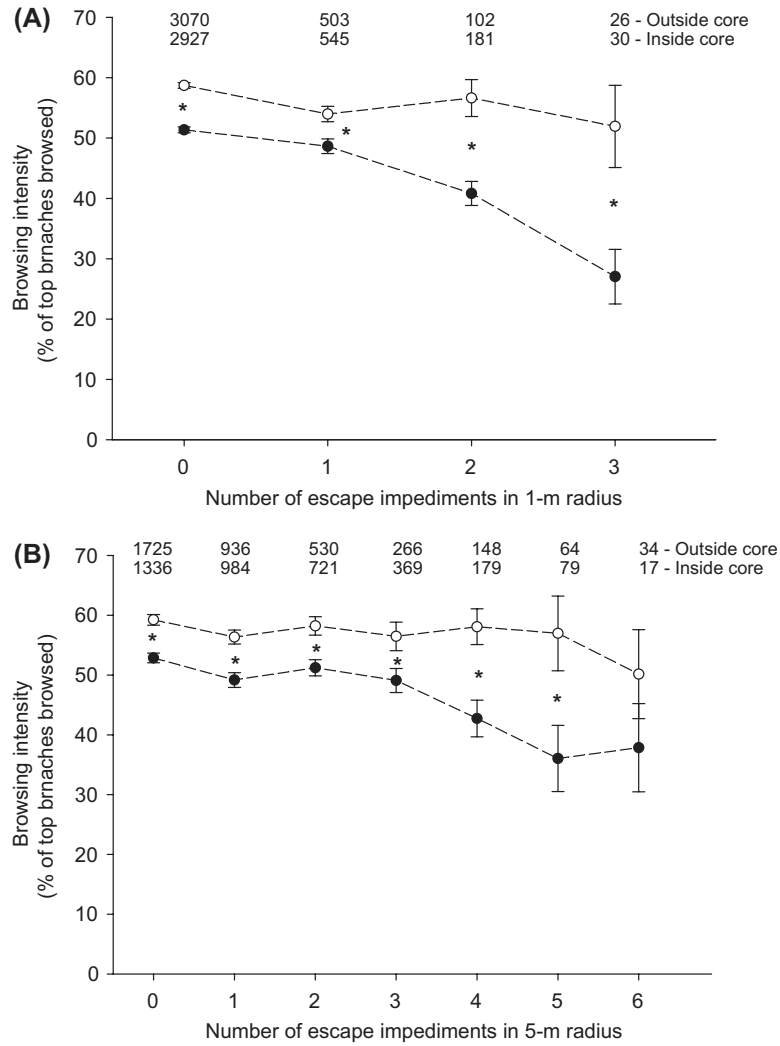
Figure 5. Browsing intensity on tree saplings (10–200 cm) outside (○) and inside (●) the wolf core area in relation to the presence of varying numbers of escape impediments only within 1 m radius (A) and within 5 m radius of each sapling (B). Sample sizes are indicated at the top in each graph, browsing intensity is only determined for samples size of > 10 trees. Asterisks indicate significant differences between inside and outside core based on Mann–Whitney test with Bonferroni correction of significance level ($p < 0.0125$ in (A) and $p < 0.007$ in (B)).
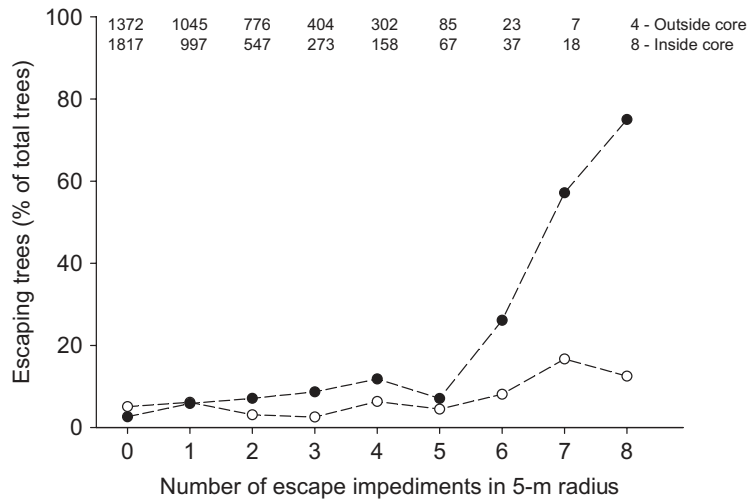

Figure 6. Percentage of trees growing out of reach of ungulate browsing (200–400 cm) of total present trees growing in relation to the amount of escape impediments within 5 m radius of a tree outside (○) and inside (●) the wolf core area. Total number of trees present in each category is indicated on top of the figure.

species showed a similar reduction in proportion of browsed branches. Since red deer is the main browser in our system (Jędrzejewska et al. 1997) and plays an important role in determining patterns of tree regeneration (Kuijper et al. 2010a, b), patters in browsing are mainly determined by this species. This fits with the observed highest browsing intensity on saplings in the preferred browsing height class of red deer of 50–150 cm (Renaud et al. 2003). The reduction in browsing intensity inside the wolf core area is most easily explained by density-mediated effects of wolves on red deer (Jędrzejewski et al. 2002). Based on the fact that wolves spend more than 50% of their time annually inside the core area of their territory (Jędrzejewski et al. 2007, Schmidt et al. 2009) and their spatial distribution in spring–summer is restricted within this core area (Jędrzejewski et al. 2001), we calculated a 5-fold higher predation pressure (using Jędrzejewski et al. 2002) inside the core area on a yearly basis. Outside the reproductive period (autumn–winter), wolves increase their daily movement distances and utilize their territory in a rotational way (Jędrzejewski et al. 2001), hence killed prey can then be found throughout their territory (Jędrzejewska and Jędrzejewski 1998). This higher predation pressure in combination with the strong range fidelity of red deer living in this area (Kamler et al. 2008) should lead to a lower red deer density and lower browsing intensity inside the core area.

In addition to these density-mediated effects, behaviorally-mediated effects can lead to a reduction in browsing intensity by ungulates avoiding risky habitats or risky times (Lima and Dill 1990, Mao et al. 2005, Creel et al. 2008, Valeix et al. 2009, Thaker et al. 2011) or changing their behavior (Pulliam 1973, Hunter and Skinner 1998, Brown et al. 1999). Although, habitat characteristics between wolf core areas and the remainder of their territories can differ (see below), forage availability for browsing ungulates seems similar in the two areas. We observed a similar tree sapling species composition, no difference in Shannon diversity index and no difference in density of recorded tree saplings inside and outside the wolf core area. We only found that sapling height was 7 cm higher outside the wolf core area, which unlikely has a large effect on forage availability for red deer. The finding that inside the core area still more than 50% of branches is being browsed of trees in the height class 50–100 cm, shows that ungulates are still abundantly present. Previous studies in the Yellowstone National park showed that deer became more vigilant once wolves returned to the area (Laundré et al. 2001). Also other studies showed that deer may directly respond by increased vigilance and lower foraging only when wolves are present (Creel and Winnie 2005, Liley and Creel 2008). These behavioral effects where observed already when wolves were within 3 km distance (Liley and Creel 2008). Similar direct effects of predator presence on prey behavior were also observed in African systems (Valeix et al. 2009). Likewise, red deer in our study area may perceive wolf core areas as more risky due to the higher frequency of occurrence of wolves (Jędrzejewski et al. 2001, Schmidt et al. 2009) and show behavioral changes leading to a lower foraging efficiency when present inside the wolf core area.

That risk effects are an important underlying mechanism explaining our observed patterns in browsing intensity is most strongly indicated by the relationship we found with the presence of coarse woody debris (CWD). Ungulates in African systems have been shown to avoid and are more vigilant in habitats with low visibility (Underwood 1982, Shrader et al. 2008, Valeix et al. 2009). Earlier American studies have found that deer reduce foraging and increase vigilance levels in the vicinity of objects that reduce habitat visibility or can serve as objects obstructing escape (Halofsky and Ripple 2008, Liley and Creel 2008). These so-called escape impediments can be river valleys, ridges, fallen trees or rocks (Halofsky and Ripple 2008). There is consensus that indirect, behaviorally-mediated effects of predators on ungulates occur in relation to habitat features, however, the scale at which these effects operate is less clear. While several American studies have illustrated effects of predator presence on large scale distribution of ungulates in relation to predation risk (Lima and Dill 1990, Kie 1999, Creel et al. 2005, Mao et al. 2005), undisputed evidence that ungulates react to fine-scale risk factors affecting foraging behavior or patch selection on a small scale is lacking (Winnie 2012). That browsing intensity on trees in the present study was more reduced with increasing CWD inside the wolf core area compared to outside the wolf core area, suggests that deer experience higher predation risk effects (perceived predation risk). Outside the wolf core area, where the encounter rate of wolves is lower, deer browsing intensity was not related to the presence of CWD. Similarly, the number of trees growing out of reach of herbivore control (> 200 cm) increased with increasing CWD only inside the wolf core area. This shows that a higher presence of wolves alone is not the sole factor, but fine-scale risk factors are important related to habitat characteristics such as the presence of CWD. The present study suggests that behaviorally-mediated effects of predators on prey can become in this way more important than density-mediated effects in affecting lower trophic levels.

According to the 'risk allocation hypothesis' vigilance levels of deer may actually drop when the predator encounter increases (Lima and Bednekoff 1999). Evidence for this theory has also been found in wolf-red deer systems (Creel et al. 2008). However, these behavioral effects of red deer in response to wolf presence have been observed in systems with an open landscape where deer often see wolves approaching and can respond to it in advance (Creel et al. 2008). How red deer respond to predator presence in closed forest systems, with low visibility and lower chance to detect predators by sight, as our present study area, is still largely unknown and may differ from these patterns. The interactive effects of (cues of) predator presence and habitat characteristics appear to influence in these systems spatial patterns of tree regeneration and provide local spots with reduced herbivore pressure and increased tree regeneration.

Landscape of fear or alternative explanation for differences in browsing?

We explain the observed lower browsing intensity of tree saplings inside the wolf core area as being the result of a combination of direct (lethal) and indirect (non-lethal) predator

effects on their prey species. However, there might be several confounding factors explaining our results.

As the core area and non-core area were not randomly chosen, other confounding factors cannot be controlled for. Previous studies in BPF showed that wolf den's are often found in parts of their territory which are associated with the least human activity and often the farthest away from any road or village (Theuerkauf et al. 2003b, Theuerkauf and Rouys 2008). To minimise these potential differences between inside and outside core areas we put transects in all cardinal directions from the core areas to exclude possible gradients in human activity. Besides we restricted our study to the BNP where motorised vehicles and hunting and forestry activities are prohibited. Anyway, the studied wolf core area is the part of the study area least visited by people mainly due to the concentration of visiting tourists in the south-western corner of the forest. This may have affected the distribution patterns of red deer and browsing intensity. Studies from other systems showed that deer can concentrate in those parts most frequently visited by humans to escape predation pressure (Kloppers et al. 2005, Muhly et al. 2011, Rogala et al. 2011). Whether deer in our study area also show similar behavioral responses is unknown. However, in case they do, lower browsing levels inside the wolf core area can still be interpreted as resulting from indirect predator effects creating a higher perceived predation risk inside core areas. Alternatively, deer in our study area may respond differently to human presence as they are intensively hunted outside the strictly protected area. Earlier studies from Białowieża Primeval forest showed that also deer avoid areas of human activity (Theuerkauf and Rouys 2008). In that case, the opposite trend in observed browsing levels of trees would have been expected, with most browsing in the least disturbed area hence inside the wolf core area. Since this did not occur we do not regard human activity as an important confounding factor explaining our results.

In addition the location of wolf core areas may be related to other habitat characteristics. Our results showed that wolf core and non-core area are comparable in tree density, Shannon diversity index and canopy cover. Only the average sapling height was higher (7 cm) outside the wolf core area compared to inside the core area. This difference cannot be explained by browsing intensity as this was higher outside the wolf core area. As there was no difference in canopy cover, as a proxy of light availability, a higher soil fertility outside the wolf core area might potentially result in higher growth rate of tree saplings and explain these results. Earlier studies showed that wolves dens and resting sites in our study area are more often located in coniferous forest compared to random locations, but occurred in all other present forest types as well (Theuerkauf et al. 2003a). We observed that the lower browsing intensity inside the wolf core area occurred within each forest type. This indicates that differences in the occurrence of forest type between inside and outside the wolf core area are not a confounding factor in our analyses. Other habitat features related to perceived predation risk such as habitat visibility (Shrader et al. 2008, Valeix et al. 2009) and the amount of escape impediments (Halofsky and Ripple 2008) were not different between location of dens (in the wolf core area)

and random location outside the den area (Theuerkauf et al. 2003a), suggesting that these are also not important confounding factor explaining our results.

Finally, the observed patterns may be caused by the second predator in the system, lynx, which also predates on red deer (Okarma et al. 1997). Growing evidence suggests that ambush predators, such as lynx, produce stronger behaviourally-induced risk effects than chase hunters such as wolves (Schmitz and Suttle 2001, Thaker et al. 2011). Home ranges of wolves and lynx in the BPF considerably overlap and in some cases the core areas of their territories overlapped (Schmidt et al. 2009). However, the wolf territory used in the present study inside the Białowieza National Park showed little overlap with the present lynx territories. Whereas the lynx territory had a core area situated in the south of the BNP, wolves had theirs in the northern parts (Schmidt et al. 2009). Moreover, the location of territories (and core area) of lynx are not stable and changes each year (K. Schmidt pers. comm.). Therefore, the location of lynx territories does not provide a likely explanation for browsing levels which are reduced for longer periods, allowing effects on the proportion of trees escaping herbivore control.

To conclude, we are inclined to interpret the lower browsing intensity of trees observed inside the wolf core areas as being mainly the result of higher predation pressure and increased perceived predation risk by ungulates rather than other factors associated with the wolf core area.

Landscape of fear in European systems

Apex carnivores have been extirpated in many areas across the globe, leading to cascading effects on ecosystem functioning (Estes et al. 2011). Especially in densely populated areas, such as Europe, the function of large carnivores has often been lost or their numbers have dropped below ecological meaningful level. However, there has been a recent expansion from wolf and lynx from thriving populations in eastern Europe to areas in western Europe (Breitenmoser 1998, Enserink and Vogel 2006, Trouwborst 2010). This recolonisation by apex predators may restore antipredator behaviour of ungulates with important consequences for ecosystem functioning. The knowledge we have from predator–ungulate interactions originating mainly from American study systems is often applied to predict how recolonisation or reintroduction of predators may influence ungulate's behaviour (Manning et al. 2009). However, especially indirect predator effects on ungulates in European systems may differ from those in American ones because of several reasons, for example smaller size and consequently lower landscape heterogeneity of nature reserves, more fragmented landscape and higher human pressure. Therefore, studying indirect predator effects on ungulate behaviour in a variety of systems is needed to accurately predict their future role. The present study is the first we are aware of that has addressed the potential for how direct and indirect predator effects on ungulates can lead to cascading effects on tree performance and affect spatial patterns of tree regeneration in a European system. It illustrates that in densely forested areas, with predators being present virtually everywhere, indirect predator effects seem to occur but also

might be more subtle (i.e. not leading to large shifts in spatial distribution or habitat selection) than observed in large scale American national parks. The underlying mechanism might also differ, for example olfactory cues might be an important attribute indicating predator risk effects in these low visibility habitats.

Whereas ungulate management often focuses only on the direct effects of predators in influencing ungulate numbers, the potential for indirect effects in European systems should be acknowledged (see also Cromsigt et al. 2013). The present study is a first step to show how predators structure ecosystems in a European context and might help to broaden the discussion on predator effects in a variety of systems.

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