Deadwood retention in commercial forest lowers short-term browsing pressure on silver fir saplings by overabundant deer

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Abstract

Humans have widely extirpated large carnivores and simultaneously promoted overabundance of deer. The intense pressure imposed by these herbivores in forests has led to extremely low rates of natural forest regeneration. In natural old-growth forests, deadwood functions as a key driver of biodiversity and promotes ecosystem functioning, such as water retention and nutrient recycling. An as yet unappreciated function of deadwood is its ability to act as a physical barrier, excluding large herbivores from given patches and thereby reducing browsing pressure. However, this benefit may be minimized by an increase in rodent herbivory in the sheltered patches. In this study, a field experiment was conducted in a total of 384 plots in which tree crowns (0–4) from logging residuals were used as increasingly dense physical barriers to shelter five newly planted saplings of silver fir (*Abies alba* Mill.). Generalized linear mixed-effects models were applied to determine whether sapling browsing by roe deer and rodents was differentially affected by these barriers. The probability of roe deer browsing decreased from 26% (no crowns) to 2% (4 crowns) while that of rodent browsing increased from 1% to 17%, respectively, as the number of deadwood crowns used in barrier construction increased. In broadleaf stands, browsing by roe deer and rodents was generally higher than in coniferous stands. In forests with high numbers of visitors, browsing by roe deer was reduced, but browsing by rodents was not influenced. The retention of large amounts of deadwood or active deadwood increments may thus provide an effective barrier to roe deer browsing but promote the browsing activity of rodents. The landscape-level heterogeneity of browsing patterns associated with the presence of deadwood suggests that deadwood shelters in homogenized forests may encourage both natural forest regeneration and forest biodiversity, despite an overabundance of roe deer.

Keywords: Browsing, *Capreolus capreolus*, Deadwood, Forest restoration, Regeneration, Rodents, Sapling growth

1 Introduction

Human impact on forest ecosystems has increased not only as a result of industrial forestry practices, but also due to management strategies that have altered the densities of large mammal species. Forestry practices in many regions across Europe include the selection of trees in young ages (<120 years) long before nature tree senescence and the removal of older as well as rotting trees (Vilén et al., 2012). In Central Europe, over 5000 years of forestry has changed the ecosystem (Grove, 2002). For example, the average amount of deadwood in the managed forests of Germany is 20.6 m^3 per hectare (BWI, 2012), which is only 10–15% of the amount in natural temperate forests (Christensen et al., 2005; Müller and Bütler, 2010). However, deadwood is important for the conservation of many species, and saproxylic fungi and beetles in particular (Stokland et al., 2012). At the same time, human management aimed at the extirpation of large carnivores (Chapron et al., 2014) together with the strict regulation of culling (Apollonio et al., 2010) has led to an overabundance of cervids, which have thus become significant ecosystem drivers in Europe (Putman, 1992), Asia (Suzuki and Ito, 2014) and North America (Côté et al., 2004). In Europe, roe deer are distributed across most of the continent (Andersen et al., 1998), inhabiting agricultural landscapes as well as forests, where they are often found at high population densities. In the forest understory, herbivory by roe deer has been shown to adversely impact forest regrowth and to alter the composition of forest plants (Boulanger et al., 2018; Fuller and Gill, 2001; Moser and Schütz, 2006). The damage caused by roe deer to nitrogen enriched agricultural land may be severe enough to result in nutrient redistribution between habitats (Abbas et al., 2012; Hothorn and Müller, 2010).

The response of a plant community to herbivory reflects a balance between herbivore selectivity and pressure, on the one hand, and the position of the plant species along the resistance–tolerance continuum, on the other (Annighöfer et al., 2015; Augustine and McNaughton, 1998). The spatial pattern of browsing is determined by the habitat selection and dietary preferences of the browsing species. In the case of roe deer and other cervids, while habitat selection is mainly driven by plant quality and quantity (Hanley, 1997, 1982; Langvatn and Hanley, 1993), habitats providing cover from predators will be browsed preferentially (Kuijper et al., 2015; Mysterud and Østbye, 1999). Limitation of accessibility for cervids by a pronounced vertical or horizontal structure can create refugia from browsing (Grisez, 1960; McGraw and Chandler, 2018). Higher rocks present refugia from browsing by deer with consequences for plant demographic and species richness of the ground vegetation (Comisky et al., 2005; McGraw and Chandler, 2018). Treefall mounds or root plates could lower browsing pressure on top and increase growth and survival of regeneration (Long et al., 1998). Dens and protective understorey as for example holly (*Ilex aquifolium* L.) have the potential for protect regeneration and lower browsing (Morgan, 1991). The debris left after logging are often called slash or logging residuals. Retention of these deadwood material may affect access and hence create refugia from browsing (Bergquist and Örlander, 1998; de Chantal and Granström, 2007; Grisez, 1960; Pellerin et al., 2010). Only a few studies of the impact of habitat selection consider that very dense habitats may prevent large species from entering a given patch (Kupferschmid and Bugmann, 2005; Maltoni et al., 2019). In other words, the physical environment itself has the potential to limit the impact of large herbivores on an ecosystem. While this has been demonstrated in old-growth forests (Pellerin et al., 2010), it has yet to be reproduced experimentally for larger scales in commercial temperate forests. Another largely unexplored topic is the extent to which the exclusion of a large herbivore is compensated by a potential increase in herbivory by the smaller-herbivore guild in more sheltered patches. The results of previous studies demonstrating competition between dense populations of ungulates and herbivorous rodents (den Herder et al., 2016; Flowerdew and Ellwood, 2001; Parsons et al., 2013; Steen et al., 2005) predict that the positive impact of deer exclusion will be weakened by an increase in rodent herbivory. Because deadwood provides rodents with both shelter from predators and nesting sites (Carey and Johnson, 1995; Suter and Schielly, 1998), an increase in the availability of deadwood may ultimately enhance rodent browsing. Whether forestry practices that include deadwood retention on the forest floor can affect browsing pressure has yet to be addressed.

Here we present the results of a field experiment, conducted at a local to regional landscape scale, in which tree crowns, obtained as logging residuals, were used to simulate increasingly dense physical barriers (0, 1, 2 and 4 crowns) for roe deer. The effect of these barriers on browsing was determined by planting five fir saplings in the absence or presence of the shelters constructed from the tree crowns. Browsing on each of the 1920 fir saplings in the 384 test plots and, if possible, the respective browsing agent were then recorded. Using generalized linear mixed-effects models, we tested whether browsing by one or the other browsing agents (i.e., roe deer vs. rodents) was prevented by the physical barriers formed by the increasing deadwood crown material. We also examined the differences in browsing between broadleaf vs. coniferous stands, the influence on the roe deer population density in the forest site and the numbers of human visitors to the forest.

2 Methods

2.1 Study area and experimental design

The field experiment was set up at a landscape scale of >150,000 km^2 in temperate commercial forests of Central Europe at 24 sites in southern Germany (Fig. 1a). Forests were managed by selective logging and broadleaved sites (9) were dominated by European beech (*Fagus sylvatica* L.) and oak (*Quercus* spp.) and coniferous sites (15) were dominated by silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H. Karst.). Forest were in the early optimum to mid-optimum stage (70-120 years; Faustmann, 2003) in an altitude of 200-500 m a.s.l. with an annual mean temperature of 7-9°C and an annual precipitation of 650-950 mm. Physical barriers of increasing density were established using an increasing number of tree crowns (average length: 7 m) obtained from logging activities. Four treatments, consisting of no crowns, one crown, two crowns and four crowns, arranged on the plots as a pile using a skidder or horses, were established. Each of the 24 study sites contained four experimental replicates, for a total of 96 replicates and 384 experimental plots. Five silver fir (*Abies alba* Mill.) saplings of similar size (30-40 cm) were obtained from tree nurseries and planted in the center of each plot. This type of sapling, both the species and its high quality due to its nursery origin, is extremely palatable to roe deer and was therefore suitable bait to examine the effect of deadwood on plot accessibility (Odermatt, 1999). The saplings were planted in a square of about one square meter, with one sapling at each of the four corners and one in the center (Fig. 1b). For the treatments that included deadwood crowns, the saplings were planted in the shelter formed by the crowns. Nine of the study sites were in broadleaf forests, in which case the crowns used in the treatments were from broadleaf trees, and 15 study sites were in coniferous forests, where the crowns were from coniferous trees. The experiment was established in autumn, between September and October, and browsing was measured the following spring, in April. Eleven sites were established in 2016 and were sampled in April 2017, and 13 sites were established un 2017 and were sampled in April 2018. For proxies of roe deer population density and the number of human visitors during the study period local forest managers conducted a questionnaire with defined categories. The roe deer population density was classified as low (roe deer only occasionally present or in low abundance; natural regeneration less effected by roe deer browsing), moderate (roe deer is present and natural regeneration is partly browsed by roe deer), or high (barley natural regeneration due to roe deer browsing). The number of human visitors to the forest was classified as low (only a few visitors per day) or high (numerous forest visitors per day).

2.2 Measurement of browsing

Browsing was evaluated on 1692 of the 1920 planted saplings (88%), because some saplings did not become established and others had been pulled out or could no longer be found. Saplings were counted as browsed if the terminal shoot showed traces of browsing. The considered browsing agents were roe deer, hares and rodents, identified according to the species-specific browsing traces described by Suchant et al. (2012). Red deer could be precluded as a browsing agent at the study sites because their exclusion from these areas is ensured by strict hunting-based management. In cases where the browsing traces could not be attributed to a particular group of herbivores, the browsing agent was noted as 'unknown'. Browsing intensity on the saplings was assessed by counting both all browsed shoots and all shoots of the sapling without browsing traces, including on the terminal shoot. Browsing intensity was assessed for roe deer and rodents, respectively.

2.3 Statistical analyses

Binomial generalized linear mixed models with logit link were applied to test for the effects of deadwood crowns as a physical barrier to browsing and to intensity of browsing (i.e. number of shoots browsed according to number of unbrowsed shoots) on fir saplings by roe deer and rodents, respectively. Further explanatory variables in the models were stand characteristics (coniferous or broadleaf), estimates of the population density of roe deer (moderate or high, as a low population density was never recorded during the study), estimates of the number of human visitors to the forest (low or high; information provided by the local forest managers) and year of establishment the experimental site (11 sites in 2016 and 13 sites in 2017). Nesting of the plots in the sites was treated as a random term in the models to control for the effects of the different site characteristics. Calculations were performed using the *glmer* function in the add-on package *lme4* (Bates et al., 2015). The differences between the four physical barrier treatments were compared simultaneously, and the p-values were adjusted for multiple testing using the function *glht* in the add-on package *multcomp* (Hothorn et al., 2008). All analyses were performed in R, version 3.3.3 (R Core Team, 2017). The dataset together with the script of the analyses is provided in Supplementary Material (Appendix S3 and S4).

3 Results

Across the 24 sampling sites and four experimental deadwood classes, 35% of all fir saplings were browsed (Fig. 2): 10% by roe deer, 18% by rodents, 1% by hares and 6% by an unknown agent (Fig. 2). After controlling for the different site characteristics (random and fixed terms), the mean probability of roe deer browsing on fir saplings decreased as the complexity of the physical barrier formed by the deadwood crowns increased, from 26% browsing on the saplings in control plots (no crowns) to 6% on plots with one crown, 3% on plots with two crowns and 2% on plots with four crowns (Fig. 3a; Table 1). By contrast, the mean probability of browsing by rodents increased as the number of deadwood crowns forming the barrier increased: 1% in control plots (no crowns), 11% in plots with one crown, 20% in those with two crowns and 17% in those with four crowns (Fig. 3b; Table 1). Browsing by roe deer and by rodents was higher in broadleaf stands than in coniferous stands (Table 1). The higher degree of browsing was mainly driven by the contrasts in the treatments with deadwood crows, whereas for control plots with no deadwood crowns no significant differences were found between broadleaf stands and coniferous stands (Supporting Information, Appendix S1). Browsing by row deer was higher for moderate (11%) than for high (9%) population density of the roe deer but there was no effect of population density of the roe deer and browsing by rodents (Table 1). Forests with a high number of human visitors had less browsing by roe deer but there was no influence on rodent browsing (Table 1). Browsing by roe deer differed between the two different years of experimental site establishment (11 sites in 2016 and 13 sites in 2017) but there was no effect for rodents (Table 1). Analyses of browsing on the plot level showed congruent results to analyses for single samplings (Supporting Information, Appendix S2).

Overall, the intensity of browsing on a single sapling, i.e., number of shoots browsed according to number of unbrowsed shoots, was such that, on average, half of all shoots in a plot were browsed, with no difference in terms of the density of the physical barrier formed by the deadwood crowns. Roe deer browsed a sapling with greater intensity in plots without than with crowns whereas rodents browsed a sapling with lower intensity in plots without than with crowns (Table 1). In broadleaf stands, the browsing intensity by both roe deer and rodents was higher (overall average 58%) than in coniferous stands (33%; Table 1). Forests with a high number of human visitors had a lower intensity of browsing by roe deer but there was no influence on rodent browsing intensity (Table 1). Browsing intensity by both roe deer and rodents were not affected by population density of the roe deer and year of experimental site establishment (Table 1).

4 Discussion

The structure of European forests has long been determined by human management, both directly, through selective logging, and indirectly, through imposed changes in the density of keystone herbivores. However, the effects of the interactions of these factors have only rarely been investigated. Using an experimental approach, we found that a physical barrier consisting of deadwood crowns decreased the probability of roe deer browsing of fir saplings from 26% to 2%, depending on the number of crowns. Conversely, the probability of rodent browsing increased with the increasing density of the physical barrier formed by the deadwood, from 1% to 17%. Our results demonstrate the effect of the physical structure of a habitat on food access by large herbivores. Moreover, they provide evidence of contrary browsing by smaller-herbivore guilds (rodents).

4.1 Physical structure of the habitat and selection by large herbivores

Natural old-growth forests are characterized by large amounts of deadwood differing in its type and its spatial distribution. These features of deadwood contribute to its importance as a habitat for a very diverse range of forest species and to its role in promoting the ecosystem functions carried out by these species (Stokland et al., 2012). The vertical and horizontal structure created by deadwood on the forest floor can provide refugia from browsing by large herbivores (Grisez, 1960). Our experiment showed that, in temperate commercial forests, the retention of deadwood crowns from logging residuals can effectively reduce browsing by large species of herbivores and thus may ultimately positive effect natural regeneration of the forest. Specifically, we compared the effect of one, two or four deadwood crowns, arranged as a pile, on the probability of browsing of silver fir saplings by roe deer, a large herbivore that due to human management actions has become overabundant in many temperate regions (Côté et al., 2004; Putman, 1992). The largest decrement in the browsing of silver fir saplings by roe deer, from 26% to 6%, as well as a significant decrease in browsing intensity was obtained already with one deadwood crown. A further intensification of the physical barrier, by increasing the number of deadwood crowns to four, lowered the probability of roe deer browsing to 2%. Thus, at least in German forests, where the amount of deadwood is currently only 10–15% of that of natural temperate forests (Christensen et al., 2005; Müller and Bütler, 2010), we recommend the retention of at least one deadwood crown as a physical barrier to reduce roe deer browsing. In practical terms, this means that deadwood should remain at the place of origin, which has additional cost-saving advantages since the expense of removal, or a particular arrangement is avoided. However, the retention of larger amounts of lying deadwood may not have additional advantages, as this may force roe deer to overcome the barrier and consume saplings in its shelter. It should also be noted that our experiment was limited to an examination of short-term effects, whereas to escape browsing pressure fir saplings may need several years under the canopy of mature trees. Over the long-term, more deadwood crowns and thereby a denser physical barrier may indeed better hamper browsing, considering that the decay of deadwood branches results in a loss of their function as obstacles.

4.2 A human “landscape of fear” affects browsing pressure

Anthropogenically induced fear in wild animals can change their behavior, including an avoidance of previously preferred habitats (Rösner et al., 2014; Taylor and Knight, 2003). The exploitation of this fact has been proposed as a novel strategy in ungulate management (Cromsigt et al., 2013). We found the browsing probability and intensity of roe deer was lower in forests with a high number of human visitors, presumably because roe deer have been and continue to be hunted in all of our study areas and humans are therefore a well-recognized enemy. The "landscape of fear" imposed by humans suggests that the habitat use of a species is driven not only by habitat forage quality but also by the potential for interactions with other species, including humans (Kuijper et al., 2015; Laundré et al., 2010; Taylor and Knight, 2003). Our results suggest that anthropogenic fear causes roe deer to change their browsing patterns, which may alter ecosystem functioning, as the natural regeneration of trees is better in forests used for recreation and hunting.

4.3 Browsing pressure, plant quality and the population density of roe deer

A positive correlation between browsing pressure and roe deer density over a wide range of densities has been reported in several studies (e.g., Partl et al., 2002). Yet, most studies of browsing pressure and impact have been based on comparisons of activity inside vs. outside of exclosures, such that the difference in the effective density of deer is enormous (Olofsson et al., 2007; Speed et al., 2014). Other authors have suggested that the relief of browsing pressure on preferred forage requires the almost complete absence of ungulates rather than a reduction in their density (Wright et al., 2012). According to our results the roe deer browsing was slightly higher for moderate (11%) roe deer population density than for high (9%) roe deer population density and differed between years. However, we were only able to evaluate moderate and high roe deer densities, as no site had a low roe deer density. This situation is increasingly common in Central Europe, where both hunting bags and roe deer collisions with vehicles are high (Hothorn et al., 2015; Hothorn and Müller, 2010) whereas the culling of roe deer populations to low levels by hunting is locally restricted and generally rare (Hothorn and Müller, 2010).

We also found that fir saplings planted in a deciduous forest were browsed by roe deer with a higher probability and with higher intensity than fir saplings planted in a coniferous forest. This pattern was mainly driven by contrasts between coniferous and deciduous forest for the treatments with addition of deadwood crowns, which suggests that the effect should be dominantly driven by the different crown material rather than the different stand characteristics itself. Coniferous trees are characterised by a thicker crown structure compared to deciduous trees, which may result in a higher protective function of coniferous tree crowns on the forest floor hampering the access by row deer.

Fir is prone to browsing and is more highly browsed than other tree species, such as spruce (Hothorn and Müller, 2010). Moreover, as a high-quality food resource for cervids, fir saplings from tree nurseries are subject to a higher browsing pressure than naturally regenerated saplings (Odermatt, 1999). Thus, our in general high values for browsing could not directly transferred to natural regenerated silver fir or to other tree species. However, we assume that the protective function of a deadwood shelter may be even higher for naturally regenerated saplings and for other tree species less exposed to browsing (Hothorn and Müller, 2010; Odermatt, 1999). If roe deer do not reach high-quality browse, it is even less likely they will enter these areas for low quality saplings. Accordingly, our demonstration of a positive effect of deadwood retention in forests on the probability of browsing by roe deer should be interpreted as a conservative estimate. For conclusions on future growth capacity and tree survival there is the need of long-term studies following all life stages of the three.

4.4 Contrary browsing by the small-herbivore guild

The probability of rodent browsing was the inverse of that of roe deer browsing and was lower on plots with no deadwood crown than on plots with a dense physical barrier of four deadwood crowns (1% vs. 17%). Lying deadwood is an important habitat element that produces a diverse vertical structuring of the forest floor. For rodents, this structuring offers shelter from predators, nesting sites, an enhanced food supply and a suitable humid microclimate (Carey and Johnson, 1995; Suter and Schielly, 1998). Thus, for rodents browsing of saplings in shelter of deadwood is favourable. Although similar benefits for rodents may be supplied by tall ground vegetation cover, this may also increase negative interactions both with larger mammals and with other small mammals (Bakker et al., 2009; den Herder et al., 2016; Flowerdew and Ellwood, 2001). The considerable contribution of rodent browsing to the total amount of browsing at our study sites highlights the importance of distinguishing between browsing agents to better understand browsing patterns and their consequences for forest regeneration (Belsky, 1984).

Based on browsing traces and other habitat properties, the mainly granivorous bank vole (*Myodes glareolus*) and the omnivorous to insectivorous yellow-necked mouse (*Apodemus flavicollis*) were probably the dominant species involved in rodent browsing at our study sites. In line with the browsing pattern of roe deer, the probability and intensity of rodent browsing were higher in deciduous than in coniferous stands. This no doubt reflected the fact that the artificial provision of fir saplings in a deciduous forest in autumn offered an attractive food resource for rodents and thus led to more intense browsing than in a forest that, in addition to the saplings, contained naturally regenerated fir. The population dynamics of rodents are such that abundance is high in some years and low in others (Hansson and Henttonen, 1988). This pattern is linked to the mast seeding of forest trees, resulting in years with large food supplies that support extremely high densities of rodents (Bogdziewicz et al., 2016; Hansson, 1998; Schnurr et al., 2002). Consequently, the probability of rodent browsing may differ from year to year (Nopp-Mayr et al., 2012), however in this study we found no effect between the two years where experimental sites were established. Independent of their browsing impact, rodents represent part of the forest's biodiversity and include endangered species (Temple and Terry, 2009). They are also involved in seed dispersal (Tiffney, 2004) and play a key role in the food web (Hanski et al., 2001).

4.5 Conclusions

The economic costs attributable to overabundance of cervids are difficult to estimate. In Germany, based on forest and browsing inventories, a preliminary estimate was at least 175 million Euros per year (Clasen and Knoke, 2013), although this did not include the expenses incurred by the intensive browsing protection measures conducted annually. Our study demonstrated the potential benefits of retaining deadwood from logging residuals as an effective and cost-effective means of protecting saplings from roe deer browsing. At the same time, the activities of other browsing agents, especially rodents, may be favored by the increased amounts of deadwood. Nonetheless, retention on the ground of logging residuals and naturally fallen trees not only serves as a barrier to roe deer browsing but also has the advantage of promoting the diversity of deadwood-dependent species and their relevant ecosystem functions.

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Figure 1. (a) Distribution of the study sites in southern Germany. Each site contained four replicates of the four treatments. (b) The impact of an increasingly dense physical barrier comprising deadwood crowns on roe deer and rodent browsing was tested by comparing the effects of no crowns, 1 crown, 2 crowns and 4 crowns. Five fir saplings were planted at the center of each plot, which in the case of the three deadwood treatments were thus located within the shelter of the crown(s).

Figure 2. Browsing of the terminal shoots of fir saplings planted in plots with no crowns or 1 crown, 2 crowns or 4 crowns in a field experiment at 24 sites across southern Germany. For each treatment, the frequency of unbrowsed and browsed saplings is shown by grouped bars. Browsed saplings are separated according to the browsing agent: roe deer, rodents, hares and unknown.

Figure 3. Predicted probability of (a) roe deer and (b) rodent browsing on the terminal shoots of fir saplings in the absence or presence a physical barrier constructed from 1 crown, 2 crowns or 4 crowns in a field experiment involving 24 sites located across southern Germany. Prediction of the browsing probability controlled for the different site characteristics (random and fixed terms) and was based on generalized linear mixed-effects models.

Figure 1

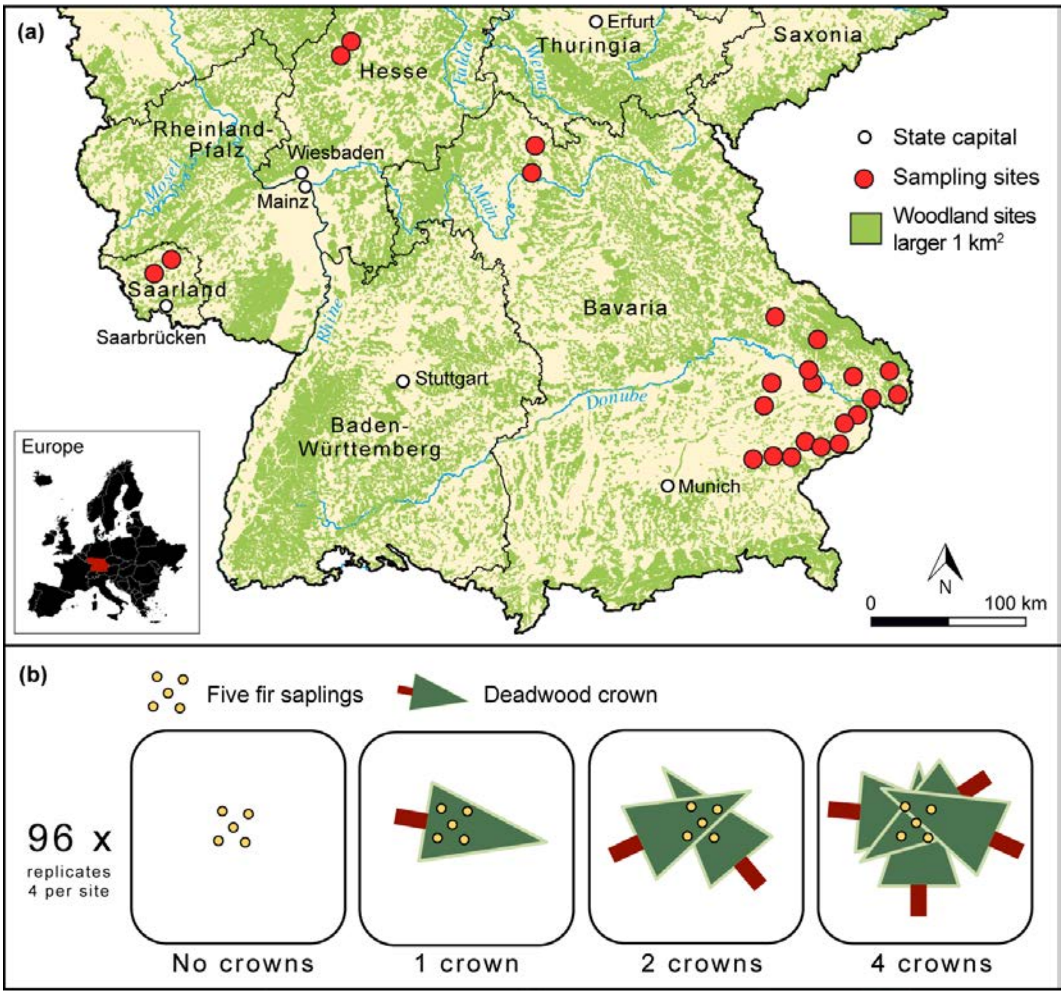
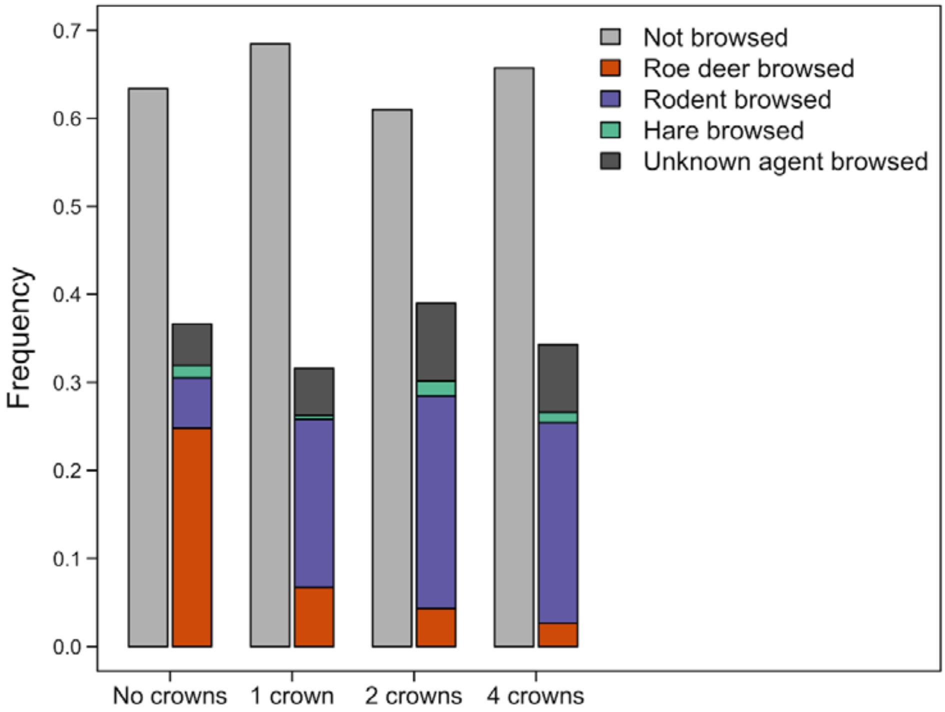

(a)
Erfurt
Thuringia
Saxonia
Hesse
Fulda
Werra
Rheinland-Pfalz
Wiesbaden
Mainz
Mosel
Main
State capital
Sampling sites
Woodland sites larger 1 km²
Saarland
Saarbrücken
Rhine
Bavaria
Stuttgart
Donube
Baden-Württemberg
Munich
Europe
N
0
100 km
(b)
Five fir saplings
Deadwood crown
96 x
replicates
4 per site
No crowns
1 crown
2 crowns
4 crowns

Figure 2



Frequency
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
No crowns
1 crown
2 crowns
4 crowns
Not browsed
Roe deer browsed
Rodent browsed
Hare browsed
Unknown agent browsed

Figure 3

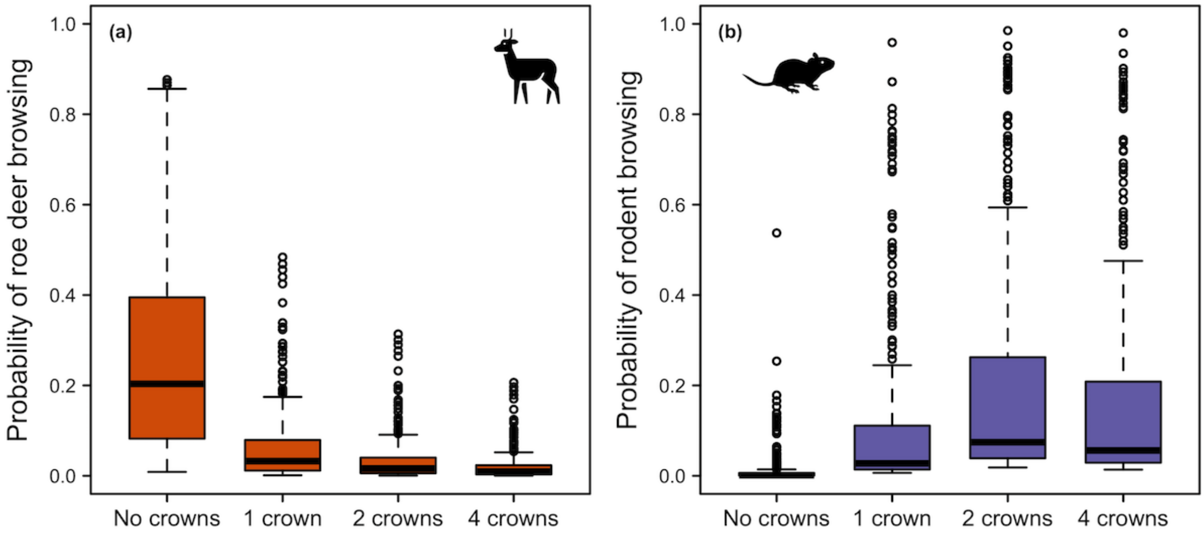

(a)
Probability of roe deer browsing
0.0
0.2
0.4
0.6
0.8
1.0
No crowns
1 crown
2 crowns
4 crowns
(b)
Probability of rodent browsing
0.0
0.2
0.4
0.6
0.8
1.0
No crowns
1 crown
2 crowns
4 crowns

Table 1. Results from generalized linear mixed-effects models of the browsing of the terminal shoots of fir saplings and the browsing intensity of single saplings, i.e., number of shoots browsed according to number of unbrowsed shoots. Separate models were used for roe deer browsing and rodent browsing. The effects of an increasingly complex physical barrier on browsing were tested by the sequential addition of tree crowns (i.e., no crowns, 1 crown, 2 crowns, 4 crowns). The impacts of the stand characteristics (coniferous or broadleaf), population density of the roe deer (moderate or high) and number of human visitors to the forest (low or high) were also evaluated. A further explanatory variable in the models was the year of establishment the experimental site (11 sites in 2016 and 13 sites in 2017). Values in bold indicate significant effects. Asterisks indicate variables with adjusted p-values for multiple testing.

	Browsing of the terminal shoots				**Browsing intensity of single saplings**			
Roe deer browsing	Estimate	Std. error	z-value	p-value	Estimate	Std. error	z-value	p-value
No crowns–1 crown*	**−2.026**	**0.352**	**−5.757**	**<0.001**	**−3.025**	**0.530**	**−5.710**	**<0.001**
1 crown–2 crown*	−0.719	0.425	−1.690	0.091	−0.612	0.585	−1.047	0.295
1 crown–4 crown*	**−1.282**	**0.471**	**−2.724**	**0.006**	**−1.332**	**0.667**	**−1.999**	**0.046**
2 crown–4 crown*	−0.563	0.498	−1.130	0.258	−0.720	0.702	−1.026	0.305
Coniferous–broadleaf stand	**2.070**	**0.619**	**3.348**	**<0.001**	**1.969**	**0.506**	**3.890**	**<0.001**
Population density of roe deer	**−1.246**	**0.613**	**−2.033**	**0.042**	−1.165	0.490	−2.377	0.017
Number of forest visitors	**−2.566**	**0.806**	**−3.182**	**0.001**	**−2.471**	**0.719**	**3.440**	**<0.001**
Year	**1.315**	**0.661**	**1.988**	**0.047**	0.880	0.543	1.621	0.105
Rodent browsing								
No crowns–1 crown*	**2.996**	**0.650**	**4.607**	**<0.001**	**3.039**	**0.449**	**6.772**	**<0.001**
1 crown–2 crown*	**1.047**	**0.407**	**2.572**	**0.010**	0.720	0.394	1.830	0.067
1 crown–4 crown*	0.746	0.407	1.832	0.067	0.486	0.394	1.235	0.217
2 crown–4 crown*	−0.301	0.386	−0780	0.435	−0.234	0.394	−0.594	0.553
Coniferous–broadleaf stand	**1.873**	**0.676**	**2.770**	**0.006**	**5.023**	**0.910**	**5.522**	**<0.001**
Population density of roe deer	0.104	0.646	0.161	0.872	−0.216	0.887	−0.243	0.808
Number of forest visitors	0.427	0.721	0.593	0.554	−0.411	0.985	−0.417	0.676
Year	−0.720	0.711	−1.012	0.312	1.234	0.963	1.282	0.200