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Presenter Information

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Red deer browsing decelerates shrub regrowth despite increasing wolf presence

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Key words: *Canis lupus*; *Cervus elaphus*; Europe; open habitat conservation; shrub encroachment.

Abstract

Semi-natural open habitats in Europe have been shaped by traditional land use practices, such as extensive mowing or livestock grazing. However, socio-economic transformations have led to the abandonment of many grassland and heathland areas and conservation management is now required to maintain these biodiverse habitats. Grazing by wild red deer (*Cervus elaphus*) can be a convenient alternative to laborious mechanical management or livestock grazing. Yet it remains unclear if free-ranging ungulates can counteract shrub growth sufficiently to maintain open habitats—especially with natural predators, i.e. wolves (*Canis lupus*), recolonizing Europe. To assess red deer effects on shrub regrowth after clearance, we installed a cohort of open and fenced plots (17 pairs) in 2016, when wolf presence in our study area (Grafenwöhr military training area, DE) was negligible. When wolf presence had become frequent in 2020, we set up a second cohort (41 paired plots). For both cohorts, the vegetation in the shrub and herb layer was significantly higher in fenced than open plots already after one year. Shrub height increased continuously and dead herbaceous biomass accumulated under red deer exclusion. Consequently, wild red deer can slow down shrub succession in open habitats even under increasing predation pressure. Regardless of wolf presence, a wildlife management that enables red deer to forage in open landscapes could thus reduce the required frequency of conservation management interventions.

Introduction

Traditional forms of agricultural land use, such as low-frequency mowing or extensive livestock grazing, have shaped Europe's semi-natural open habitats in the past (Poschlod et al. 2009). In modern landscapes, many of these grassland or heathland areas have been either agriculturally intensified or abandoned due to low profitability, so that many of the plant and animal species associated with those semi-natural open habitats have become rare (EEA 2020). A particular challenge for conservation management is to counteract shrub encroachment in open habitats (Valkó et al. 2018) because without biomass removal, e.g., through grazing, mowing or fire, most parts of Europe would become forested (Leuschner and Ellenberg 2017). Mechanical clearance of shrubs is laborious and expensive (Day et al. 2003). Among livestock species, only goats are known to browse woody species intensely (Elias and Tischew 2016) but are rarely available and challenging to handle. Wild red deer (*Cervus elaphus*) have been proposed as an alternative for open habitat management, especially for large and inaccessible areas where implementing livestock grazing is difficult (Riesch et al. 2019). Red deer can remove similar amounts of biomass from grasslands and heathlands as livestock stocked at rates recommended for conservation purposes, which comes along with benefits for open vegetation structure and diversity (Riesch et al. 2020, 2022). Whether the free-ranging ungulates can counteract shrub growth sufficiently to maintain open habitats has not yet been tested. It is further not clear how the return of the wolf (*Canis lupus*) to European landscapes affects the impact of red deer on the vegetation in open habitats. Findings from remote parts of the US and Europe have shown that wolves can under certain conditions impact on vegetation processes by affecting their herbivorous prey's density and/or behavior (Ripple and Beschta 2012, Kuijper et al. 2013).

To investigate the effect of red deer on the vegetation development and a potential influence of wolves, we set up an experiment with paired open and fenced plots in sites freshly cleared from shrubs on a military training area in Germany. The experiment started in 2016 under negligible wolf presence and was replicated in 2020, when wolf presence in the study area had become frequent. Each year, we measured the height of the shrub regrowth in open and fenced plots to assess the efficacy of red deer in controlling the shrub regrowth.

Methods

Our study area was the Grafenwöhr military training area in south-eastern Germany (49°40′56″N, 11°47′20″E). The area covers approximately 223 km^2 including almost 40% open habitats (Raab et al. 2019). Red deer are the most abundant game species, estimated at 7000-8000 individuals in summer. Other large mammals are roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). The red deer regularly forage in the open landscape (Richter et al. 2020), mainly because hunting in open areas is strictly limited by the Federal Forestry Administration. The first verified evidence of a wolf in the region dates back to a camera trap picture on the training area from autumn 2016. From that time on, at least one single wolf or a wolf pair was present on the training area. Additionally, in 2018, a pack established in a forest adjacent to the training area (cf. Fig. 1), producing litters with five, four, four, and three pups in the following years. A second wolf pack established in another neighboring forest, producing five pups in 2020 and one pup in 2021 (DBBW 2022). Analyses of wolf scats found in our study area show that about one third of the wolves' diet comes from red deer (unpublished data).

To assess the effect of red deer on shrub regrowth, we installed 17 pairs of open and fenced plots (3.5×3.5 m) after clearance of woody vegetation (mostly thorny shrubs *Crataegus* and *Prunus* sp.) in one forestry district (A) on the training area in 2016 (first cohort). In spring 2020, after further shrub removal, we installed a second cohort composed of 16 additional plot pairs in the same district and 25 plot pairs in another district (B) on the training area. Approximately half of the plot pairs in district B represented birch (*Betula* sp.) succession, few were dominated by conifers (*Pinus* sp., *Picea* sp.) or included broom (*Cytisus* sp.), the rest were similar to those in district A. Each year in autumn, usually at the end of November, we measured the height of the woody vegetation in open and fenced plots at 20 randomly chosen spots, while keeping a distance of 1 m to the plot edge. If there was no woody plant within a 10 cm radius around the selected measuring spot, we recorded zero height. From 2017 on, we additionally estimated the percentage of dead biomass in the herbaceous vegetation layer. We analyzed the interaction effect of sampling year (2016 to 2021) and plot (open, fenced) on the mean vegetation height per plot (log-transformed) in a linear mixed effects model with the sampling plot as random effect. For the data of the second cohort, we included the district (A, B) as further interacting explanatory factor. The proportion of necromass in the herb layer was analyzed by linear mixed effects models with similar explanatory and random factors. Where necessary, we accounted for unequal variances between factor levels. We compared nested models based on AIC_c but model simplification did not seem appropriate. We calculated estimated marginal means to test for pairwise differences between open and fenced plots per year. Data processing and analyses were done in R 4.2.1. Figures show means and standard errors (se) of the raw data.

Results and Discussion

In the initial measurement after shrub removal, the height of the woody vegetation was similar in open and fenced plots for both the first cohort of plots established in 2016 and the second cohort established in 2020. One year (cohort 1; Fig. 1) or six months (cohort 2; Fig. 2) after the installation of the fences, the shrubs were already significantly higher in the fenced plots than in the open plots ($p<0.0001$). The shrubs accessible to red deer in the open plots remained more or less at the height at which they had been cut. After five years, the

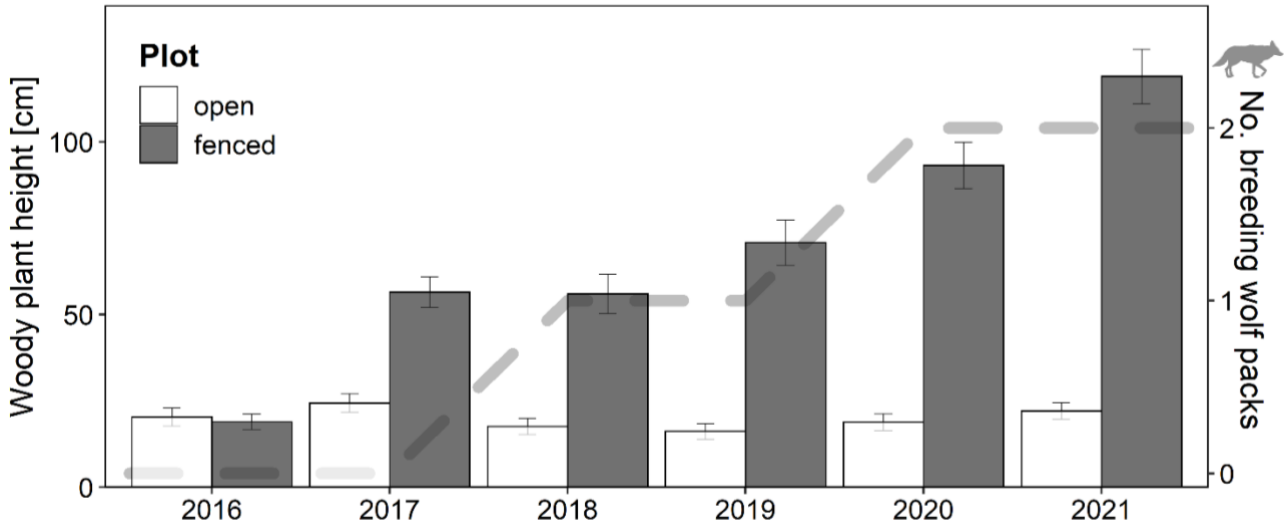

Figure 1. Mean (±se) height of woody plants (cm) in paired open and fenced plots (n=17) from 2016 (first measurement after shrub removal) to 2021. The dashed grey line symbolizes the development of the wolf population in the region.

shrubs in the fenced plots had reached a mean height of approximately 1.2 m with some shoots extending up to more than 2.5 m. For the second cohort, the development of the vegetation height in the fenced plots was similar in both districts, but the increment in woody plant height was less pronounced in the district B (Fig. 2). This might be related to differences in floristic composition and growing conditions because district A is situated in a calcareous area, while district B is characterized by mostly acidic and sandy soils, which are less favorable for plant growth.

In addition to the increasing shrub height, the fenced plots were characterized by a higher share of herbaceous necromass than the open plots. The percentage of dead herb biomass in cohort 1 was at least 12 percentage points higher in fenced than open plots ($p<0.05$) from 2017 on, despite yearly variation related to phenology and weather conditions. Similarly, in cohort 2, the share of dead herb mass in fenced plots exceeded the share of dead herb mass in open plots by 10 and 18 percentage points in district A and B after one and a half years ($p<0.001$). This is likely to be explained by the fact that the red deer, being ungulates with intermediate feeding strategy (Hofmann 1989), do not only browse on the shrubs but also graze on the herbaceous understory vegetation in the open plots. In the fenced plots, senescent plant material accumulates because it is not removed by the herbivores. Such an increase in litter can have detrimental effects on plant biodiversity due to increased light competition and reduced chances for seedling emergence (Kelemen et al. 2013).

Despite the impressive deceleration of shrub succession, it is obvious in our study area that red deer are not able to remove existing shrubs. This means that implementing red deer grazing is not sufficient for restoring shrub-infested open habitats. The same is true for goat grazing, which has to be combined with occasional mechanical clearing for effective control of shrub regrowth and expansion (Álvarez-Martínez et al. 2016).

Shrub browsing under wolf presence

Our data do not provide any indication that the suppressive effect of the browsing of the red deer on the shrubs changed over the course of time. Thus, the presence of wolves as natural predators on the training area, increasing from a single individual to various members of different packs, did not seem to compromise the red deer browsing behavior. This is in contrast to what has been observed, for example, in the US Yellowstone National Park and the Polish Białowieża National Park, where the return of wolves is supposed to have triggered a trophic cascade leading to increased tree regeneration because of reduced herbivore numbers and shifts in their habitat use behavior (Kuijper et al. 2013, Beschta et al. 2018). Still, the red deer in our study area might have adapted their behavior at a fine spatio-temporal scale to decrease encounter rates with wolves, which has been found, for instance, for fallow deer in Italy (Rossa et al. 2021). They might use the shrubby areas at different times of the day than before the return of wolves. Whether such fine-scale behavioral responses to wolf presence exist could be detected in further studies using camera traps.

So far, our exclusion experiment provides evidence that the ecological function of red deer browsing on shrubby vegetation is maintained under wolf presence. Therefore, considering wild ungulate browsing as a future conservation management strategy for open habitats appears to be particularly promising because livestock grazing might become more of a challenge in the future when wolves disperse more widely in Europe.

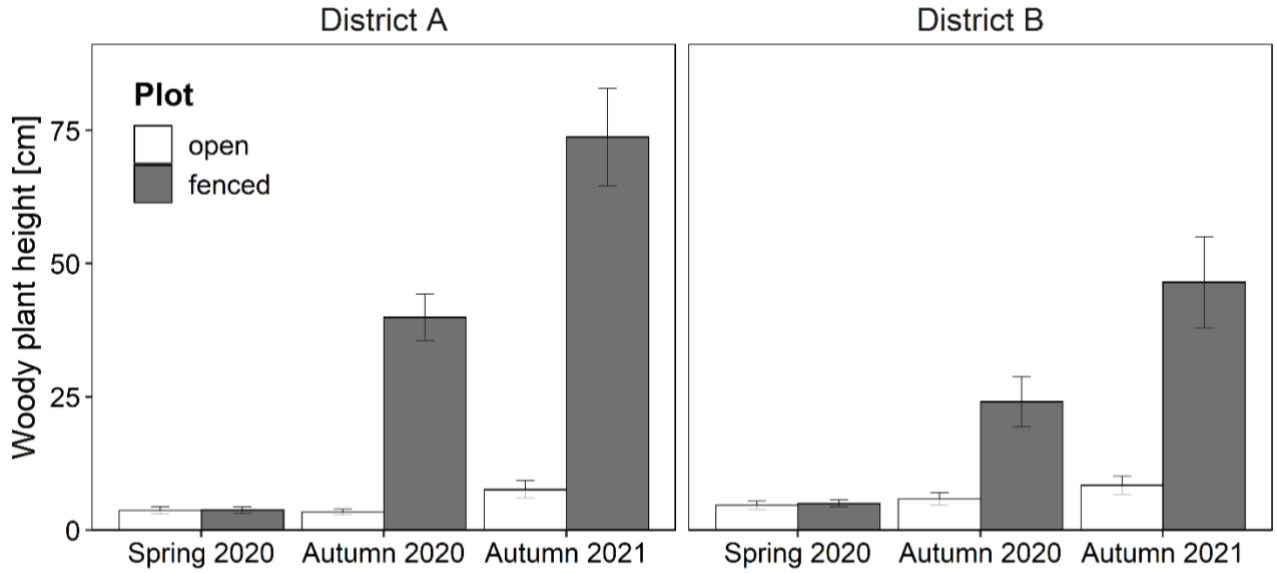

Figure 2. Mean (±se) height of woody plants (cm) in paired open and fenced plots of the second experimental cohort established in district A (n=16) and district B (n=25) in spring 2020.

Conclusions and Implications

Over several years, the red deer in our study area have maintained shrubs at the height of the stubbles that had remained after shrub clearance. Red deer continued to suppress the shrub regrowth under increasing wolf presence. This effect did not qualitatively differ between districts with different soil conditions and plant communities. Consequently, browsing by wild red deer appears to be an effective strategy to counteract the regrowth of shrubs after mechanical removal in open habitats. A targeted wildlife management allowing red deer to forage in open habitats can thus help to reduce the frequency and costs for mechanical conservation measures and contribute to the preservation of open habitats and associated endangered species. Providing an alternative to livestock grazing, a wildlife-based strategy for managing open habitats might reduce the potential of conflict that comes along with recolonizing wolves in Europe.

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