

Local trophic cascading impact of wolves on tree regeneration in summer and winter areas of ungulates

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Abstract

Wolves can change the abundance and the spatio-temporal use of habitats of wild ungulates and thus have an impact on the browsing of tree regeneration. In the Calanda region of Switzerland, ungulate browsing was monitored in tree regeneration inventories before, during and after wolf settlement. Within the core zones of wolves the deer density and browsing on tree saplings decreased but not in frequently used zones that were within winter areas of deer. Trophic interactions are supposed to be complex because of the influence of forestry, hunting and wildlife protection areas.

Keywords

Canis lupus, ungulate browsing, herbivory, forest regeneration, red deer

Introduction

The wolf (*Canis lupus* L.) currently returns to its original distribution areas in central Europe. Since about 1995, it has been migrating from Italy to Switzerland. In the region around the mountain range of Calanda (Canton of Grisons) the first couple of wolves in the modern time of Switzerland settled down in 2012 and reproduces each year.

The wolf will change the interactions between the organisms, as wolves eat wild ungulates like chamois (*Rupicapra rupicapra* L.), roe deer (*Capreolus capreolus* L.) and red deer (*Cervus elaphus* L.) to meet their energy needs as a large, year-round active carnivore. This reduces the species abundance of the prey species and can affect the frequency and distribution of browsing on tree regeneration (RIPPLE & BESCHTA 2012). Besides such direct, numeric effects of wolves on the abundance and demography of their prey populations, functional effects through mediated behaviour of wild ungulates are reported. For example, the presence of wolves can affect the spatio-temporal use of wild ungulates (KULJPER et al. 2013). This in turn affects the vegetation development and the tree regeneration indirectly (GÄRTNER & NOACK 2009). The group size (BARJA & ROSELLINI 2008) and the food selection of the wild ungulates (CHRISTIANSON & CREEL 2008) can also change in the presence of wolves, and thus the browsing pressure on the site increases or decreases locally. As forest ecosystems in central Europe are strongly influenced by hunting, the trophic cascading impact of carnivores on forests may be limited (RATIKAINEN et al. 2007). Thus, trophic interactions between predators, herbivores and forest regeneration are complex, multi-layered and difficult to anticipate.

In a first phase of wolf recolonization in a region with still a low density of wolves, the functional effects as changes in the spatio-temporal use of habitats and resources are considered to be dominant because the wild ungulates attempt avoiding to become a prey (KUPFERSCHMID & BOLLMANN 2016). Later, in phases with higher wolf densities and in particular in wolf core areas, numeric effects on the abundance of prey species should become more obvious. Since the spatio-temporal habitat use of prey species is not only influenced by the occurrence and abundance of large predators but also by forestry, hunting practises and wildlife protection areas, a gradual decrease in the browsing level cannot be assumed in general.

In this study I used regeneration assessment areas that were installed previous to wolf settlement i) in the core area of the wolf pack, ii) in areas used by deer and wolves in winter and iii) in areas with only sporadic presence of wolves. The aim of this pilot study was to compare the regeneration density and browsing intensity over time to see if there was a large and thus measurable effect of wolves on tree regeneration.

Methods

In order to control the influence of ungulate browsing on tree regeneration, the canton of Grisons established regeneration assessments in different areas with 14-25 circular sampling plots on a rectangular grid with a fixed distance of 100 m. The plot radius varied between 2 and 9 m and the plot centres were permanently marked. Each plot was sampled in autumn by the cantonal authorities in various years (1996, 2007/08, and 2013/15). Thereby, the amount of tree regeneration was counted in height classes (10 cm till 130 cm height) and it was noted if the terminal shoot was browsed. For this study, seven sites were chosen with regeneration of *Abies alba* that also had silver fir trees in the canopy.

Four sites were situated in the Calanda region:

- 2 sites in the core area of the wolf pack located in a summer area of red deer (hunting area Felsberg)
- 2 sites with frequent wolves in winter located in a winter area of roe and red deer and belonging to the wildlife protection area of 'Chimmiwald' (hunting area Untervaz).

Three sites were situated in the nearby Prättigau region:

- 2 sites with infrequent wolf presence located in a winter area of red deer, one of them belonging to the wildlife protection area of 'Eggwald' (hunting areas Vorderprättigau or Seewis)
- 1 site with infrequent wolf presence located in a summer area of red deer (hunting area Seewis).

The sites were resampled by students in early spring before budburst in 2016 (Calanda) or 2017 (Prättigau). Ungulate density was approximated in each area by taking the number of ungulates culled by hunting per year and forest area (red and roe deer) or area (chamois) within each hunting district and calculating the Ungulate Density Index (following MOTTA 1996) as $UDI = 1/5 \text{ roe deer} + 1/4 \text{ chamois} + \text{red deer}$. Analysis was done separately for each tree species with the R 3.3.1 (2016), function 'lm' of the package lme4. For the number of saplings browsed on their leader shoot in percentage of all saplings, i.e. the browsing intensity, additional subset analyses per each region were carried out.

Results and discussion

The region Calanda with frequent wolves and deer in a winter area had significantly less tree regeneration (apart from more beech saplings, probably due to lower elevation of one site) than the region Calanda with deer in summer (Tab. 1). The values varied over time with more regeneration of the preferentially browsed tree species *Abies*, *Acer* and *Sorbus* after compared to before wolf settlement (Tab. 1). An increase in UDI tended to have a negative influence on *Acer* and *Abies* sapling density. Generally, the models explained rather poorly, indicating that some major factor explaining tree regeneration density is missing in the models.

	<i>Acer pseudoplatanus</i>	<i>Fagus sylvatica</i>	<i>Sorbus aucuparia</i>	<i>Abies alba</i>	<i>Picea abies</i>
Browsing intensity	-0.0021±0.0014	-	0.0015±0.0008	-	-
Basal area	<i>-0.0709±0.0275</i>	-0.4319±0.0816	0.0558±0.0158	<i>0.0241±0.0114</i>	0.0643±0.0135
UDI	<i>-0.0158±0.0062</i>	-	-	<i>-0.0049±0.0025</i>	-
Region: Calanda deer in winter	-0.3866±0.1090	6.3768±1.3087	<i>-0.4954±0.2118</i>	-0.6179±0.1718	-1.1242±0.2154
Region: Prättigau deer in summer	<i>1.6656±0.7654</i>	19.4311±3.5602	-2.4205±0.6313	-1.3351±0.4829	-2.8720±0.5871
Region: Prättigau deer in winter	<i>0.6319±0.3201</i>	9.2997±1.9071	-1.1346±0.3305	-0.7586±0.2568	-1.6247±0.3144
Year: during wolf establishment (2013)	0.1422±0.0951	-	0.1025±0.0535	0.0408±0.0434	-
Year: after wolf establishment (2015-2017)	0.1887±0.0579	-	<i>0.0761±0.0350</i>	0.0712±0.0230	-
pH	-	4.6548±1.2074	-0.6624±0.1925	-0.5457±0.1555	-0.9093±0.1987
Adjusted R-squared	0.0833	0.2316	0.1811	0.0564	0.0911
Degree of freedom	8/343	5/388	8/348	8/385	5/390

Table 1: Linear regression coefficients (± standard error) for tree regeneration density of saplings between 10 cm and 130 cm separately for the most frequent tree species. The tree density was square root transformed (except for *Fagus* where a natural logarithm transformation was carried out). The reference for 'Region' is 'Calanda deer in summer' and for 'Year' it is 'before wolf establishment (1996 – 2008)'. The results were considered as significant below a p-value of 0.01 (in bold) and as a tendency between 0.01-0.05 (in italics).

The browsing intensity decreased for maple and spruce saplings with increasing sapling density. UDI had a combined effect with region as the UDI decreased in the core zone of wolf in the Calanda, remained more or less stable in the region of Calanda with deer in winter and increased in region Prättigau (cf. Tab. 3). The results were therefore almost not interpretable and a subset analysis for each region was therefore performed.

With the exception of beech, for all tree species the browsing intensity decreased in Felsberg in the wolf core zone over time (Tab. 2 and Fig. 1). In contrast, the browsing intensity increased over time for all species in Untervaz (only significant for *Fagus*, tendency for *Picea*, Tab. 2 but see Fig. 1). In the region Prättigau, the UDI values increased over time but only the browsing intensity of *Acer* significantly increased over time in Seewis. Note however, that there were only a limited amount of sampling plots with tree regeneration (between 29 and 102 depending on the tree species) and the result would clearly gain accuracy with more sites and plots within sites.

	Region	Calanda		Prättigau	
	Hunting area	Felsberg	Untervaz	Seewis	Vorderprättigau
Tree	Wolf establishment	Wolf summer core zone	Wolves in winter	Infrequent wolf presence	
<i>Acer</i>	during	-	0.0472 ±0.1033	-	-
	after	-0.3306 ±0.0816	0.1470 ±0.1075	0.2613 ±0.0829	0.0777 ±0.1203
<i>Fagus</i>	during	<i>0.3793 ±0.1628</i>	0.0879 ±0.0531	-	-
	after	0.1862 ±0.1484	0.1667 ±0.0526	-0.0545 ±0.0642	0.0427 ±0.1461
<i>Sorbus</i>	during	-0.4115 ±0.1299	0.1147 ±0.1951	-	-
	after	-0.5795 ±0.1756	0.1414 ±0.1947	0.0627 ±0.1252	-0.0328 ±0.1152
<i>Abies</i>	during	-0.4004 ±0.1357	-0.2645 ±0.1965	-	-
	after	-0.3971 ±0.1413	0.1592 ±0.2034	-0.1673 ±0.0888	0.0942 ±0.0866
<i>Picea</i>	during	-0.0632 ±0.0324	0.0023 ±0.1057	-	-
	after	<i>-0.0752 ±0.0339</i>	<i>0.2487 ±0.1089</i>	0.0101 ±0.0587	-0.0155 ±0.0207

Table 2: Linear regression coefficients (\pm standard error) for the subset analysis of browsing intensity before, during or after wolf settlement for the most frequent tree species in each region. The reference for 'wolf establishment' is before. The results were considered as significant below a p-value of 0.01 (in bold) and as a tendency between 0.01-0.05 (in italics).

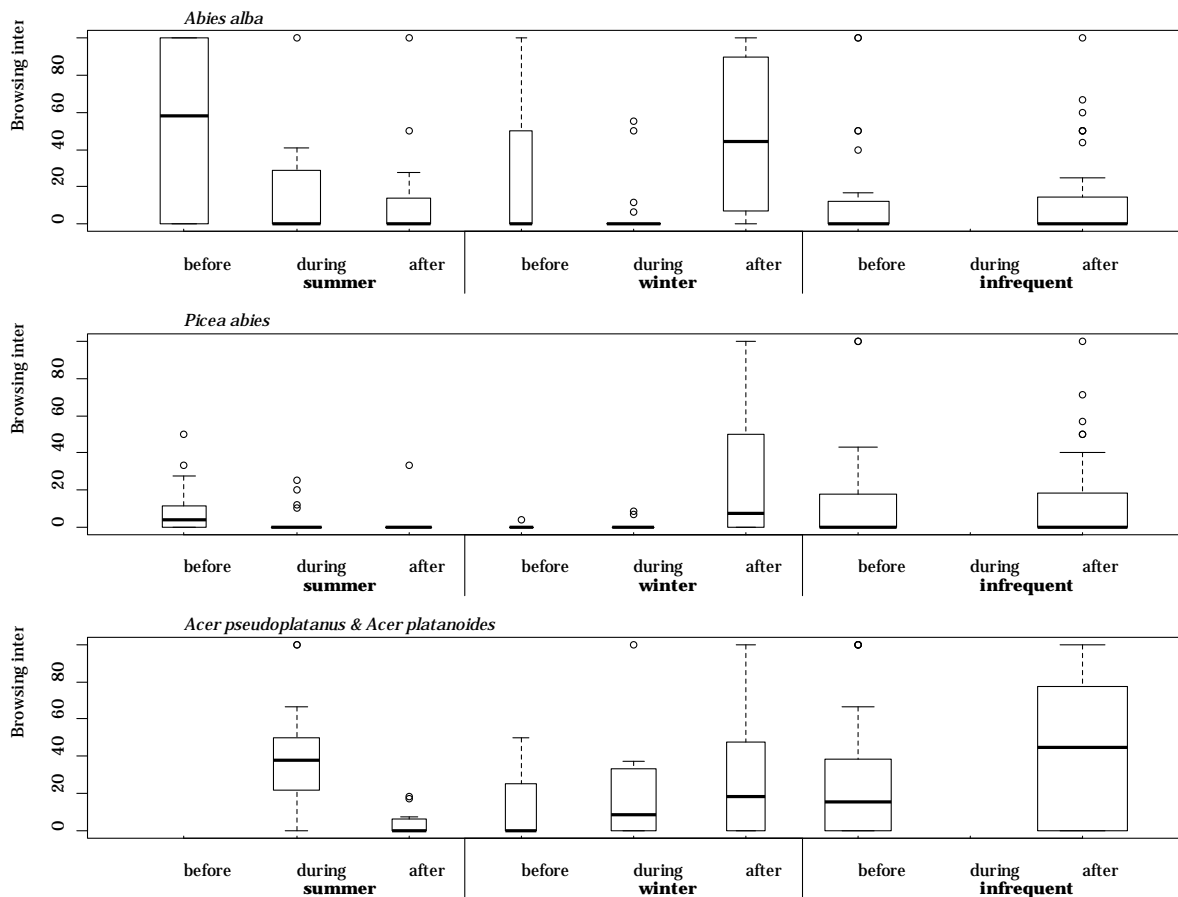


Figure 1: Browsing intensity for fir, spruce and maple before, during and after wolf settlement in the region Calanda with wolves in summer or winter and in the Region Prättigau with infrequent wolf occurrence.

	Calanda		Prättigau	
Region	Wolf summer core zone	Wolves in winter	Infrequent wolf presence	
	Felsberg	Untervaz	Seewis	Vorderprättigau
Ungulate density Index	↘	→	↗	↗
Browsing intensity	↘	↗	→	→
Sapling density	↗	↗	↗	↗

Table 3: Summary of the main factors in the two regions and their effect over time.

Conclusion

The direct effect of wolves on the population size of wild ungulates naturally depends on the preferred prey species. In the core wolf area of Felsberg in the region of Calanda, the UDI decreased dramatically in 2013 and thus probably also the browsing intensity which probably lead to more tree regeneration (Tab. 3). In Untervaz with frequent wolves in winter, the browsing intensity rather increased over time. Both sites in the hunting district Untervaz are core winter habitats for roe and red deer and are situated within a winter wildlife protection area. There might have been shifts in the spatio-temporal use, in the group size and/or in the food selection of the wild ungulates due to the stress induced by the wolves. However, the effect of wolves may simply be overruled by other factors, such as decreased hunting. Hence, our study demonstrates that the equation 'wolf = less ungulates = fewer browsing' is not a general rule, in particular because of the small – scaled landscape of Switzerland that is strongly influenced by forestry, hunting and wildlife protection areas.

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