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# Deer browsing promotes Norway spruce at the expense of silver fir in the forest regeneration phase



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#### ABSTRACT

Deer populations have dramatically increased over the last decades in Western Europe and their browsing has affected forest vegetation, especially plant community composition. High deer browsing pressure may threaten forest ecosystems and needs to be assessed over the long run. However, few studies to date have addressed the long-term impact of deer on forest regeneration.

During one regeneration phase, we assessed the impact of deer (*Cervus elaphus* L. and *Capreolus capreolus* L.) browsing on mixed silver fir (*Abies alba* Mill.)/Norway spruce (*Picea abies* L. H. Karst.) stands in the Vosges Mountains in North-eastern France. For both tree species, we measured seedling and sapling density, height and diameter in 28 paired fenced – unfenced plots distributed over two sites that had been fenced 27 years ago, for 10 and 23 years respectively.

We demonstrated that the presence of deer decreased the density, height and diameter of silver fir saplings, while it increased the height of Norway spruce saplings. We also noticed that the effect of fencing was very different depending on fencing duration, and that even 10 years of fencing led to changes that were still visible 17 years later.

Our results confirm that deer browsing has a long-term impact on the regeneration of silver fir. Furthermore, they suggest that deer browsing may cause a species substitution, with Norway spruce gradually replacing silver fir. Such a trend would have an impact on the ecological and economical value of these forests. How browsing impacts the forest's ability to adapt to global warming should also be considered, since browsing might impede the implementation of management policies designed to address this issue.

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#### 1. Introduction

How forest composition and large herbivore populations co-evolve has repeatedly questioned forest ecologists. The very long-term action of large herbivores on forest structure and composition is still poorly understood. For instance, the prevalent theory that original temperate vegetation consisted of a closed forest hosting low herbivores concentrations which had no influence on forest succession has been challenged by the theory of original park-like landscapes with high concentrations of various large herbivorous species playing a steering role in plant community succession (Vera, 2000). Over the last few decades, forests have experienced significant human-induced environmental changes such as acid rain, nitrogen deposition, land use change, climate change, changes in wood harvesting intensity (Coomes et al., 2014), but also increasing deer populations. Indeed, deer overpopulation is considered a major threat to forest ecosystem sustainability, especially for stand structure and composition stability (Rackham, 2008). This recent, world-wide and large increase in deer populations is attributed to the extirpation of large predators (Breitenmoser, 1998) and changes in silviculture, agriculture and

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game management (Van Hees et al., 1996; Waller and Alverson, 1997). Hence, understanding the long-term interplay between deer and forest stands dynamics has become of critical importance in order to plan adaptation strategies to maintain the associated services provided by forest ecosystem (Beguin et al., 2016).

High deer densities are able to modify the survival and growth of tree seedlings, influence community composition, and modify the trajectory of ecosystems (Augustine et al., 1998). In European temperate forests, both red deer (Cervus elaphus L.) and roe deer (Capreolus capreolus L.) include silver fir (Abies alba Mill.) and Norway spruce (Picea abies (L.) Karst) in their winter diets, as coniferous species are a main resource throughout the low food availability season (Redjadj et al., 2014; Storms et al., 2008). Furthermore deer browsing intensity varies among tree species, silver fir being more palatable to deer than Norway spruce (Heuzé et al., 2005a). It has been reported worldwide that when overabundant. deer may have an important impact on tree species composition in forest communities (McGarvey et al., 2013; Motta, 2003; Olofsson et al., 2005; Tamura, 2015). In particular, the case of spruce being favoured by large ungulates in comparison with fir has been reported (Heuzé et al., 2005b; Thompson and Curran, 1992). Similarly, on Anticosti Island, Potvin et al. (2003) showed that deer is about to eradicate balsam fir (Abies balsamea (L.) Mill.) in favour of white spruce (Picea glauca (Moench) Voss) within a few decades

Silver fir and Norway spruce are two coniferous species that partially share their ecological niches so that they often cooccur (Mauri et al., 2016). They have different light requirements, however. Norway spruce is considered a post-pioneer species as it is able to physiologically acclimate in full-light conditions, while silver fir is less competitive than Norway spruce when colonizing open areas, but has better long-term survival rates in shady conditions (Vieilledent et al., 2009). Regenerating mixed stands is currently a critical issue in forest policy for economic and ecological reasons. The productivity of mixed stands has been showed to remain, on average, more stable through time than monospecific stands (Morin et al., 2014), and the loss of admixed tree species because of deer browsing presents a substantial financial risk (Clasen et al., 2011). Finally, silver fir is considered to be better adapted and more resistant than Norway spruce to anticipated future conditions, *i.e.* climate changes and associated biotic risks (Knoke et al., 2008; Wermelinger, 2004).

In the meantime, the current pressure exerted by deer populations on vegetation is considered problematic for natural forest renewal. Fencing is often used as a protection tool for forest stand regeneration (Vacek et al., 2014; VerCauteren et al., 1997) and is a common experimental approach for studying the impact of browsing by deer (Castleberry et al., 2000; Rooney, 2009; Tremblay, 2005; Trumbull et al., 1989). Numerous studies have already been carried out using fencing designs (Waller et al., 2009), but they are often conducted in deer overabundance contexts and mostly concern relatively short periods of exclosure. From a silvicultural point of view, the duration of the experiment is hardly thought with respect to the length of the regeneration phase in commonly managed forests. Fencing experiments conducted over long periods are likely to produce sound results for forest managers, namely assessing more precisely the benefit of long-term fences against deer, and, for researchers, better quantifying the long-term impact of deer browsing on mixed forest stands.

In the present study, we aimed to assess the long-term impact of managed deer populations on the regeneration of mixed silver fir – Norway spruce stands, using an experimental design. More precisely, we tested the following hypotheses: **H1.** High deer browsing pressure has a negative impact on the establishment and growth of silver fir (Heuzé et al., 2005b; Motta, 1999);

**H2.** High deer browsing pressure does not impact the establishment and growth of Norway spruce (Rozman et al., 2015; Vacek et al., 2014);

Consequently we predicted that, in presence of deer, Norway spruce has a competitive advantage over silver fir due to a lower palatability, resulting in a regeneration layer dominated by Norway spruce (Casabon and Pothier, 2007; Potvin et al., 2003).

**H3.** Deer exclusion for 10 years still has visible effects even 17 years after fences removal.

We used an exclosure design set up in forests under a multipleuse management scheme where deer is hunted. This experimental design consists of two sites, each with 7 replicates of paired fenced/unfenced plots. The fences at the first site had been maintained for 23 years (Fencing Duration (FD): 23 years), whereas those at the second site had fallen down during a windstorm after 10 years (FD: 10 years). Therefore, the observation period was 23 years for site A (with 23 years of fencing) while it was of 27 years for site B (with only 10 years of fencing), which made it possible to assess the persistence of the effect of a 10-year fencing period 17 years later.

#### 2. Materials and methods

#### 2.1. Stand and site characteristics

The experimental sites are located in the Vosges Mountains, in north-eastern France (48°31'N to 48°35'N, 7°01'E to 7°12'E) (Fig. 1), in even-aged managed forests, on a podzolic soil (Picard et al., 1994). The mean annual temperature was 9.2 °C (from 1.1 °C to 18.0 °C) and the mean annual cumulative precipitation was 1437 mm between 1981 and 2010 (AURELHY database, Canellas et al., 2014). Site A was a 150-180-year-old stand with a S - SE aspect, a slope of 28 ° and an elevation of 720 m above sea level (a.s.l.). The mean basal area was  $54.1 \text{ m}^2 \text{ ha}^{-1}$  (between 42.7 m<sup>2</sup> ha<sup>-1</sup> and 64.1 m<sup>2</sup> ha<sup>-1</sup> among plots) at the time of fencing, in 1989. Site B was a 110-160-year-old stand, with a NW to E aspect, a slope of 12° and an elevation of 580–630 m a.s.l. At both sites, the overstory was dominated by coniferous species, nearly exclusively Abies alba accompanied by Picea abies, Scots pine (Pinus sylvestris) and a few beech trees (Fagus sylvatica). The low abundance of understory trees and the already large height of reproductive trees allowed sufficient light at ground level to support forest regeneration (Picard et al., 1994). Thus, no cuttings were made before storm Lothar occurred in 1999.

Free-ranging populations of red deer and roe deer are present at both sites. These populations have been increasing for the last several decades (Supplementary tables A to D). Over 1985–2015, 4.8 and 4.1 red deer were culled per 100 ha in the management units associated to sites A and B respectively. Over the same period, 2.2 and 2.7 roe deer were culled per 100 ha in the forest area of the three municipalities surrounding sites A and B respectively (data from the "Réseau Ongulés sauvages ONCFS-FNC-FDC").

#### 2.2. Experimental design

At each site, 14 plots, each 25 m \* 25 m, were delimited in 1989. These plots were grouped in seven pairs (fenced - unfenced), split in three blocks. Fences were 2.5 m tall, with a 10 cm mesh size. One block contained three pairs of plots (3 fenced - 3 unfenced Download English Version:

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