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Rewilding with large herbivores: The importance of grazing refuges for sapling establishment and wood-pasture formation

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ABSTRACT

Rewilding is a novel nature management type that aims at restoring natural processes with minimal human intervention. It is increasingly employed on abandoned agricultural lands in Europe, but empirical studies are scarce. Rewilding may lead to formation of wood-pastures, arguably the primeval landscape in parts of Europe before Neolithic times. We investigated sapling establishment, a key process for wood-pasture formation, in the Oostvaardersplassen: Europe's oldest large-scale rewilding area, with high densities of free-roaming large herbivores. We transplanted saplings of pioneers, spiny shrubs, and hardwood species and studied how herbivore accessibility (grazed control, partial and full exclosure), vegetation type (tall roughs; short lawns) and soil-tillage (mimicking wild boar rooting) affected sapling survival for four years. No single sapling survived in grazed controls, while survival in exclosures was 25%. Differences in survival between partial and full exclosures were minor, indicating that reduced herbivore access is sufficient for sapling survival. Survival was higher in lawn than in rough in both exclosure types and for all species, indicating positive effects of preceding grazing. Soil tillage initially benefitted all species, but effects lasted for pioneers only, suggesting that – once introduced – wild boar rooting may affect woody species composition. We conclude that rewilding with herbivores can successfully form wood-pasture landscapes on abandoned agricultural land as long as grazing refuges are present that allow for sapling establishment. As grazing refuges are generally lacking on abandoned agricultural lands, where most rewilding is foreseen, we recommend that future projects consider the presence – or creation – of grazing refuges.

1. Introduction

Rewilding is rapidly emerging as a novel concept within restoration and conservation management (Donlan et al., 2006; Navarro and Pereira, 2012). The general aim of rewilding is to restore natural processes with minimal human intervention (Bauer et al., 2009; Navarro and Pereira, 2012). It does allow for short-term human interventions to start-off natural processes at an early stage, e.g. by reintroducing keystone species such as wolves (Manning et al., 2009), wild boar (Sandom et al., 2013), or large herbivores (Navarro and Pereira, 2012; Sandom et al., 2012), but long-term recurring interventions are avoided. In Europe, rewilding is typically considered on abandoned agricultural areas (Navarro and Pereira, 2012). Over the past decade, much discussion has taken place on the merits and dangers of rewilding (Bauer et al., 2009; Caro, 2007; Donlan, 2005; Oliveira-Santos and Fernandez, 2010; Rubenstein et al., 2006). To date, however, little research has been done on rewilding and our understanding of its potential effects is therefore limited. More knowledge is currently highly desired given the multiple foreseen rewilding projects in Europe (www.rewildingeurope.com).

The openness of Europe's primeval landscape, i.e. before humans significantly affected their environment (Neolithicum, ca. 7000 years ago), has been the subject of a long-standing discussion (e.g. Svenning, 2002; Szabo, 2009). The classical view is that Europe was predominantly a closed woodland landscape (e.g. Mitchell, 2005). A more controversial view is that Europe was predominantly an open wood-pasture landscape maintained by now extinct large herbivores (Vera, 2000). Empirical evidence for this wood-pasture hypothesis at European scale is limited, although it did get recent support from a study on (sub) fossil beetles from Great Brittain (Sandom et al., 2014). Regardless of this discussion on the openness of Europe's pre-Neolithic landscape, rewilding got proposed to be instrumental in restoring such wood-pasture landscapes (Sandom et al., 2014), known for their associated high biodiversity (Bergmeier et al., 2010; Hartel et al., 2013). Impacts

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of free-ranging large herbivores on vegetation structure have been studied quite extensively in Europe, where grazing by large herbivores for nature conservation purposes is commonly applied since the 1980s (Smit and Putman, 2011; Van Wieren and Bakker, 2008). Several studies show that wood-pasture landscapes with mosaics of short grasslands, roughs, shrubs and trees can indeed arise and be maintained by large herbivore grazing (Bakker et al., 2004; Olff et al., 1999; Smit et al., 2010; Smit et al., 2005; Smit et al., 2006; Smit and Ruifrok, 2011; Van Uytvanck et al., 2008). However, in contrast to rewilding, herbivore densities were all strongly human-regulated in these studies. Also, the majority of these studies have been carried out in nature areas on low productive sites, as the more productive sites have generally been reserved for agricultural purposes (Scott and Sullivan, 2000). Yet, most rewilding projects are foreseen on abandoned agricultural lands (Navarro and Pereira, 2012) that are generally more productive (despite the fact that reduced productivity is an important driver of land abandonment (Benayas et al., 2007)). Thus, an essential and unanswered question is to which degree rewilding with large herbivores can form wood-pasture landscapes on productive abandoned agricultural lands? A key-process for the development of wood-pasture landscapes is the establishment of woody species (Olff et al., 1999; Vera, 2000). Here we consider the phase of sapling establishment, i.e. after successful arrival and germination of seeds.

Several factors are known to affect sapling survival (Clark et al., 1999). First of all, browsing and trampling by large herbivores limit sapling survival, especially at high herbivore densities (Côté et al., 2004). Secondly, light competition with herbaceous plants can limit sapling survival (Vandenberghe et al., 2006), particularly in the more productive ecosystems (Smit and Olff, 1998). Thirdly, soil properties such as low nutrients, high moisture and limited oxygenation can limit sapling survival (Kozlowski, 1999; Kuijper et al., 2010). The strength of these three limiting factors for sapling survival is expected to vary between different functional groups (Niinemets and Valladares, 2006; Vandenberghe et al., 2009). For instance, thorny shrubs are less limited by herbivore browsing than pioneer and hardwood species, while hardwood species are less limited by light competition than pioneer and shrub species, and pioneers are better at establishing in disturbed soils (Finegan, 1984). Furthermore, the strength of the limiting factors for these different functional groups may also interact with the surrounding vegetation type. For instance, tall herbaceous vegetation attract fewer herbivores than short vegetation (e.g. grazing lawns) due to the relatively low nutritional quality of the former (Augustine and McNaughton, 1998), and thus indirectly reduce impacts of herbivores (Smit and Ruifrok, 2011; Van Uytvanck et al., 2008; Vandenberghe et al., 2006). On the other hand, tall vegetation will lead to increased competition for light (Vandenberghe et al., 2008).

In grazed ecosystems, temporal absence or reduced densities of herbivores may open a window of opportunity for the establishment of woody species (Olff et al., 1999; Smit et al., 2010). This can occur through (seasonal) animal migrations, population crashes due to diseases or harsh winters, or through avoidance of high-risk areas for encountering predators or hunters (Ripple and Beschta, 2004; Cromsigt et al., 2013). At smaller scale, this window may arise through natural barriers such as coarse woody debris (Smit et al., 2012), dense patches of herbivore-defended plants (Smit et al., 2006, 2008), or rock outcrops (Smit et al., 2005). In general, these natural barriers do not simply exclude all herbivores, but rather selectively reduce herbivore access: smaller browsers may still have (limited) access to thickets, while larger grazers cannot enter (Bakker et al., 2004; Smit and Verwijmeren, 2011). However, agricultural lands – where most rewilding projects are foreseen – are generally characterized by spatially uniform conditions, particularly at smaller scales (Benton et al., 2003). Also, restricted surface areas may hamper the ability of (seasonal) migration of herbivores over larger distances. However, temporary absence or limited access of herbivores can simply be manipulated by erecting exclosures (Smit et al., 2010).

In this study, we investigated establishment of woody species in the Oostvaardersplassen, the oldest large-scale rewilding area in Europe where free-ranging Heck cattle, Konik horses and red deer were released in the 1980–1990s (Marris, 2009; Sandom et al., 2012). We set up a full-factorial manipulative study to test the effects of herbivore accessibility (no, partial or full access), surrounding vegetation type (tall roughs or short lawns) and soil-disturbance (undisturbed or soil-tillage) on transplanted saplings of six shrub and tree species (two pioneers, two thorny shrubs, two hardwood species). We followed sapling survival for 4 years. Here, we report the results and discuss the implications of rewilding with large herbivores for the formation of wood-pasture landscapes.

2. Materials and methods

2.1. Study area

Our study was performed in the Oostvaardersplassen (OVP) (52°26′N, 5°19′E), a 5600 ha nature reserve situated on reclaimed land (from lake IJsselmeer in 1968), 2–5 m below sea level, in the province of Flevoland, the Netherlands. Average yearly temperatures are between 9.6–9.9 °C and average annual rainfall is between 825–875 mm (averages over 1981–2010, data from www.knmi.nl). The OVP contains an undrained wet area of 3600 ha (open water and reed beds) and a drained dry area of 2000 ha (short lawns and tall roughs) (Fig. 1). The original soil profile consists of a several metres thick clay layer that remained after the embankment of the area, which rests on a Pleistocene sandy base layer.

The area was originally designated for industry and agricultural use, and partly already prepared for agriculture in the 1970's. It got re-designated as a nature reserve in the mid 1970's due to surprising breeding bird occurrences of which several were at that time country-wide extinct. Later, three large herbivore species were successively introduced in the area to keep the grasslands open and short. In 1983, 32 Heck cattle (*Bos primigenius taurus*) were introduced, followed by 18 Konik horses (*Equus ferus caballus*) in 1984, and 52 red deer (*Cervus elaphus*) in 1992–1993 (Cornelissen et al., 2013). Since then, the herbivore assemblage consisted of three functional types: ruminants (Heck cattle), hindgut fermenters (Konik) and intermediate feeders (red deer). These three large herbivores mostly use the drained dry area of the ecosystem, while only the red deer irregularly use the wet reed beds (Cornelissen et al., 2014a).

Herbivore population sizes are not human-regulated in the sense that there is no culling or supplementary feeding, but managers do apply an early reactive management to minimize animal suffering: individuals that are unlikely to survive are shot at the end of winter (ICMO, 2010). Consequently, herbivore densities are bottom-up regulated with recorded annual mortality rates of up to 30% in harsh winters and similar recruitment rates during favourable growing seasons (ICMO 2010; Vera, 2008). Since their introduction, the herbivore population increased to 360 heads of cattle (0.18 ha^{-1}), 1220 horses (0.61 ha^{-1}) and 3580 red deer (1.8 ha^{-1}) in 2012 (Cornelissen et al., 2013), resulting in a total number of 5160 large herbivores (2.6 ha^{-1}, considering the dry 2000 ha only). This density is very high compared with human-controlled densities of free-ranging large herbivores in natural areas, that typically varies between 0.1 and 1.0 animals/ha^{-1} (e.g.

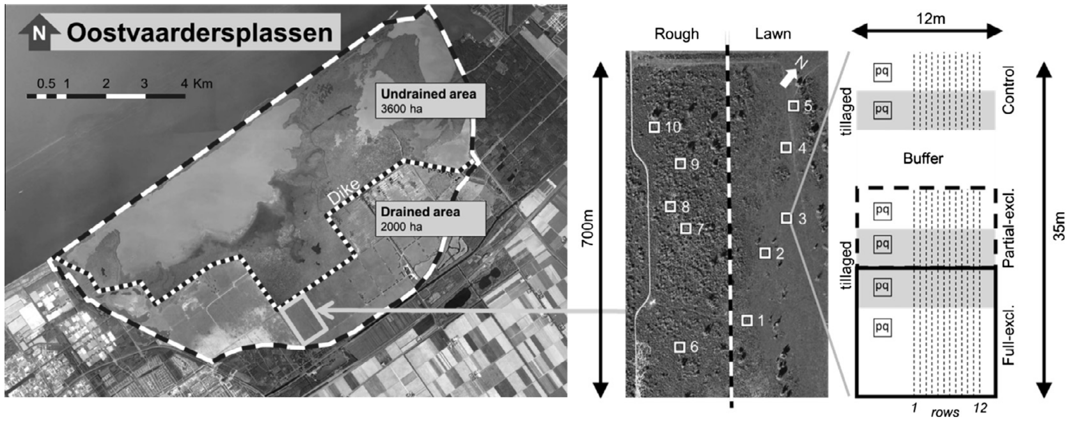

Fig. 1. Location and set-up of the experiment in the Oostvaardersplassen with the drained and undrained zone, separated by a low dike. The undrained zone contains open water with reed beds, while the drained area consists mostly of short lawn (65%) and tall rough (35%). Five plots were located in lawn (nr. 1–5) and five plots in rough (nr. 6–10). Each plot consisted of a full exclosure (2 m fence), a partial exclosure (1 m fence) and a grazed control (no fence). Within each treatment part of the soil is tillaged (grey area). Saplings are transplanted in rows, one species per row, and two rows per species. Vegetation composition was followed in 1 × 1 m permanent quadrats (pq) in the left compartment where no trees were planted. Image from Bing Maps, © 2013.

van Uytvanck et al., 2008; Smit and Ruifrok, 2011). As a result of this high density in the OVP, the dominant vegetation type in the dry drained area shifted from roughs with shrubs towards short-grazed lawns (Cornelissen et al., 2013). Also, the now-mature shrub and tree species that once established in the OVP before the herbivore introductions in the 1980s (mainly the softwood pioneers *Sambucus nigra* and *Salix alba*) are currently dying due to old age and herbivore debarking, while new recruitment of woody species appears inhibited (Cornelissen et al., 2014b).

Our study focused on the dry area of the OVP (2000 ha) that consists of lawns (ca. 65%) and roughs (ca. 35%). Lawns are dominated by short palatable grasses (mainly *Poa trivialis* and *Lolium perenne*,) and are intensely grazed during the growing season (May–October) by all three large herbivores, as well as by large numbers of geese in winter and early spring (predominantly *Branta leucopsis*, ca. 20.000). Roughs are dominated by tall plant species (mainly *Phragmites australis* and *Carduus crispus*) and are particularly used after the growing season when the short lawns are depleted (ca. November–April). Other (not introduced) mammalian herbivores known to browse saplings, such as Roe deer (*Capreolus capreolus*) and hare (*Lepus europaeus*) were not observed in our study area. A typical native 'soil disturber' such as wild boar (*Sus scrofa*) is currently not present, but may be introduced in the future (Vera, 2008). The largest mammalian carnivore present is the red fox (*Vulpes vulpes*). The wolf (*Canis lupus*) is thought to have become extinct in the Netherlands at around 1870 (de Rijk 1985), but is gradually recolonizing western Europe from the east (Trouwborst, 2010).

2.2. Experimental set-up

We set-up our experiment early April 2010, at the beginning of the growing season. The experiment consisted of 10 plots, each of which measured 35 × 12 m. Five plots were located in rough vegetation and five plots in lawn vegetation (Fig. 1). Vegetation height of both types was equally short at this period (<4 cm). Within each vegetation type, plots were spread over a distance of 500 m, while the distance between plots of different vegetation types ranged from 140 m to 280 m. Each plot contained three compartments: one compartment of 8 x 12 m with full access to the three large herbivores (grazed control), one compartment of 8 × 12 m with reduced access to red deer but excluding cattle and horses (partial exclosure: 1 m high fence, mesh width of 20 × 20 cm), and one compartment of 13 × 12 m with no access to these three herbivores (full exclosure: 2 m high fence). This full exclosure had a larger surface area than the other two compartments, as part is used in a follow-up experiment (monitoring long-term vegetation dynamics and soil-soil fauna feedbacks). The grazed control was separated from the partial exclosure by a 6 m buffer to avoid edge effects (e.g. herbivores may be attracted to the exclosures). We used a tractor to plough the soil 20–30 cm deep over an area of 4 × 12 m in each plot (*soil tillage*), with the intention to mimic wild boar rooting. A group of wild boar is able to open up extensive areas of soil vegetation in a short time span (Barrios-Garcia and Ballari, 2012) and this is found to facilitate woodland regeneration (Sandom et al., 2013). However, wild boar is presently absent in the area. A third of each compartment was not planted with saplings but used to monitor vegetation development in permanent quadrats. In total, we transplanted 7100 one-year-old saplings (origin: Staatsbosbeheer Zaad en Plantsoen, Driebergen, autochthonous material), divided over the grazed controls, partial exclosures and full exclosures. We used two pioneer shrub species, *Salix alba* (mean height ± SD after planting: 36 cm ± 9) and *Sambucus nigra* (12 cm ± 5), two thorny shrub species, *Rosa canina* (33 cm ± 11) and *Crataegus monogyna* (34 cm ± 12), and two hardwood species, *Quercus robur* (34 cm ± 9) and *Fraxinus excelsior* (23 cm ± 6). All these six species occur as seed sources in or nearby the study area. Saplings were planted in rows over the length of the plot using a tractor. First a slit of 15 cm deep was cut in the soil after which saplings were planted by hand. To avoid the saplings from being easily pulled out by the herbivores prior to establishment, the tractor drove along both sides of the slit to close it firmly. To summarize, each plot consisted out of 12 rows in total, with ca. 70 cm between rows, and each row contained one species (for practical reasons: one species per row allowed mechanical transplanting of 7100 saplings, and additionally minimalized the chance of misidentification of - particularly – browsed species during monitoring). In the first six rows all six species were present in a random order for each plot, and the next six rows were also randomly ordered, but we made sure that rows 6 and 7 did not contain the same species. Within each row distance between saplings was 50 ± 10 cm (Mean ± SD).

2.3. Measurements and analyses

To verify whether the partial exclosures were indeed visited by herbivores, we regularly checked for the presence of dung pellets, (snow) tracks and signs of browsing on the saplings. We used the drop-disc method (Styrofoam disc, Ø 24 cm, 65 g) to assess vegetation height at the peak of the growing season (August). In the grazed controls in 2010, mean vegetation height was 10 ± 3 cm and 30 ± 14 cm for lawn and rough, respectively (means ± SD). In the partial exclosures, vegetation height was 41 ± 10 and 82 ± 27 cm, and in the full exclosures this was 39 ± 9 and 80 ± 32 cm for lawn and rough. The tillaged zones remained bare for the first two months, but reached 11 ± 12 cm (lawn) and 13 ± 14 cm (rough) in grazed controls, and 66 ± 29 cm (lawn) and 86 ± 34 cm (rough) in partial and full exclosures. Each next growing season, vegetation height started at ca. 3 cm in grazed controls (lawn and rough, tillaged and undisturbed), but reached similar levels at the peak of the growing season as in 2010 (also in exclosures). By the end of 2013, the vegetation composition in the partial and full exclosures in lawn and rough had merged, with dominance of *Urtica dioica* and, to a lesser extent *P. australis*, while the vegetation composition remained unchanged in the grazed controls.

2.3.1. Sapling survival

We counted the number of living saplings the first week after transplantation ($t = 0$) and repeated these measurements after 50 days, 388 days (~1 year), 753 days (~2 years) and 1473 days (~4 years). Each survey was done in spring when saplings were best visible; in summer and fall the vegetation in the exclosures was too tall and dense (up to 200 cm) to locate saplings without severely damaging the surrounding vegetation. Saplings without leaves and without living stem (brownish colour under bark), as well as saplings that had been removed by herbivores were considered dead. As sapling survival in the grazed controls was already very low after 50 days (6%) and nearly zero after 1 year, we decided not to perform any further statistical analyses on these data. All statistical analyses were performed in R 2.14.1 (R Foundation for Statistical Computing, Vienna, AT).To analyse how sapling survival was affected by vegetation type and soil tillage in the partial and full exclosures, we used a generalized linear model (GLZ) for each species separately, for each survey. We used GLZs with a binomial error distribution and logit-link function, with sapling survival (alive/dead) as the dependent variable and vegetation type, soil tillage presence, exclosure type (full vs. partial) and plot id as independent variables. We nested plot id within vegetation type to correct for possible random variation between the plots. Some exclosures had been shortly visited by cattle and horses due to a break-through event in early spring 2011. To control for this we used breakthrough as an independent factor in the analyses of sapling survival in those compartments.

2.3.2. Sapling height

After 1, 2 and 4 years, we measured the height of three randomly selected living individuals per row per treatment combination. Saplings were measured from ground level to the highest green part. If less than three saplings were alive per row, we measured the available saplings. We used full factorial ANOVA's for each species separately and for each year (1, 2, 4), with sapling height as dependent variable and vegetation type, soil tillage presence, exclosure type (full vs. partial) and plot id (nested in vegetation type) as independent variables. Saplings that had been

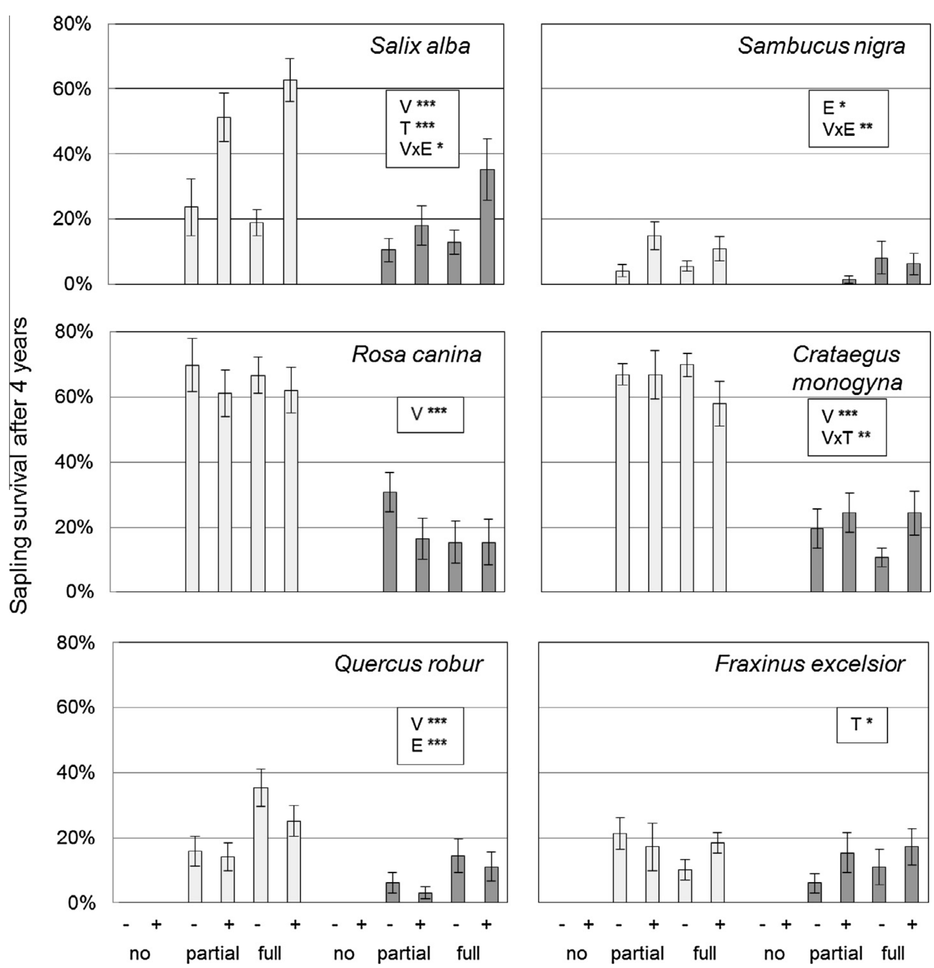

Fig. 2. Sapling survival (means ± 1 se) of the six woody species after four years in lawn (light bars) and rough (dark bars), in the three exclosure types (no, partial and full), with (+) and without (−) soil tillage. Indicated are significant variables and interactions of: vegetation type (V), exclosure type (E), soil tillage (T). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

affected by a breakthrough event were excluded from analysis. Sapling height outside exclosures and *Sambucus* saplings were not considered due to very low survival.

3. Results

3.1. Sapling survival in grazed controls

No sapling survived outside the exclosures (Fig. 2). After 50 days, sapling survival in grazed controls was already very low (6%) compared to survival in the partial and full exclosures (66% and 62%, respectively; see Appendix A for data of all years). After 1 year, only nine individuals were alive: six *Crataegus*, two *Rosa,* and one *Quercus*. All were found in lawn, except for one *Crataegus*. After 2 years, all saplings planted outside the exclosures had died.

3.2. Sapling survival in partial and full exclosures

Overall sapling survival in the partial and full exclosures combined declined from 67% after 50 days, to 42%, 32% and 25% after 1, 2 and 4 years, respectively. Survival differed strongly between species, and there were some clear treatment effects. After 4 years, survival was lowest for *Sambucus* (6%) and highest for the spiny species *Rosa* and *Crataegus* and (42% and 43%, respectively). Vegetation type was consistently significant for most species (not for *Sambucus* and *Fraxinus*) with higher survival in lawn than in rough (Table 1, Fig. 2). Soil tillage had significant positive effects for all species at the first survey, but this effect only remained for the pioneer species *Sambucus* and *Salix*. Soil tillage was consistently negative for *Crataegus* in lawn (interaction tillage $*$ vegetation after 1, 2 and 4 years). Impacts of exclosure type on survival were limited: only *Quercus* survived consistently better in full exclosures. The significant vegetation $*$ exclosure type interaction for *Sambucus* in year 4 is caused by a better survival in roughs in full exclosures than in partial exclosures (Fig. 2).

3.3. Sapling height in partial and full exclosures

Sapling height varied largely between species. After four years, saplings of *Salix* were the tallest (overall mean: 390 cm) while saplings of *Quercus* were the shortest (overall mean: 87 cm) (Fig. 3; Appendix B). Exclosure type and soil tillage affected heights of most species in all years: species were taller in the full exclosures, while soil tillage was consistently positive for *Salix*, *Rosa* and *Crataegus* (Table 2). Vegetation type irregularly affected some species, but saplings were generally higher in lawn. This effect was consistent for *Crataegus* over four years.

4. Discussion

We found that sapling establishment is currently strongly limited for all species where herbivores have full access, while establishment is comparably successful where herbivores have reduced or no access. Absence of natural grazing refuges in combination with the high herbivore density play an important role for the observed establishment limitation in the OVP, which has important implications for the numerous ongoing and newly planned rewilding projects on abandoned agricultural lands in Europe.

The high herbivore impact may be no surprise given the productivity of the system and bottom-up regulation of herbivores (Oksanen et al., 1981). For comparison, in a comparably productive abandoned agricultural area in Belgium, but with human top-down regulated herbivore densities ($0.4\ ha^{-1}$ vs. $2.6\ ha^{-1}$ in the OVP), sapling survival of *Quercus* and *Fraxinus* after two years was up till 60% higher (Van Uytvanck et al., 2008). Also, under these conditions, roughs (notably *Carex* sp. and *Juncus* sp.) facilitated saplings against browsing. Similar effects of roughs (*Juncus effusus*, *U. dioica*,

Table 1
Results from the generalized linear mixed model (GLZ) on effects of Vegetation type (V), Exclosure type (E), Soil tillage (T), plot number (ID), breakthrough (B) and their interactions on sapling survival of the six woody species after 50 days, 1, 2 and 4 years. Indicated are deviances for the independent variables and their interactions.

	Species	Res. Dev.	Res. DF	V	E	T	$V \times E$	$E \times T$	$V \times T$	$V \times E \times T$	ID (V)	B
	DF			1	1	1	1	1	1	1	2	1
50 days	*Sambucus nigra*	248	78	**13*****	2	**54*****	2	2	**10****	1	3	
	Salix alba	212	79	**8*****	0	**28*****	2	1	1	1	**8***	
	Rosa canina	197	79	**44*****	1	**6***	4	2	**3***	4	3	
	Crataegus monogyna	212	79	**74*****	**13*****	**13*****	1	1	1	0	0	
	Quercus robur	200	78	**23*****	**5***	**22*****	0	2	1	0	**12*****	
	Fraxinus excelsior	248	79	1	**9****	**14*****	**5***	0	0	1	**6***	
Year 1	*Sambucus nigra*	155	78	**2*****	2	2	**4***	0	**8****	1	**17*****	**13*****
	Salix alba	354	79	**45*****	1	**47*****	0	2	**7****	1	**52*****	0
	Rosa canina	346	79	**166*****	3	0	0	0	1	2	**9****	0
	Crataegus monogyna	279	79	**127*****	3	1	1	1	**7****	**4***	**13****	**4***
	Quercus robur	201	78	**31*****	**21*****	3	**6***	1	0	2	**16*****	2
	Fraxinus excelsior	189	79	**6***	1	3	3	0	1	**5***	**8***	1
Year 2	*Sambucus nigra*	146	78	3	4	**5***	**11****	2	3	1	**28*****	**10****
	Salix alba	305	79	**32*****	0	**65*****	1	3	3	0	**24*****	**9****
	Rosa canina	473	79	**216*****	1	0	1	0	0	0	**14****	**5***
	Crataegus monogyna	397	79	**236*****	**11****	0	0	0	**17*****	3	**12****	0
	Quercus robur	253	78	**70*****	**14*****	1	2	0	**9****	2	**31*****	0
	Fraxinus excelsior	180	79	2	2	2	0	0	3	0	2	**4***
Year 4	*Sambucus nigra*	143	78	2	**4***	4	**11****	3	2	1	**27*****	**9****
	Salix alba	266	79	**26*****	1	**65*****	**7***	3	2	0	**13****	**25*****
	Rosa canina	407	79	**184*****	1	4	31	2	1	0	**31*****	**7****
	Crataegus monogyna	382	79	**228*****	2	0	3	0	**8****	2	**18*****	0
	Quercus robur	205	78	**44*****	**25*****	2	0	0	0	1	**38*****	3
	Fraxinus excelsior	199	79	2	1	**5***	4	1	1	2	5	1

Significant values are in bold.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

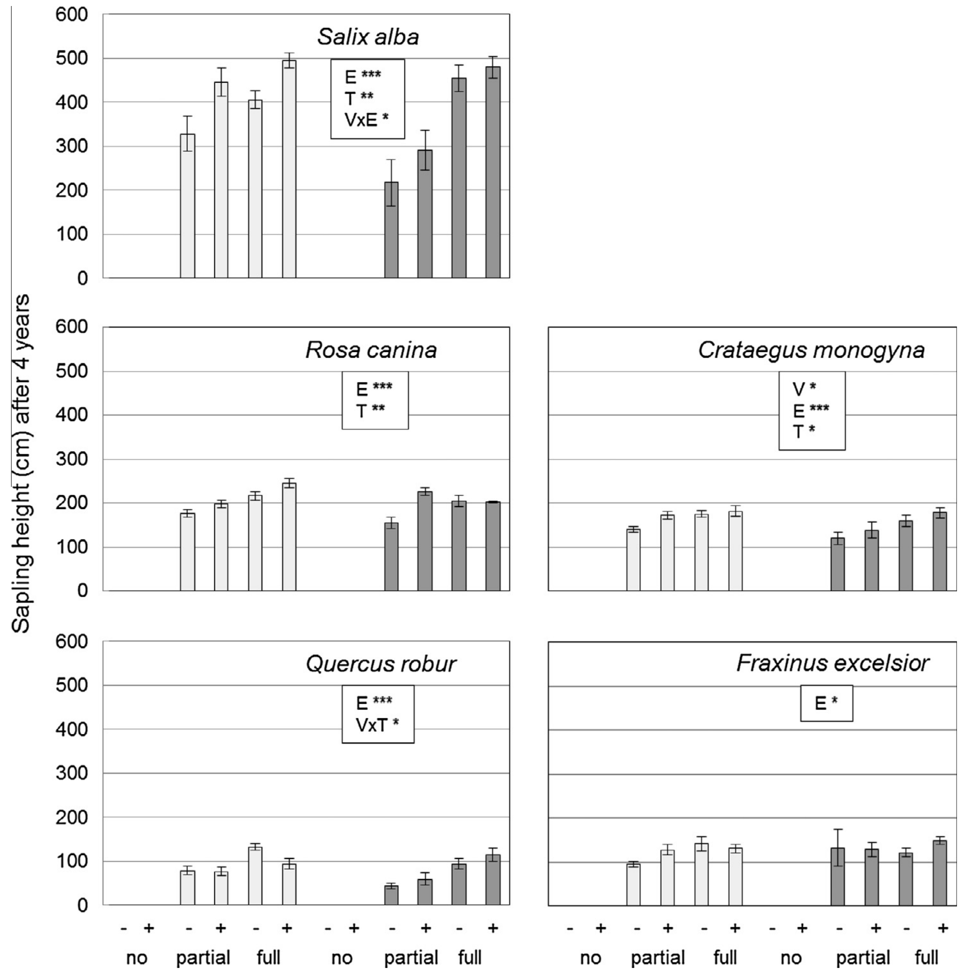

Fig. 3. Sapling height in cm (means ± 1 se) of the five woody species (*Sambucus* not included) after four years in lawn (light bars) and rough (dark bars), in the three exclosure types (no, partial and full), with (+) and without (−) soil tillage. Indicated are significant variables and interactions of: vegetation type (V), exclosure type (E), soil tillage (T). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Deschampsia caespitosa) were found for *Prunus* and *Crataegus* saplings in ancient wood-pastures in the Netherlands (Smit and Ruifrok, 2011). We expected similar protective effects of roughs for sapling survival in our study, but no single sapling survived outside exclosures in roughs (nor in lawns). Current herbivore densities are probably too high for saplings to profit from potential facilitative effects of roughs. This finding is in line with Smit et al. (2007) who found that facilitative effects of surrounding 'nurse' plants disappeared at high grazing pressure (181.7–204.1 livestock unit-days per hectare; 1 livestock unit = 600 kg) as nurse plants themselves got browsed and trampled. Indeed, the roughs in the OVP got intensely grazed in winter and early spring when lawns were depleted, resulting in equally short roughs and lawns (3 cm) by the end of winter. Height differences between roughs and lawn rapidly reappeared again in the growing season, when food was no longer limiting. Thus, the selectivity of the herbivores changed with the reduced availability of preferred food, resulting in increased consumption of the less attractive species, as is in line with literature (e.g. Crawley, 1983). This means that under the current high herbivore densities, more robust protective structures than roughs are needed for successful establishment of woody species.

Indeed, sapling survival was successful in our partial exclosures that effectively realized reduced and selective accessibility to herbivores. While indications for visiting Heck cattle or Konik horses were not detected, deer pellets, deer tracks, browsing signs, sapling heights, and personal observations indicate that red deer regularly entered these plots (in winter mostly). Correspondingly, sapling height after four years was lower in the partial exclosures than in the full exclosures for all studied species. Nevertheless, sapling heights of all species steadily increased in these partial exclosures over the last four years, and most will soon reach the 'browse line' of 200 cm above which shoots of saplings are considered relatively safe from browsing (Palmer and Truscott, 2003). Hence, we expect that under current conditions – with regular red deer browsing in winter – these saplings will be able to become adults. However, it is highly questionable whether these saplings will also be able to reach the adult phase when herbivore browsing increases, e.g. after removal of the current partial exclosures. *Rosa* and *Crataegus* may stand a chance as their protective thorns had already fully developed by the second year. However, highly intense browsing and bark stripping of saplings – and even of adults – of *Salix*, *Fraxinus*, *Quercus* and *Sambucus* are likely to result in mortality. The sharp decline in *Salix* and *Sambucus* cover in the OVP after 1996 when the herbivore densities went up far beyond 0.5 ha^{-1} certainly points in that direction (Cornelissen et al., 2014b).

Thus, robust grazing refuges with (temporal) limited access to large herbivores do enhance sapling establishment. We aimed at mimicking natural grazing refuges such as coarse woody debris, spiny thickets, rock outcrops or islands that are not only important for grazing-sensitive plants, but for plant diversity in grazed ecosystems in general (Milchunas and Noy-Meir, 2002). Our study

Table 2
Results of ANOVA for effects of Vegetation type (*V*), Exclosure type (*E*), Soil tillage (*T*), plot number (ID), and their interactions on sapling height of *Salix, Rosa, Crataegus, Quercus* and *Fraxinus* (*Sambucus* not included) after 1, 2 and 4 years. Indicated are the *F* values.

	Species	Res. DF	V	E	T	$V \times E$	$E \times T$	$V \times T$	$V \times E \times T$	ID (V)
	DF		1	1	1	1	1	1	1	2
Year 1	*Salix alba*	105	0	**73*****	**21*****	4	**4***	**8****	0	2
	Rosa canina	127	**8*****	**28*****	**33*****	**4***	1	**5***	1	1
	Crataegus monogyna	148	1	**44*****	**21*****	**6***	**5***	2	2	**8*****
	Quercus robur	127	0	**64*****	5	**8****	0	1	0	3
	Fraxinus excelsior.	128	**8****	**36*****	**9****	**7***	0	**7***	3	0
Year 2	*Salix alba*	109	**8****	**46*****	**12*****	1	4	0	2	4
	Rosa canina	121	**11****	**25*****	**23*****	1	1	0	2	**6***
	Crataegus monogyna	140	**12****	3	**6***	0	0	3	0	1
	Quercus robur	91	2	**13****	**10***	0	0	**5***	1	2
	Fraxinus excelsior.	59	0	2	**6***	2	1	1	3	0
Year 4	*Salix alba*	106	2	**19*****	**12****	**9***	1	1	0	0
	Rosa canina	117	3	**22*****	**12****	1	0	0	4	1
	Crataegus monogyna	132	**5***	**15*****	**7***	2	2	0	1	**12*****
	Quercus robur	73	2	**23*****	1	1	1	**7***	1	0
	Fraxinus excelsior	66	2	**4***	3	0	1	0	3	0

Significant values are in bold.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

shows the importance of grazing refuges for sapling establishment in a productive system with a high density of free ranging large herbivores. It is important to notice that such natural grazing refuges are generally lacking on abandoned agricultural land where most rewilding projects are ongoing or foreseen.

Vegetation type had strong impact on sapling survival in both exclosure types, with higher survival in lawn than in rough for most species. We attribute this effect to reduced light competition in lawns compared to roughs. Light competition strongly affects tree sapling survival (Vandenberghe et al., 2008; Vandenberghe et al., 2006). In absence of herbivores, the vegetation gets dominated by tall roughs, which reduces sapling survival, especially in productive ecosystems (Smit and Olff, 1998). Because lawns are the result of intensive grazing (Augustine and McNaughton, 1998; Díaz et al., 2007), we argue that high herbivore densities may have indirect positive effects on sapling survival, but only when followed by a period of low herbivore densities or temporal absence (window of opportunity), as has also been proposed by others (Bakker et al., 2004; Smit et al., 2010). This also pleas for more dynamic herbivore management in other nature areas where populations are human- controlled and generally kept at relatively constant (high) densities without such fluctuations. In general, such spatio-temporal fluctuations of herbivore densities can enhance vegetation structure (Smit et al., 2010), allowing for shifting mosaics of grasslands, roughs, shrubs and trees over space and time, with positive impacts on associated floral and faunal diversity (Olff et al., 1999). To which degree rewilding indeed contributes to such enhanced associated diversity requires more empirical testing, but such studies are currently underway.

Initially, soil tillage benefitted all species, but the positive effects only remained for *Salix* and, to a lesser extent *Sambucus*, the two pioneers. Tillage most likely reduced the competition for resources and light, as it temporarily removed the surrounding vegetation. Particularly fast growing pioneer species can benefit from these temporal conditions (Finegan, 1984). This also implies that, if wild boar gets added to the current herbivore guild and sufficient grazing refuges are available, its rooting will not only facilitate woody recruitment (Sandom et al., 2013) but also affect the woody species composition by particularly benefitting pioneers.

In this study we focused on the sapling phase as this is often the limiting phase (establishment limitation) for recruitment of woody species in grazed ecosystems (Moe et al., 2009; Rao et al., 2003). However, besides this establishment limitation, also other life stages have to be completed for successful recruitment (Gill and Marks, 1991). For instance, prior to establishment limitation also seed dispersal and germination may be limiting for recruitment (Clark et al., 1999; Nathan and Muller-Landau, 2000). Our follow-up studies performed in the full exclosures revealed that seed removal by rodents, predominantly of acorns by wood mouse *Apodemus sylvatica*, may indeed contribute to the recruitment limitation in the OVP (unpublished data), although such seed removal may also reflect the redistribution of seeds to grazing refuges rather than seed mortality (Smit and Verwijmeren, 2011). In addition, we frequently encountered natural saplings of *Crataegus*, *Prunus spinosa*, *Cornus sanguinea*, *Quercus*, and *Sambucus* under solitary mature shrubs and trees in the drained area of the OVP. In one occasion, we found up till 200 *Crataegus* saplings under an adult *Crataegus*, where birds regularly roosted (unpublished data). This indicates that seed dispersal is not limited and that germination is possible for at least these species. On the other hand, we did not find back any of these natural saplings in the following years, indicating the importance of – again – establishment limitation in this system.

5. Conclusion

Our findings have important implications for the numerous ongoing and planned rewilding projects on abandoned agricultural lands elsewhere. Most projects that apply a bottom-up control of large herbivores will face relatively high herbivore densities, particularly on the more productive sites. Our study shows that under such conditions, the lack of grazing refuges limits sapling establishment – and thus the formation of wood-pasture landscapes. At the same time, our study indicates the potential of simple one-time interventions to enhance sapling establishment, while the bottom-up control of herbivores can be maintained. If establishment of saplings is seen as important in the short run (next 5–10 years) these interventions may include the creation of grazing refuges by deposition of coarse woody debris, simulating wind-throw or forest fires (de Chantal and Granström, 2007; Smit et al., 2012). They could also include the creation of small water bodies, islands or increasing the water table that would make parts of the area (temporarily) inaccessible to herbivores (we observed successful recruitment of *Salix* on such small islands in the OVP). Another measure would be to create ecological corridors to adjacent areas (Gilbert-Norton et al., 2010) that would stimulate fluctuations in herbivores densities and possibly reduce grazing pressure during winter and early spring when food is scarce. If such one-time interventions are not desired there are more natural opportunities for sapling establishment, but which' occurrence in time is harder to predict. For example, harsh winters in combination with scarce food stocks at the onset of winter may cause herbivore population crashes that could result in woody recruitment events. Also, the arrival of a large predator in rewilding areas is not unlikely, giving the recent return of wolves, lynx and bears to various areas in Western Europe (Trouwborst, 2010). Their impact on the landscape may not only be direct – reducing herbivore numbers by predation – but also by altering the behaviour of herbivores that may start avoiding 'risky' areas, and so locally reduce browsing pressure and facilitate woody establishment (Kuijper et al., 2013; Kuijper et al., 2014). Such 'ecology of fear' (sensu Brown et al., 1999) and resulting changes on the vegetation may even be enhanced without the actual presence of a predator, e.g. by innovative 'hunting for fear' types of management (Cromsigt et al., 2013).

To which degree our results apply to systems with different land-use trajectories (former arable land vs. former pastures), environmental conditions (productivity, climate) or (initial) large herbivore density remains to be tested, but it is clear that these factors will importantly determine the speed of the processes and final outcome at landscape level. For instance, the establishment of shrubs and trees will occur more quickly, and will be more abundant, on grazed abandoned arable land than on grazed former pastures (e.g. Van Uytvanck, 2009). Also, in very low productive systems, it is questionable whether unmanaged herbivore populations will be able to reach high densities (McNaughton et al., 1989) at such levels that they can limit shrub and tree establishment as currently observed in the OVP. Furthermore, when large herbivores are not yet present in an area and rely on natural (re)colonization, the initial uniform conditions of the abandoned land may quickly disappear due to natural succession, with the speed depending on the abovementioned prior land-use and environmental conditions.

Hence initial human interventions can largely determine the outcome of rewilding. All human interferences should be carefully balanced against maintaining the benefits of an unaffected large-herbivore guild and resulting natural processes. After all, we are only beginning to understand how rewilding with large herbivores affects the long-term community dynamics and ecosystem development. Our study shows that a wood-pasture landscape does not arise easily when grazing refuges are lacking. Future rewilding projects may benefit from a careful consideration of the initial conditions prior to initiating rewilding to maximize returns with respect to the restoration of natural processes, wood-pastures landscapes and associated biodiversity values.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.11.047.

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