



# FOREST FACTS



Photo: Carl-Gustaf Thulin (upper left, lower right), Pablo Garrido (upper right, lower left).

## Novel herbivores and functions in ancient ecosystems:

### *Large herbivores for wood-pasture restoration*

**Pablo Garrido, Anna Jansson, Grzegorz Mikusiński, Vladimir Naumov, Erik Öckinger, Anna Skarin, Alessia Uboni and Carl-Gustaf Thulin**

**Large herbivores play key roles** in terrestrial ecosystems, including ecosystem engineering functions.

**They affect the vegetation structure and composition**, nutrient cycling and even climate.

Herbivore-rich communities, including large herbivores, **promote more open landscape conditions**.

**Prehistoric large herbivore faunas have been largely depleted by humans** with cascading effects on ecosystems.

Some of the **ecosystem functions of extinct large herbivores were replaced by human agriculturalists** through animal domestication, and agriculture and husbandry practices.

Today the **abandonment of such traditional management practices threatens the biodiversity of wood-pastures** and makes it urgent to find novel alternatives for their conservation.

**M**ammalian fauna of large and megaherbivores (see Definitions) have been decimated worldwide during the late Quaternary. They had key functions in ecosystems and their extinction in the wild produced cascade effects on plant community composition, vegetation structure, fire regimes, nutrient cycling and even climate. Hence, the reverse process, i.e., restoring ecosystems by (re-)introducing missing large herbivores, could have major effects on plant communities and vegetation structure, with positive effects for biodiversity and ecosystem functioning.

In Europe, wood-pastures are rich in biodiversity and thus of particular conservation value. They were common in former herbivore-richer ecosystems of pre-historical times. As many wild large herbivores went extinct, so did their functions in ecosystems, although their role was partly replaced by domestic herbivores with the advent of agriculture (including animal domestication, and agriculture and husbandry practices). Such traditional management practices, including grazing by domestic large herbivores, have maintained open wood-pasture structures and associated biodiversity for millennia. Today however, traditional practices have largely been abandoned, threatening the biodiversity and ecosystem services provided by wood-pastures and semi-natural grasslands. Novel solutions for their long-term conservation are therefore urgently needed.

## What we study and expect

To test the hypothesis that the re-introduction of an ecologically functional substitute of an extinct large herbivore could halt current biodiversity declines and restore wood-pastures, we designed a 28-month rewilding experiment where an endangered horse breed, the Gotland Russ (*Equus ferus caballus* L.), was introduced in three 10-hectare enclosure replicates (Figure 1) without supplementary feeding. From 2004 to 2014, the experimental area was abandoned, pastures were not tilled, and were only occasionally harvested and/or grazed (including the forest) by cattle. By adding a horse into a community dominated by roe deer and moose, we expected effects on the forest structure and composition via selective browsing, especially during winter when grasses are not available. Additionally, horses were expected to limit tree colonization of grasslands and

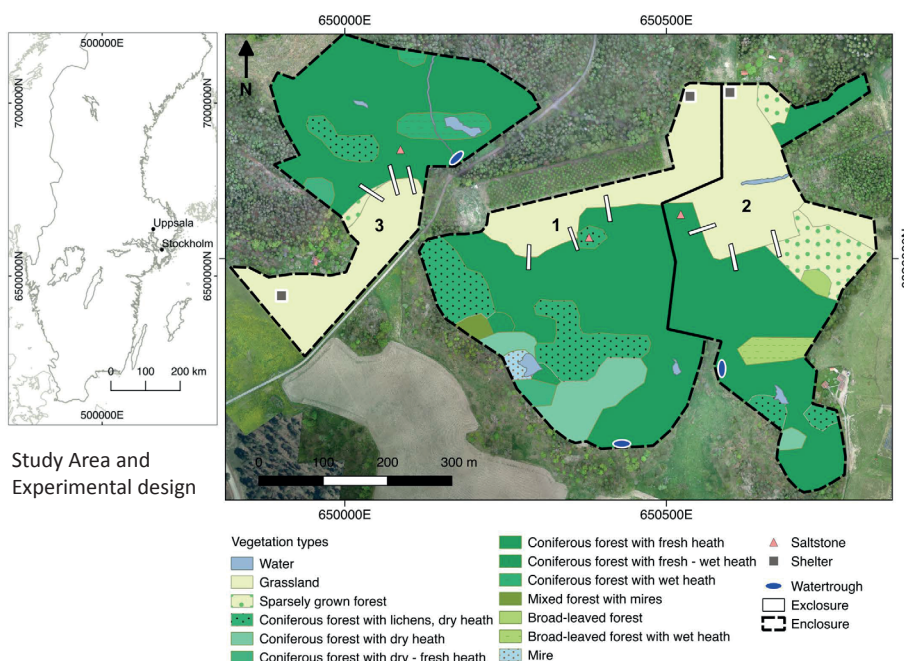


Figure 1. Location map and experimental design at Krusenberg estate close to Uppsala (Sweden). Enclosures represent control plots where herbivores were excluded. Their location on the map is approximate.

mitigate biodiversity declines, as grazing may impede competitive plant species from dominating the vegetation community. A higher plant diversity of grasslands would also benefit pollinators.

## Effects on the forest component

After a 28-month rewilding (without supplementary feeding) experiment, horses reduced tree density, particularly among small diameter classes (e.g., seedling and saplings). Diameter of trees higher than three meters was measured at breast high (DBH = 1.30 m); five centimetres from the ground otherwise. The effect on forest vegetation was clearly distinct among tree species, resulting from different browsing

pressure and tree preferences (Table 1). In forest-dominated areas horses reduced tree height for ash, rowan, willow, blackthorn, aspen, and birch, in relation to abandonment conditions (areas without horses). For oak, pine and Norway spruce no effect was detected due to either horse avoidance or, in the case of oak, due to tree resistance to browsing and perhaps protection from other species such as blackthorn. Horses were then able to reduce the vegetation structure and affect tree composition (Figure 2).

## Effects on the grassland component

Horses controlled the colonization of woody vegetation in grassland-dominated

## DEFINITIONS

### Ecological substitute or replacement

**species:** Animal species that have functions equivalent to formerly extinct species. These species include distinct and/or domesticated forms of extinct animals.

**Ecosystem functions:** Ecosystem processes fundamental for the stability and maintenance of ecosystems. Nutrient cycling, photosynthesis and primary productivity are some examples.

**Ecosystem engineering functions:** Actions normally induced by animals that alter a given ecosystem. For instance, the introduction of

large herbivores can change woody vegetation into grasslands.

**Cascade effects:** Normally, effects of one species on other species at lower levels of the food web. For instance, horse grazing induced a higher plant diversity which induces pollinators to use grasslands.

**Large herbivores and megaherbivores:** Mammals that feed on vegetation (herbivores). Large herbivores have an adult body mass from 45 to 999 kg; megaherbivores  $\geq 1000$  kg in body mass.

**Browsers:** Herbivores whose feeding habits mainly include woody vegetation.

**Grazers:** Herbivores whose feeding habits mainly include grassland plant species.

**Rewilding:** Here we use the concept of trophic rewilding defined as species (re-) introductions to restore top-down trophic cascades to promote self-regulating biodiverse ecosystems (*sensu* Svenning et al. 2016).

**Wood-pasture:** A kind of habitat in which trees are interspersed among grasslands like a savanna, or mosaics of forest and grassland habitats at a given landscape unit. Herbivores, either wild or domestic, are important components for the ecosystem stability.



Table 1. Mean values ± SD for tree species availability and horse browsing pressure estimates. Preference estimates are also shown per tree species. Norway spruce was excluded due to horse avoidance. Scots pine was used as reference species to calculate preference estimates due to its lower relative browsing pressure.

	Ash	Rowan	Oak	Sallow	Blackthorn	Aspen	Birch	Pine
Tree availability	0.11±0.12	0.13±0.07	0.11±0.11	0.08±0.10	0.13±0.13	0.31±0.17	0.10±0.08	0.02±0.04
Browsing pressure	0.71±0.10	0.55±0.12	0.53±0.11	0.47±0.13	0.36±0.14	0.35±0.14	0.27±0.13	0.19±0.11
Relative preference	3.73	2.89	2.79	2.49	1.89	1.86	1.40	****

Note: Tree species (forage) availability was estimated as the number of focal tree species divided by the total number of all species recorded in experimental plots. Browsing pressure was obtained as the ratio between the number of browsed twigs divided by the total number of twigs up to three meters per selected tree species.

areas. Horse grazing also induced a change in the grassland community where plants adapted to grazing by reducing plant height and generating faster growing, more palatable leaves, characteristic of ruderal plant communities (i.e., plant communities adapted to disturbances). These changes at community level are intimately related to ecosystem processes and functions such as photosynthesis and litter decomposition. Likewise, ruderal communities have high nitrogen mineralization rates positively linked to primary productivity. Horse grazing additionally mitigated plant species declines (Figure 3a), in particular bee-pollinated plants (Figure 3b). The higher diversity of plants in grazed areas attracted butterflies and bumblebees to feed and use that habitat more, and thus foster the delivery of important ecosystem services (e.g. pollination).

**Concluding remarks and outlook**

Rewilding or year-round horse grazing without supplementary feeding may be an alternative to restore herbivore-dependent ecosystems that are rapidly disappearing. Horse grazing may tackle biodiversity declines and boost ecosystem functioning. Horse browsing has clear effects on vegetation structure and composition which may additionally lead to positive effects on climate and wildfire mitigation strategies. However, rewilding may not materialize due to strict national and international policy. In Sweden, current regulations stipulate that horses have to be checked on daily basis, be provided with shelter during wintertime, and be protected from e.g., predation and starvation. EU and national policies may then limit or even jeopardize future rewilding efforts. In this situation, the applicability of rewilding projects for

habitat restoration is very limited and up-scaling rewilding interventions might require additional innovations in conservation finances.

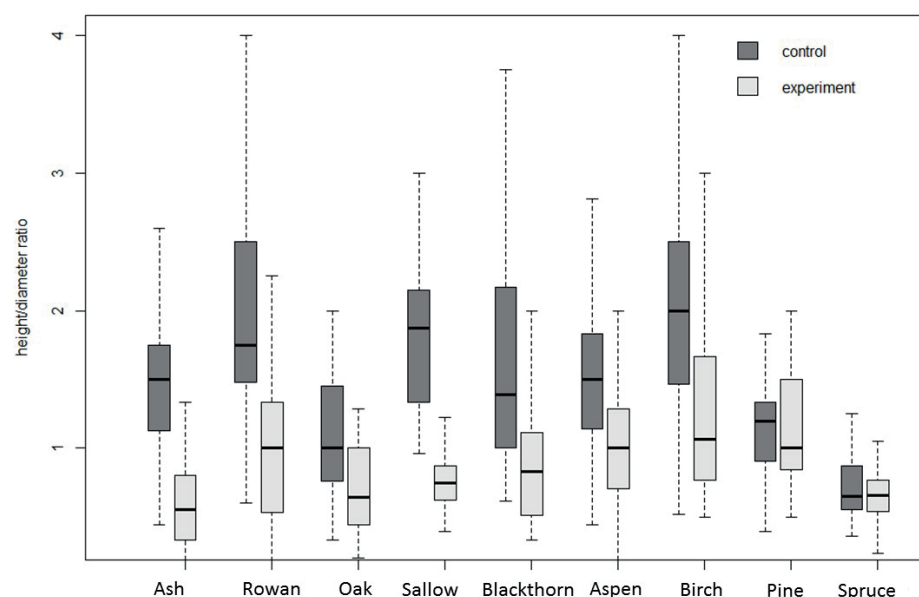


Figure 2. Effect of horse browsing on tree height in experimental (with horses) and control plots.

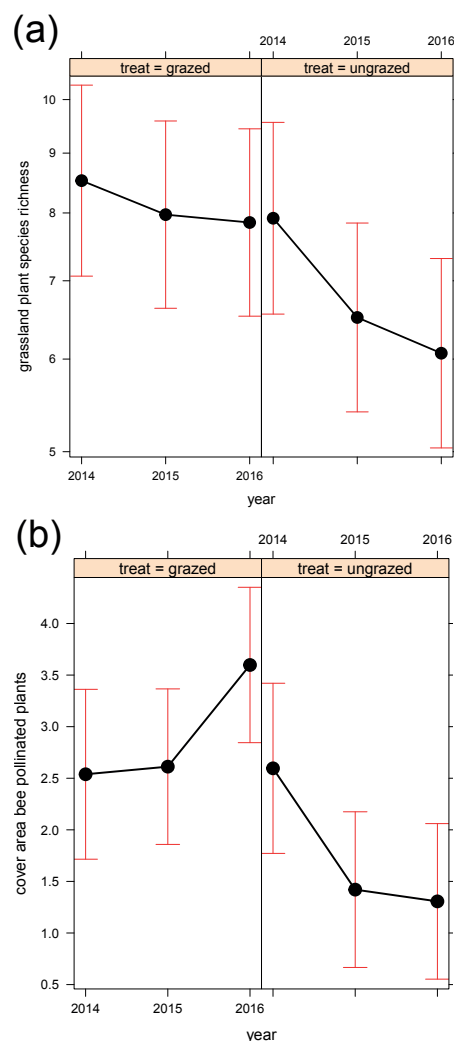


Figure 3. a) Effect of plant species richness and b) cover of bee-pollinated plants in relation to time and treatment (grazed vs. ungrazed). Reproduced with the permission of John Wiley and Sons (permission number: 4763711081359).

In Sweden, traditional management practices that maintained wood-pastures and semi-natural grasslands are threatened as a result of land use changes. About 66 % of the most valuable oak wood-pasture habitats in Östergötland (Sweden) are, for example, currently abandoned with subsequent secondary woodland development. Grazing cannot be resumed due to lack of farmers and livestock. This is also the general pattern in Europe, which poses great uncertainty for the conservation of the biodiversity and cultural values of wood-pastures. Therefore, novel management alternatives are urgently needed. Rewilding with horses and other large herbivores may be a way to restore many abandoned European agricultural landscapes ■

**”Rewilding with horses ... may be a way to restore many abandoned European agricultural landscapes.”**

**Keywords**

Ecological replacement species, horses, paradigm shift, political constrain, rewilding, wood-pasture restoration

**Read more:**

► **Garrido, P., Mårell, A., Öckinger, E., Skarin, A., Jansson, A. & Thulin, C.-G. 2019.**

Experimental rewilding enhances grassland functional composition and pollinator habitat use. *Journal of Applied Ecology*. 56: 946–955.

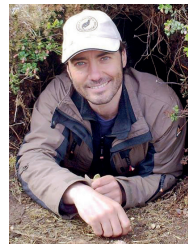
► **Garrido, P., Edenius, L., Mikusiński, G., Skarin, A., Jansson, A. & Thulin, C.-G. 2020.**

Experimental rewilding may restore abandoned wood-pastures if policy allows. *AMBIO*. DOI: 10.1007/s13280-020-01320-0

► **Svenning, J.-C., et al. 2016.**

Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *PNAS* 113: 898–906.

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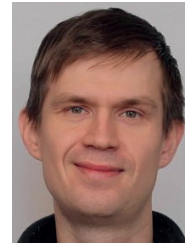
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