Long-term impact of wild ungulates on natural forest regeneration in the Donau-Auen National Park, Austria

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In the Donau-Auen National Park, since 1999 systematic vegetation surveys have been carried out on browsing control plots in order to record the long-term effects of wild ungulates (red deer, roe deer, fallow deer, mouflon, wild boar) on the development of forest regeneration. The method used is the Ungulate Impact Control System (UICOS) that works with comparison area-pairs (unfenced control areas vs. fenced areas). There were clear differences in the development of tree and shrub species influenced by ungulates compared with the forest development under ungulate exclusion. However, the goals and benchmarks for the national park have so far been achieved. Most of the negative as well as positive effects of ungulates in terms of forest benchmarks resulted from changes in height increment of the tree species. Related to biodiversity, the impact of ungulates had different effects on the tree species, depending on the biodiversity index. For shrub species there was mostly a negative ungulate impact on their biodiversity.

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Im Nationalpark Donau-Auen werden seit 1999 systematische Vegetationserhebungen auf Verbiss-Kontrollflächen durchgeführt, um die langfristigen Auswirkungen der wildlebenden Huftiere (Rothirsch, Reh, Damhirsch, Mufflon, Wildschwein) auf die Entwicklung der Waldverjüngung zu erfassen. Als Methode wurde das Ungulate Impact Control System (UICOS) verwendet (Vergleichsflächenverfahren, paarweiser Vergleich von Zaunflächen mit ungezäunten Flächen). Es ergaben sich deutliche Unterschiede in der Entwicklung der Baum- und Straucharten mit Huftiereinfluss im Vergleich zu ihrer Entwicklung unter Ausschluss der Huftiere. Die Ziele und Richtwerte für den Nationalpark wurden jedoch bisher erreicht. Die meisten huftierbedingten negativen wie auch positiven Wirkungen, gemessen an forstlichen Richtwerten, resultierten aus dem Einfluss auf den Höhenzuwachs der Baumarten. Im Hinblick auf die Biodiversität wirkte sich der Huftiereinfluss auf die Baumarten je nach Biodiversitätsindex unterschiedlich aus. Für Straucharten ergab sich zumeist ein negativer Huftiereinfluss auf die Biodiversität.

Keywords: forest regeneration, ungulate impact, long-term development, ungulate exclosures, Donau-Auen, National Park, Austria.

Introduction

Browsing on forest vegetation by mammals (ungulates, hares, mice etc.) is basically one of a series of different drivers of regeneration dynamics and a natural process in young forest development (e.g. Crawley 1983). When assessing the impact of ungulates on the development of forest vegetation, there are considerable problems in science and practice (see e.g. Gossow & Reimoser 1985, Donaubauer et al. 1990, Reimoser & Putman 2011). Hasty and wrong conclusions often led to conflicts between forestry, hunting and nature conservation. The different methods of browsing assessment are controversial with regard to their general applicability and informative value (Reimoser et al. 2014).

The most authoritative but also the most complex method to objectively determine the concrete effects of the respective ungulate impact on the forest development (through browsing, fraying, trampling etc.) is the construction of fence-control areas (about 25–100m^2 in size) that are as similar as possible in site and the multi-year observation of the forest development within the fence (without ungulate influence) in comparison with areas outside the fence (with ungulate influence) (Nopp-Mayr et al. 2020, Millett & Edmondson 2013, Pellerin et al. 2012, Casabon & Pothier 2007, Bellingham & Allan 2003, Reimoser et al. 1999, Reimoser & Suchant 1992). Of course, fencing of forest patches is not a natural situation (forest totally without ungulates), but it is a treatment that allows an objective assessment and evaluation of herbivore impacts. The fence works so to say as a filter to make the effects of ungulates within the complex, multifactorial forest-regeneration system clearly visible.

Therefore, as a part of the wildlife monitoring in the Donau-Auen National Park, since 1999 systematic vegetation surveys are carried out on pairs of ungulate impact control areas (unfenced vs. fenced area) in order to record the effects of wild ungulates on the development of forest vegetation. The ungulate species include roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and, rarely, mouflon (*Ovis ammon musimon*) and fallow deer (*Dama dama*). The presented dataset is a rare case of long-term records with a stringent survey design and a large number of control-treatment pairs.

The aims of this study are (1) to develop objective bases for understanding the effects of wild ungulates on the growth of forest vegetation in the Donau-Auen National Park, (2) to record the changes in various biodiversity indices caused by ungulates, and (3) to assess these effects with regard to reference values (benchmarks) in the national park. The results also serve as the basis for coordinating ungulate management in the national park with its ecologically relevant environment. In order to minimize anthropogenic influences caused by unnaturally high ungulate population densities, interventions in the national park may be necessary to regulate the ungulate populations, if this regulation will not be possible via an appropriately coordinated ungulate management in the surrounding areas of the national park.

Material and Methods

Study area

The Donau-Auen National Park (Fig. 1) is located in the Danube floodplains between the cities Vienna and Bratislava. It was established in 1996 and extends over the federal states of Lower Austria and Vienna. The current total area is about 9,600 hectares; of these, approx. 65 % is riparian forest (softwood and hardwood floodplains), 15 % meadow, and approx. 20 % is covered by water. Due to its elongated shape, in view of the wild-ungulate distribution the national park interacts closely with its environment, which is mainly used for agriculture.

Autochthonous tree species in the national park (31 species, Gilli 2021): *Acer campestre* (field maple), *Acer platanoides* (Norway maple), *Alnus glutinosa* (black alder), *Alnus incana* (grey alder), *Betula pendula* (European white birch), *Carpinus betulus* (European hornbeam), *Fagus sylvatica* (common beech), *Fraxinus angustifolia* (narrow-leafed ash), *Fraxinus excelsior* (common ash), *Malus sylvestris* (crab apple), *Populus alba* (white poplar), *Populus nigra* (black poplar), *Populus tremula* (European aspen), *Populus x canescens* (grey poplar), *Prunus avium* (sweet cherry), *Prunus padus* (bird cherry). *Pyrus pyraster* (wild pear), *Quercus cerris* (European turkey oak), *Quercus pubescens* (downy oak), *Quercus robur* (common oak), *Salix alba* (white willow), *Salix cinerea* (grey willow), *Salix eleagnos* (rosemary willow), *Salix fragilis* (cack willow), *Salix x rubens* (hybrid crack willow), *Sorbus aria* (common whitebeam), *Sorbus torminalis* (wild service tree), *Tilia cordata* (small leafed lime), *Tilia platyphyllos* (broad leafed lime), *Ulmus glabra* (wych elm), *Ulmus laevis* (European white elm), *Ulmus minor* (field elm).

Allochthonous tree species and questionable allochthonous tree species in the national park (27 species, Gilli 2021): *Acer negundo* (ash-leafed maple), *Acer pseudoplatanus* (sycamore maple), *Acer saccharinum* (silver maple), *Aesculus hippocastanum* (horse chestnut), *Ailanthus altissima* (tree of heaven), *Broussonetia papyrifera* (paper mulberry), *Castanea sativa* (European chestnut), *Eleagnos angustifolia* (oleaster), *Ficus carica* (common fig), *Fraxinus americana* (American ash), *Fraxinus pennsylvanica* (red ash), *Juglans nigra* (black walnut), *Juglans regia* (common walnut), *Malus domestica* (cultivated apple), *Morus alba* (white mulberry), *Morus nigra* (black mulberry), *Picea abies* (common spruce), *Pinus nigra* (black pine), *Pinus sylvestris* (red pine), *Populus balsamifera* (balsam poplar), *Populus x canadensis* (hybrid black-poplar), *Prunus cerasifera* (cherry plum), *Prunus domestica* (cultivated plum), *Prunus serotina* (black cherry), *Pyrus communis* (common pear), *Quercus rubra* (red oak), *Robinia pseudacacia* (black locust), *Sorbus aucuparia* (rawon tree), *Taxus baccata* (common yew).

The area of the national park was strongly affected from an intensive hunting history, as it served as hunting ground in the Habsburg era and later under National Socialists rule, which led to unnaturally high ungulate densities.

Number of living ungulates: In the planning phase of the national park estimated ungulate numbers (minimum numbers) were published on the base of assessments and surveys (Tab. 1; Leditznig & Fraissl 1996). More recent estimations with FLIR (Forward Looking InfraRed) in 2015 and 2017 showed numbers of between 900 and 1.050 red deer just for the national park areas on the northern side of the Danube (Franke 2017). For wild boar a strong increase of the numbers in the years after 1990 was stated in the planning phase, because of several successive years with rich acorn mast, a low hunting bag in the year 1986 (Tschernobyl) and the opening of the eastern borders after the fall of the iron

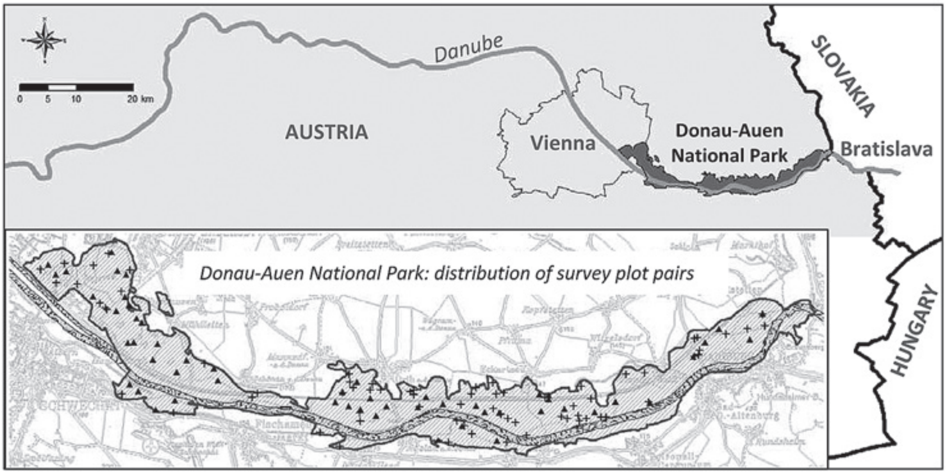

Fig. 1: Donau-Auen National Park with the spatial distribution of the two series of survey plot pairs (comparison areas). Cross = 1st series (1999–2019). Triangle = 2nd series (2011–2020). – Abb. 1: Nationalpark Donau-Auen mit der räumlichen Verteilung der beiden Serien von Vergleichsflächenpaaren. Kreuz = 1. Serie (1999–2019). Dreieck = 2. Serie (2011–2020).

Tab. 1: Estimated numbers of ungulates alive and the annual mortality (hunting bags and animals found dead by other reasons) for the former planning area of the national park with 11,500 ha (Lediztnig & Fraissl 1996). – Tab. 1: Geschätzte Anzahl lebender Huftiere und jährlicher Abgang (Jagdstrecken und aus anderen Gründen tot aufgefundene Tiere) für das ehemalige Planungsgebiet des Nationalparks mit 11.500 ha.

Ungulate species	Red deer	Roe deer	Mouflon	Fallow deer	Wild boar
Estimated number of ungulates living in the area	700	2.100	30	?	?
Hunting bag and animals found dead	350	970	18	?	560

curtain in 1986 (Lediztnig & Fraissl 1996). A precise assessment of the number of wild boars does not exist till today.

Beside the hunting history of the area, the loss of hydrological dynamics and thereby floodwater events after control of river flow in the 19th century as natural regulator of the game populations, led to higher numbers of ungulates. Since this time extraordinary flooding events with regulating impact on the ungulate numbers were rare, exceptions were the floodwater events in 2002, 2005–2006 and 2013.

Hunting bag numbers (including carrion/animals found dead): The numbers of yearly hunting bags and dead found individuals of red deer, fallow deer and mouflon within the conservation area since the year 2000 show a more or less constant trend without large fluctuations (Fig. 2). Hunting bag and carrion numbers of roe deer declined over the years from more than 200 in the first years to around 120 animals in the last years. The numbers of hunting bags and wild boars found dead are constantly high and irregular with counts between nearly 250 up to 670. In 2020 the very high number of 666 animals was due to intensive regulation because of imminent African Swine Fever (ASF). Fluctuations between single years were caused by foregoing impacts of floodwater events (e.g. 2006, 2013) or animal diseases (e.g. swine fever in 2001), which mostly led to lower shooting numbers in the following years (C. Egger, ÖBf AG, personal communication 2021).

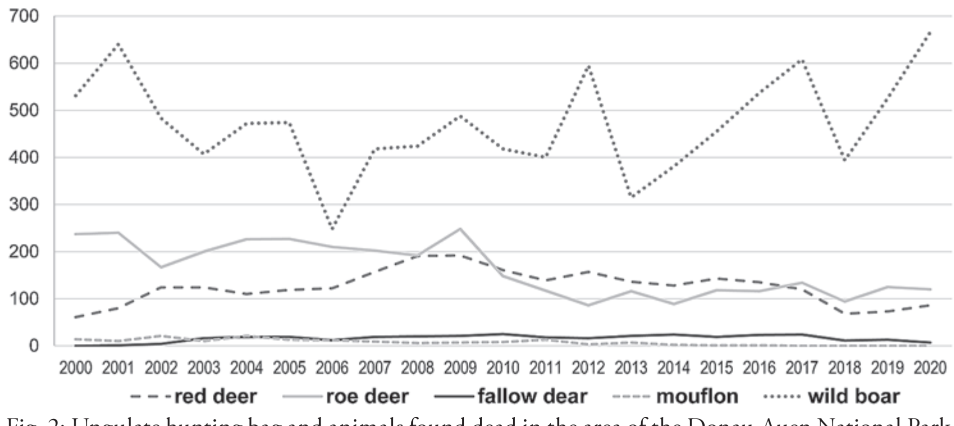

Fig. 2: Ungulate hunting bag and animals found dead in the area of the Donau-Auen National Park from 2000 to 2020. – Fig. 2: Jagdstrecke an wildlebenden Huftieren und Fallwild im Nationalpark Donau-Auen von 2000 bis 2020.

By establishment of the Donau-Auen National Park in 1996 the management of game changed from economic and traditional hunting to straight regulating management of only ungulate species. From that time on the general principle was to allow natural processes and reduce anthropogenic control as much as possible (Nationalpark Donau-Auen GmbH 1999, 2009, 2019). Although the ungulate density in the region was high, the majority of hunters in the vicinity of the national park claimed to stop or at least to reduce the regulation of game within the conservation area. A reason for this reaction may be due to the destruction of fences, which had enclosed parts of the park area in the years before, so that now ungulates could be more easily hunted by the hunters outside the park when the animals cross the border line (F. Kovacs, ÖBf AG, personal communication 2021). However, crucial factors to continue the game management inside the park were on one hand expectable impacts caused by ungulates in forest regeneration sites of the park and on the other hand damages by wild ungulates in surrounding agricultures. The planning targets for the game populations were modified since that time fundamentally. The targeted numbers and constitutions of ungulate populations from that time on were orientated on typical natural social structures and not as before on economic hunting parameters, like trophies etc. The huntable animals within the conservation area were limited to the ungulates red deer, roe deer, wild boar and the allochthonous species fallow deer and mouflon (Nationalpark Donau-Auen GmbH 1999, 2009, 2019). In the Lower Austrian part of the national park, roe deer have not been shot since 2012 (Nationalpark Donau-Auen GmbH 2011). The parasite *Fascioloides magna* (American giant liver fluke), which has been found in the national park since 2000 (Winkelmayer & Prosl 2001), is partly lethal for roe deer.

With establishment of the national park also the designation of non-hunting zones and areas with strongly reduced hunting pressure (short hunting intervals) was implemented and different monitoring programs were started. The non-hunting areas were not enforced consequently, so regulation was possible also within these areas on few days per year and battues with a large number of hunters (~60 persons) were organised. Other hunting types outside of the non-hunting zones up to the present are single hunts from high seats with or without baiting station (Nationalpark Donau-Auen GmbH 1999, 2009, 2019). The methods had been evaluated and discussed regularly (science and hunting boards of the Donau-Auen National Park), therefore part of the former hunting infrastructures, particularly in the non-hunting zones, have since then been destroyed. To point out particularly is the cessation of supplementary feeding of ungulates, since 2004 in the Lower Austrian part (Nationalpark Donau-Auen GmbH 2007), and since 2016 in the Viennese part of the park (A. Faltejsek, Municipality of Vienna, personal communication 2021). Since that time the distribution of ungulates within the park changed somewhat, with the population of red deer shifting more and more to the eastern part of the area with lower visitor numbers.

The visitor behaviour in the national park differs a lot between the Viennese and the Lower Austrian part (Arnberger & Brandenburg 2001, Arnberger & Hinterberger 2003, Arnberger et al. 2009). The western part of the conservation area bordering to the City of Vienna is highly frequented from visitors all over the week and especially on weekends and holidays, whereas in the eastern part the visitor numbers are much lower and concentrate on a few visitor hotspots.

Data collection

The first series of comparison-area pairs (unfenced control areas vs. fenced areas) was erected in 1999, and a second series was set up in 2011. In 2020, new comparison-area pairs were set up for a third series of surveys in order to continue the wildlife impact monitoring with a comparable method and to document the long-term effects of ungulates on the forest development. The present study comprises the results of 70 comparison-area pairs from the first series after a 20-year period of investigation (1999–2019) and of 54 area pairs from the second series after a 9-year period (2011–2020); Fig. 1.

Method

The comparison-area pairs (Fig. 3) are established on areas where forest regeneration is in an initial phase. The survey and evaluation methods are standardized (ungulate impact control system – UICOS/WIKOSYS, REIMOSER et al. 1999, 2014, REIMOSER 2002, REIMOSER & REIMOSER 1997, 2003). The ungulate impact on tree seedlings can only be clearly identified or made visible with this method. Comparison-area procedures offer the possibility of directly and reliably assessing the concrete effects of the ungulate impacts on forest regeneration (REIMOSER et al. 2014, 1999).

One area of each pair of the comparison areas is accessible to ungulates (unfenced area = control area), the second area is inaccessible to ungulates (fenced area = treatment area, ungulate exclosure). Which of the two previously demarcated areas is fenced is made at random (decision by lot). Suitable comparison sites are forest areas (1) that are able to regenerate (sufficient light in the lower layer), (2) where forest regeneration is at the beginning (trees predominantly less than approx. 0.5 m in height), and (3) are distributed as evenly as possible over the study area. A comparison-area pair consists of two 6 × 6 m areas (each with a 5 × 5 meter survey area, Fig. 3) at a distance of 5 to 20 meters between the two plots (on comparable sites).

Within a few weeks after the fences have been erected, the first survey of the vegetation is carried out with regard to site characteristics, present tree and shrub species, their number and height, browsing characteristics etc. The follow-up surveys are usually carried out at 3-year intervals. In each survey, the respective difference in the measured variables between the unfenced (control) areas (U) and the fenced areas (F) is determined. When de-

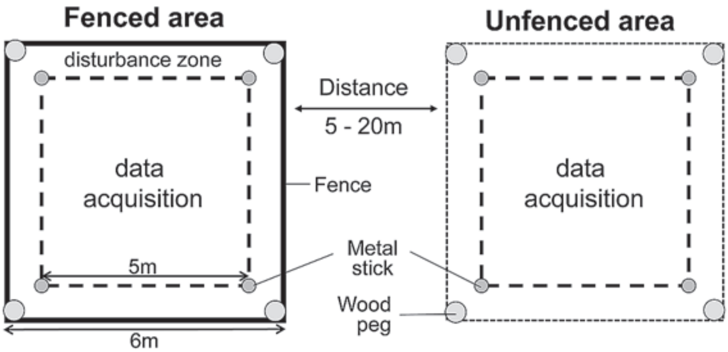

Fig. 3: Scheme of the comparison-area method (unfenced control areas vs. fenced areas). – Abb. 3: Schema des Vergleichsflächenverfahrens (ungezäunte Kontrollflächen vs. eingezäunte Flächen).

termining the effects of ungulates for the observation period, the following two differences are formed for each pair of comparison areas: The difference in the values (per indicator) between U and F for each recording year and the difference between these two difference values between the end (B) and the beginning (A) of the respective observation period.

$\Delta A = U_A - F_A$, $\Delta B = U_B - F_B$, $\Delta\Delta = \Delta B - \Delta A$ (e.g., A=1999, B=2019)

The effects of the ungulates on the vegetation determined by the fence-control comparison can be positive, negative or insignificant with regard to the achievement of a predefined desired anthropogenic benchmark. So, basically, largely differing effects can result. Since, in addition to undesired, also desired effects on forest development can be detected on a comparable scale, a neutral, mutually open approach is created, which enables a balance of positive and negative ungulate influence in terms of human targets. Positive functions of ungulates in forest ecosystems can be, for example, the spread of seeds and the penetration of plant seeds into the soil, the browsing of competing vegetation from desired tree species, the change in germination conditions through the production of excrement and nutrient redistribution (Reimoser 2002). The value-neutral ecological effects of ungulates within forest ecosystems, and the valuation (positive or negative) of ungulate impacts on human targets should be clearly separated (see below step 1 and step 2).

Due to the special framework conditions for national parks (IUCN Category II), conventional approaches assessing damages of ungulates to forest vegetation, such as those used in managed forests, cannot be used appropriately. Alternative ways of assessing the influence of herbivores on vegetation, which are compliant with the national parks´ predefined targets and guidelines, are required, which make it possible to objectively determine the necessity and extent of regulation of ungulate populations in national parks, in the case of anthropogenically disturbed plant-herbivore interactions (Reimoser 2001, 2002).

In addition to these considerations on tolerance limits of herbivore-plant interactions within protected areas that include forest cover, the avoidance of economically unacceptable game damage in the vicinity of the protected area can be of decisive importance. Such game damages outside protected areas, caused by ungulates partly living in the protected area (e.g. during the hunting season in the vicinity of the park) and partly living outside the park (e.g. when hunting season is closed there), can be decisive for the necessity and extent of a regulation of ungulate populations through ungulate shooting in the protected area too.

The legal framework (NÖ Nationalparkgesetz, LGBl, 5505-0) and management plan (Nationalpark Donau-Auen GmbH, 2019) for the Donau-Auen National Park comprise the following basic targets: Wild autochthonous ungulate species have the same protective status in the park as autochthonous plant species and forest communities. One of the goals of national park management is to promote and maintain natural forest vegetation in the park. The following criteria define the acceptable impact load from ungulates on the national park´s vegetation: (1) No ungulate-related changes in the development and regeneration of the forest communities in their typical structure and species combination (i.e. sustainable seed production through sufficient seed trees) on at least approx. 50 % of the forest area in the national park (benchmark); the remaining area may be redesigned by the ungulates, which can result in a higher biodiversity on the entire park. (2) No permanent reduction in the local species diversity of autochthone woody plants by ungulates in the national park. (3) A natural regeneration of the forest should be possible in the course of each forest generation.

The evaluation is carried out according to a standardized procedure that is also used in other countries and national parks (Reimoser et al. 1999, Reimoser 2002). The evaluation and presentation of results are divided into three steps:

Step 1: "Value-neutral" representation of the effects of ungulates for all tree and shrub species by comparison of unfenced areas and fenced areas (U-Z).

Step 2: Contrasting the determined ungulate effects (***U-Z) against regeneration benchmarks*** (Tab. 2), by comparing the actual situation with the area-specific benchmark values. This evaluation step also enables a better comparison with areas used for forestry, in which the effects of ungulates on forest development are assessed using the same method (comparison-areas method) with regard to the development of game damage and game benefit by means of a target-actual comparison. In contrast to forests used for forestry purposes, the economic component of damage caused by ungulates to the forest is not relevant in the national park. Nevertheless, it can be interesting to compare the effects of ungulates in order to assess the differences in ungulate impact compared with managed forests. The terms "damage" and "benefit", deriving from ungulate are oriented towards achieving a forest regeneration goal and they are not relevant for the national park, but are useful for comparison.

The classification "benchmark not reached" (BM-) applies if the benchmark is not achieved due to ungulate impacts (comparison of the forest development on the unfenced area with the ungulate-proof fenced area) for at least one indicator (Tab. 2). Correspondingly, "benchmark reached" (BM+) applies if the reference value is reached for at least one indicator due to the influence of ungulates or if there is an additional increase in height in a key tree species of at least 3 height classes due to ungulate impact (e.g., due to browsing by competitive vegetation).

Step 3: Representation of the ***influence of ungulates on the biodiversity of tree and shrub species*** using four biodiversity indices (Richness, Shannon, Evenness, Gini-Simpson; Mühlenberg 1993, Supriatna 2018). Undesirable neophytes are not taken into account (ashleaf maple, silver maple, black locust, tree of heaven, hybrid poplar, balsam poplar, black walnut, American ash, douglas fir).

(1) Richness: number of species

(2) Shannon index: Takes into account both the number of species and their abundance (number of individuals per species), maximum value depending on population size (Donau-Auen National Park, when calculating according to the mean value from comparison areas at approx. 2, for the entire survey area at 3)

(3) Evenness: Quotient of the Shannon index and the maximum Shannon index value, is a measure of the distribution of individuals in a population (between 0 and 1)

(4) Gini-Simpson index: expresses the probability that two individuals selected at random from all individuals in a recording belong to a different species (between 0 and 1)

The surveys are carried out by specially trained survey teams. The collected data are entered and evaluated in a standardized form (WIKOSYS 9.4, cf. Reimoser 2002, Reimoser & Reimoser 1997, 2003, Reimoser et al. 2014).

Tab. 2: Test criteria (indicators) with specific benchmarks for the forest regeneration in the Donau-Auen National Park. – Tab. 2: Prüfkriterien (Indikatoren) mit den spezifischen Richtwerten für die Waldverjüngung im National Park Donau-Auen.

Indicator		Benchmark[1]
N	**Regeneration density of trees**	≥ 2000 trees/ha (1,000 trees/ha for xeric alluvial biotope)
M	**Mixture type of trees**	Typical tree species of the 2 mixture types (softwood, hardwood, see below) present with ≥20 % of regeneration density (N), in which these tree species can be substituted for one another. *Softwood:* autochthonous willows, alders, poplars, ash species *Hardwood:* autochthonous elms, oaks, maple, linden, ash species
K	**Key tree species**	*Softwood:* each ≥5 % of regeneration density (N) of autochthonous willows, alders and poplars (each if they occur). *Hardwood:* each ≥5 % of autochthonous elms, oaks, maple, linden, ash (each if they occur). *Special sites:* individual target tree species (justification); e.g. xeric alluvial biotope
S	**Number of tree species**	≥ 4 species (without neophytes[4]), (1 species for xeric alluvial biotope)
H	**Height increment of trees[2]**	Difference >2 height classes[3]
V	**Shrub volume index**	≥ 600 m³/ha equivalent (only for xeric alluvial biotope)
Z	**Number of shrub species**	Difference >1 species (only for xeric alluvial biotope)

[1] depending on the natural forest community
[2] recorded for the highest tree individual per species in regeneration and per survey period, respectively
[3] height classes: –10cm, 11–25, 26–40, 41–70, 71–100, 101–130, 131–160, 161–200, 201–250, 251–300, 301–350, 351–400, 401–450, … cm (no upper height limit)
[4] Ashleaf maple, silver-maple, black locust, tree of heaven, American ash, hybrid and balsam poplar, black walnut

Results

The effects of ungulates on the development of young forests are shown by comparing the forest development on sample areas with ungulate influence (unfenced areas - U) with the development on sample areas without ungulate influence (fenced areas - F). The two comparison-area series (1999–2019 and 2011–2020) were each established on areas with the beginning of forest regeneration. The 1st series shows the effects of ungulates as they resulted from the ecological constellation of forest vegetation and ungulate occurrence 12 years before the constellation at the beginning of the 2nd series. This enables a long-term comparison of the development of the ungulate impact on the forest in the national park.

In the first series (1999–2019, 70 comparison pairs), 25 tree species and 17 shrub species were recorded in the first survey (1999). In the last survey after 20 years (2019) there were 22 tree species and 18 shrub species. In the 2nd series (2011–2020, 54 comparison pairs) there were initially (2011) 25 tree and 19 shrub species, and after 9 years (2020) 27 tree and 18 shrub species.

The mean regeneration density of young trees from all sample areas (sum of all tree-height classes including tree seedlings) was around 31,100 individuals per hectare at the beginning of the 1st series (1999). In the following year the density rose to around 44,800 trees/ha and then decreased. At the beginning of the 2nd series (2011) the regeneration density was around 44,100 trees/ha and decreased in the following years. At the beginning of each series, there were only minor differences in the forest regeneration density between the unfenced areas and the fenced areas. The total number of trees in regeneration was only recorded in the initial phase of the series. Later, only the (maximum) six tallest trees of each tree species ("upper height trees" - UH), which are primarily relevant for further forest development (Nopp et al. 2020), were surveyed on each sample area; individual trees were not marked, so other trees could be in the upper height classes in each census.

At the beginning of the 1st series (1999) the corresponding averaged UH-tree number was 4,755 trees/ha, in the 2nd series (2011) 5,893 young trees/ha. In the last survey of both series (2019 and 2020), the tree number had already decreased significantly reflecting the typical pattern of declining tree numbers in advanced forest regeneration with higher trees, particularly in the 1st series after 20 years (Tab. 3, 4; Fig. 4, 5).

From the 1st series of comparison areas (1999–2019), 84 % of the fenced areas and 50 % of the unfenced areas have reached the thicket stage (trees/shrubs >2 m height); maximum height of trees was 16 meters on the fenced and 14 meters on the unfenced areas, shrubs up to 9 meters on both fenced and unfenced areas. From the 2nd series (2011–2020), 76 % of the fenced areas and 37 % of the unfenced areas were already in the thicket stage; the maximum height of fenced trees was 9 m, of unfenced trees 8 m, shrubs reached up to 9 m on the fenced areas and 8 m on the unfenced areas.

Impact of ungulates on tree species

Regeneration densities, tree species composition, tree height development

The forest regeneration densities (tree numbers of the upper-height trees – UH) and the tree species composition, separated into four tree-height classes (up to 25cm, 26–100cm, 101–200cm, >200 cm) and according to fenced (F) and unfenced area (U) for the two series, each for the first (1999, 2011) and the last survey (2019, 2020) are shown in Tables 3a, 3b and 4a, 4b. The project report for the Donau-Auen National Park contains a detailed long-term evaluation of all surveys (Reimoser & Reimoser 2021).

In the 1st series, the mean number of the UH-trees per hectare after 20 years of ungulate impact (2019) on the unfenced comparison areas (U) was 3,080 trees/ha; there were 21 tree species; field maple dominated, followed by ash and sycamore maple (Tab. 3b, Fig. 4a). When the ungulates on the fenced areas (F) were excluded, the mean UH-tree number was 2,929 trees/ha; there were 19 species; field maple also dominated, followed by sycamore maple and ash (Tab. 3b, Fig. 4a). If only the trees over 2 meters high are taken into account, a clear influence of ungulates can be seen, which delays the height development of the trees on the U-plots. While after 20 years an average of 2,340 young trees per hectare reached a height of more than 2 meters within the fence, so far there have been only 771 trees/ha on the unfenced area (Tab. 3b, Fig. 4b). Crab apple, bird cherry and tree of heaven only reached heights of over 2 meters within the fence.

In the 2nd series, the mean number of UH-trees per hectare after 9 years of ungulate influence (2020) on the U-plots was 4,715 trees /ha; there were 22 tree species; as in the first series, field maple dominated (30.4 %), followed by ash (21.6 %) and sycamore maple (13.7 %, Tab. 4b, Fig. 5a). When ungulates were excluded (F-plots), the mean UH-tree number was 4,581 trees/ha; there were 26 species; field maple dominated (36.1 %), followed by elm

(13.3 %, *Ulmus laevis* + *Ulmus minor*) and ash (13.1 %). While an average of 1,808 young trees per hectare reached a height of over 2 meters within the fence after 9 years, on the U-area it were only 600 trees/ha (Tab. 4b, Fig. 5b). Norway maple, American ash, black locust, oak (*Quercus robur* + *Quercus cerris*), beech, hornbeam, crab apple and bird cherry reached heights of over 2 meters only within the fence. Tree of heaven reached a height of over 2 m only outside the fence (Tab. 4b).

The ungulate impact on the development of tree species can be seen primarily from the comparison of the ingrowth into the higher tree-height classes, which results from the first to the last survey. Distinctly more trees have grown into the height class over 200 cm on the F-plots than on the U-plots. Overall, the ingrowth of trees in the upper tree-height class on the U-area was changed, mostly delayed, by the impact of the ungulates; depending on the tree species, there were different effects (Tabs. 3a and b, Tabs. 4a and b).

Tab. 3a: 1st series, first survey (1999). Tree species composition in percentage of UH-tree number per hectare (UH = 6 highest trees per species) in the 4 tree-height classes and over all height classes (Total) and stem density of UH trees (UH-trees/ha); order of species according to total U+F, U=unfenced area, F=fenced area. – Tab. 3a: 1. Serie, erste Erhebung (1999). Baumartenzusammensetzung in Stammzahlprozent der Oberhöhenbäumchen je Hektar (6 h*öchste* Bäume je Art) nach 4 Baumhöhenklassen und über alle Höhenklassen hinweg (Total) sowie Stammzahldichte der Oberhöhenbäumchen (UH-trees/ha); Reihenfolge der Arten nach gesamt U+F, U=ungezäunte Fläche, F=Zaunfläche.

Tree species	**1–25 cm**		**26–100 cm**		**101–200 cm**		**> 200 cm**		**Total**		
	U	**F**	**U**	**F**	**U**	**Z**	**U**	**F**	**U**	**F**	**U+F**
Field maple, *Acer campestre*	32,2	26,5	31,0	31,4	12,7	16,8	29,4	12,5	29,9	28,8	29,4
Ash, *Fraxinus excelsior*	26,5	17,3	26,0	26,8	25,4	24,1	35,3	0,0	26,3	24,4	25,3
Syc. maple, *Acer pseudoplatanus*	11,3	12,3	8,3	7,9	4,8	8,5	0,0	0,0	8,7	8,7	8,7
Elms, *Ulmus laevis, U. minor*	4,4	9,3	9,0	7,9	3,2	9,7	0,0	0,0	7,2	8,3	7,7
White poplar, *Populus alba*	0,4	1,2	7,4	6,8	9,5	10,8	0,0	0,0	5,5	6,0	5,8
Walnut, *Juglans regia*	0,4	1,2	3,3	3,8	14,3	15,7	0,0	0,0	3,3	4,4	3,9
Bird cherry, *Prunus padus*	4,8	5,6	3,0	3,0	3,2	7,3	0,0	0,0	3,4	3,9	3,7
Black locust, *Robinia pseudoac.*	0,0	1,2	1,8	3,4	23,8	6,0	11,8	49,9	3,2	3,7	3,4
Ashleaf maple, *Acer negundo*	3,0	2,5	3,0	2,5	3,2	0,0	0,0	0,0	2,9	2,2	2,6
Norway maple, *Acer platanoides*	5,7	5,0	1,3	1,4	0,0	0,0	0,0	0,0	2,4	2,0	2,2
Lime, *Thilia cordata, T. platyp.*	1,3	1,8	2,2	1,1	0,0	0,0	0,0	0,0	1,8	1,1	1,4
Black poplar, *Populus nigra*	0,0	0,0	1,1	1,1	0,0	0,0	23,5	37,6	1,2	1,1	1,1
Sweet cherry, *Prunus avium*	1,7	2,5	0,4	0,9	0,0	0,0	0,0	0,0	0,7	1,1	0,9
Crab apple, *Malus sylvestris*	1,7	2,5	0,4	0,7	0,0	0,0	0,0	0,0	0,7	1,0	0,8
Hornbeam, *Carpinus betulus*	1,7	2,5	0,9	0,2	0,0	0,0	0,0	0,0	1,1	0,6	0,8
Red pine, *Pinus sylvestris*	2,6	3,7	0,0	0,0	0,0	0,0	0,0	0,0	0,7	0,7	0,7
Tree of heaven, *Ailanthus altiss.*	2,2	0,6	0,0	0,4	0,0	0,0	0,0	0,0	0,6	0,4	0,5
Wild pear, *Pyrus pyraster*	0,0	3,7	0,2	0,2	0,0	0,0	0,0	0,0	0,1	0,9	0,5
Oaks, *Quercus robur, Q. cerris*	0,0	0,6	0,4	0,5	0,0	0,0	0,0	0,0	0,2	0,5	0,4
Willow sp., *Salix sp.*	0,0	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,2	0,0	0,1
Grey alder, *Alnus incana*	0,0	0,0	0,0	0,0	0,0	1,2	0,0	0,0	0,0	0,1	0,1
Black walnut, *Juglans nigra*	0,0	0,0	0,0	0,2	0,0	0,0	0,0	0,0	0,0	0,1	0,1
Deciduous trees	97,4	96,3	100,0	100,0	100,0	100,0	100,0	100,0	99,3	99,3	99,3
Conifers	2,6	3,7	0,0	0,0	0,0	0,0	0,0	0,0	0,7	0,7	0,7
TOTAL	100	100	100	100	100	100	100	100	100	100	100
UH-trees/ha	**1314**	**924**	**3097**	**3200**	**360**	**473**	**97**	**46**	**4868**	**4642**	**4755**
Ratio U/F	1,42		0,97		0,76		2,12		1,05		

Tab. 3b: 1st series, last survey (2019). Tree species composition in percentage of UH-tree number per hectare (UH = 6 highest trees per species) in the 4 tree-height classes and over all height classes (Total) and stem density of UH trees (UH-trees/ha); order of species according to total U+F, U = unfenced area, F = fenced area. – Tab. 3b: 1. Serie, letzte Erhebung (2019). Baumartenzusammensetzung in Stammzahlprozent der Oberhöhenbäumchen je Hektar (6 höchste Bäume je Art) nach 4 Baumhöhenklassen und über alle Höhenklassen hinweg (Total) sowie Stammzahldichte der Oberhöhenbäumchen (UH-trees/ha); Reihenfolge der Arten nach gesamt U+F, U = ungezäunte Fläche, F = Zaunfläche.

Tree species	1–25 cm		26–100 cm		101–200 cm		> 200 cm		Total		
	U	F	U	F	U	Z	U	F	U	F	U+F
Field maple, *Acer campestre*	45,8	59,8	35,1	30,3	37,3	33,4	36,3	45,4	37,3	42,9	40,0
Ash, *Fraxinus excelsior*	12,5	0,0	22,1	3,8	18,2	4,5	15,6	9,3	18,4	8,2	13,4
Syc. maple, *Acer pseudoplatanus*	20,8	40,2	9,5	15,1	7,3	6,6	15,6	10,0	12,1	10,5	11,3
Elms, *Ulmus laevis, U. minor*	6,9	0,0	6,3	3,8	20,0	11,1	0,7	8,1	7,8	7,8	7,8
White poplar, *Populus alba*	8,3	0,0	16,7	24,5	4,5	0,0	3,0	2,0	9,6	4,1	6,9
Bird cherry, *Prunus padus*	0,0	0,0	0,5	11,3	0,0	20,0	3,0	8,3	0,9	9,6	5,1
Walnut, *Juglans regia*	0,0	0,0	2,3	1,9	7,3	6,6	9,6	3,4	4,8	3,5	4,2
Norway maple, *Acer platanoides*	1,4	0,0	3,2	0,0	0,0	4,5	0,7	4,2	1,7	3,7	2,7
Lime, *Thilia cordata, T. platyp.*	0,0	0,0	0,0	1,9	4,5	0,0	5,9	2,4	2,4	2,1	2,3
Black locust, *Robinia pseudoac.*	0,0	0,0	0,0	5,7	0,0	0,0	2,2	3,2	0,6	3,1	1,8
Ashleaf maple, *Acer negundo*	1,4	0,0	0,5	0,0	0,0	2,2	5,9	1,5	1,9	1,4	1,6
Sweet cherry, *Prunus avium*	0,0	0,0	0,9	0,0	0,0	11,1	0,0	1,2	0,4	2,0	1,1
Bird cherry, *Prunus padus*	0,0	0,0	1,8	0,0	0,0	0,0	0,0	0,5	0,7	0,4	0,6
Tree of heaven, *Ailanthus altiss*	0,0	0,0	0,9	0,0	0,0	0,0	0,0	0,5	0,4	0,4	0,4
Hornbeam, *Carpinus betulus*	0,0	0,0	0,5	0,0	0,0	0,0	0,7	0,2	0,4	0,2	0,3
Oaks, *Quercus robur, Q. cerris*	2,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,2
Chestnut, *Aesculus hippocastan.*	0,0	0,0	0,0	1,9	0,0	0,0	0,0	0,0	0,0	0,2	0,1
Wild pear, *Pyrus pyraster*	0,0	0,0	0,0	0,0	0,0	0,0	0,7	0,0	0,2	0,0	0,1
Americ. ash, *Fraxinus americana*	0,0	0,0	0,0	0,0	0,9	0,0	0,0	0,0	0,2	0,0	0,1
Deciduous trees	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0
Conifers	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
TOTAL	100	100	100	100	100	100	100	100	100	100	100
UH-trees/ha	**411**	**29**	**1268**	**303**	**629**	**257**	**771**	**2340**	**3080**	**2929**	**3004**
Ratio U/F	14,34		4,18		2,45		0,33		1,05		

Tab. 4a: 2nd series, first survey (2011). Tree species composition in percentage of UH-tree number per hectare (UH = 6 highest trees per species) in the 4 tree-height classes and over all height classes (Total) and stem density of UH trees (UH-trees/ha); order of species according to total U+F, U = unfenced area, F = fenced area. – Tab. 4a: 2. Serie, erste Erhebung (2011). Baumartenzusammensetzung in Stammzahlprozent der Oberhöhenbäumchen je Hektar (6 höchste Bäume je Art) nach 4 Baumhöhenklassen und über alle Höhenklassen hinweg (Total) sowie Stammzahldichte der Oberhöhenbäumchen (UH-trees/ha); Reihenfolge der Arten nach gesamt U+F, U = ungezäunte Fläche, F = Zaunfläche.

Tree species	1–25 cm		26–100 cm		101–200 cm		> 200 cm		Total		
	U	F	U	F	U	Z	U	F	U	F	U+F
Field maple, *Acer campestre*	28,6	33,9	22,9	24,2	24,0	10,4	0,0	0,0	24,8	25,2	25,0
Ash, *Fraxinus excelsior*	27,4	18,0	25,5	23,3	10,0	26,9	0,0	100,0	25,1	22,6	23,8
Syc. maple, *Acer pseudoplatanus*	13,3	14,2	13,1	12,4	2,0	3,0	0,0	0,0	12,4	12,0	12,2
White poplar, *Populus alba*	5,2	6,0	13,9	13,6	20,0	10,4	0,0	0,0	11,5	11,6	11,6
Elms, *Ulmus laevis, U. minor*	8,5	2,2	6,3	8,0	30,0	34,3	0,0	0,0	8,5	8,9	8,7
Walnut, *Juglans regia*	0,8	6,6	3,1	3,1	2,0	0,0	0,0	0,0	2,3	3,6	3,0

Tree species	1–25 cm		26–100 cm		101–200 cm		> 200 cm		Total		
	U	F	U	F	U	Z	U	F	U	F	U+F
Bird cherry, *Prunus padus*	2,8	1,7	2,5	2,6	2,0	1,5	0,0	0,0	2,5	2,3	2,4
Ashleaf maple, *Acer negundo*	1,2	0,6	3,1	2,2	4,0	4,5	0,0	0,0	2,5	2,0	2,3
Norway maple, *Acer platanoides*	4,4	1,1	0,8	3,3	0,0	0,0	0,0	0,0	1,9	2,5	2,2
Hornbeam, *Carpinus betulus*	1,2	2,2	1,6	2,4	0,0	0,0	0,0	0,0	1,4	2,1	1,8
Tree of heaven, *Ailanthus altiss*	0,0	2,7	2,5	1,6	0,0	0,0	0,0	0,0	1,5	1,7	1,6
American ash, *Fraxinus americ.*	0,0	0,0	1,0	1,3	2,0	7,5	0,0	0,0	0,8	1,5	1,1
Oaks, *Quercus robur, Q. cerris*	0,4	4,4	1,2	0,4	0,0	0,0	0,0	0,0	0,9	1,3	1,1
Beech, *Fagus sylvatica*	1,7	3,4	0,4	0,0	0,0	0,0	0,0	0,0	0,8	0,8	0,8
Lime, *Thilia cordata, T. platyp.*	2,0	0,6	0,2	0,4	2,0	0,0	0,0	0,0	0,9	0,4	0,6
Sweet cherry, *Prunus avium*	1,6	2,2	0,0	0,2	0,0	0,0	0,0	0,0	0,5	0,6	0,6
Black locust, *Robinia pseudoac.*	0,0	0,6	0,6	0,6	2,0	1,5	0,0	0,0	0,5	0,6	0,6
Black poplar, *Populus nigra*	0,4	0,0	1,0	0,2	0,0	0,0	0,0	0,0	0,8	0,1	0,4
Crab apple, *Malus sylvestris*	0,4	0,0	0,2	0,4	0,0	0,0	0,0	0,0	0,3	0,3	0,3
Black walnut, *Juglans nigra*	0,0	0,0	0,2	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,1
Wild pear, *Pyrus pyraster*	0,0	0,0	0,0	0,2	0,0	0,0	0,0	0,0	0,0	0,1	0,1
Deciduous trees	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0	100,0
Conifers	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
TOTAL	100	100	100	100	100	100	100	100	100	100	100
UH-trees/ha	**1838**	**1358**	**3632**	**4075**	**370**	**497**	**0**	**15**	**5841**	**5945**	**5893**
Ratio U/F	1,35		0,89		0,75		0,00		0,98		

Tab. 4b: 2nd series, last survey (2020). Tree species composition in percentage of UH-tree number per hectare (UH = 6 highest trees per species) in the 4 tree-height classes and over all height classes (Total) and stem density of UH trees (UH-trees/ha); order of species according to total U+F, U=unfenced area, F=fenced area. – Tab. 4b: 2. Serie, letzte Erhebung (2020). Baumartenzusammensetzung in Stammzahlprozent der Oberhöhenbäumchen je Hektar (6 höchste Bäume je Art) nach 4 Baumhöhenklassen und über alle Höhenklassen hinweg (Total) sowie Stammzahldichte der Oberhöhenbäumchen (UH-trees/ha); Reihenfolge der Arten nach gesamt U+F, U=ungezäunte Fläche, F=Zaunfläche.

Tree species	1–25 cm		26–100 cm		101–200 cm		> 200 cm		Total		
	U	F	U	F	U	F	U	F	U	F	U+F
Field maple, *Acer campestre*	53,9	55,0	26,1	31,6	28,2	34,2	29,6	38,9	30,4	36,1	33,2
Ash, *Fraxinus excelsior*	16,7	15,0	28,1	20,3	14,5	17,4	8,6	4,9	21,6	13,1	17,4
Syc. maple, *Acer pseudoplatanus*	12,8	5,0	9,3	13,3	22,6	12,2	19,8	7,4	13,7	10,4	12,0
Elms, *Ulmus laevis, U. minor*	2,6	15,0	8,8	8,2	5,6	7,7	19,8	20,9	8,8	13,3	11,0
Bird cherry, *Prunus padus*	3,9	0,0	5,4	5,7	4,8	6,1	1,2	8,6	4,6	6,8	5,7
Silver poplar, *Populus alba*	3,9	0,0	5,7	5,1	8,9	3,1	8,6	2,5	6,4	3,2	4,9
Walnut, *Juglans regia*	0,0	5,0	2,3	6,3	8,1	4,1	4,9	2,9	3,5	4,2	3,8
Norway maple, *Acer platanoides*	0,0	0,0	2,3	0,6	0,8	3,6	0,0	0,8	1,4	1,6	1,5
American ash, *Fraxinus americ.*	0,0	0,0	1,7	0,0	0,0	1,5	0,0	3,7	0,9	1,9	1,4
Ashleaf maple, *Acer negundo*	0,0	0,0	1,7	0,6	0,8	2,6	0,0	1,6	1,1	1,6	1,4
Tree of heaven, *Ailanthus altiss*	0,0	0,0	1,4	0,6	1,6	0,0	7,4	0,0	2,0	0,2	1,1
Beech, *Fagus sylvatica*	0,0	0,0	1,5	3,2	0,8	0,5	0,0	0,0	1,0	1,0	1,0
Black locust, *Robinia pseudoac.*	1,3	0,0	1,4	0,6	0,8	0,0	0,0	2,9	1,1	1,3	1,2
Lime, *Thilia cordata, T. platyp*	2,6	0,0	1,7	0,6	0,0	0,5	0,0	0,0	1,3	0,3	0,8
Oaks, *Quercus robur, Q. cerris*	1,3	5,0	0,9	1,3	0,0	1,0	0,0	0,4	0,6	1,0	0,8
Hornbeam, *Carpinus betulus*	0,0	0,0	0,3	0,0	0,0	2,0	0,0	1,6	0,2	1,3	0,7
Crab apple, *Malus sylvestris*	1,3	0,0	0,9	0,6	0,0	1,5	0,0	0,4	0,6	0,8	0,7
Sweet cherry, *Prunus avium*	0,0	0,0	0,6	0,0	0,0	0,0	0,0	1,6	0,3	0,7	0,5

Tree species	1–25 cm		26–100 cm		101–200 cm		> 200 cm		Total		
	U	F	U	F	U	F	U	F	U	F	U+F
Wild pear, *Pyrus pyraster*	0,0	0,0	0,3	0,0	0,0	0,5	0,0	0,4	0,2	0,3	0,2
Black poplar, *Populus nigra*	0,0	0,0	0,0	0,0	2,4	0,0	0,0	0,0	0,5	0,0	0,2
Prunus sp.	0,0	0,0	0,0	0,6	0,0	1,0	0,0	0,0	0,0	0,5	0,2
Red pine, *Pinus sylvestris*	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,2	0,1
Yew, *Taxus baccata*	0,0	0,0	0,0	0,6	0,0	0,0	0,0	0,0	0,0	0,2	0,1
Black pine, *Pinus nigra*	0,0	0,0	0,0	0,0	0,0	0,5	0,0	0,0	0,0	0,2	0,1
Deciduous trees	100,0	100,0	100,0	99,4	100,0	99,5	100,0	99,6	100,0	99,5	99,8
Conifers	0,0	0,0	0,0	0,6	0,0	0,5	0,0	0,4	0,0	0,5	0,2
TOTAL	100	100	100	100	100	100	100	100	100	100	100
UH-trees/ha	**578**	**148**	**2618**	**1173**	**919**	**1453**	**600**	**1808**	**4715**	**4581**	**4648**
Ratio U/F	3,90		2,23		0,63		0,33		1,03		

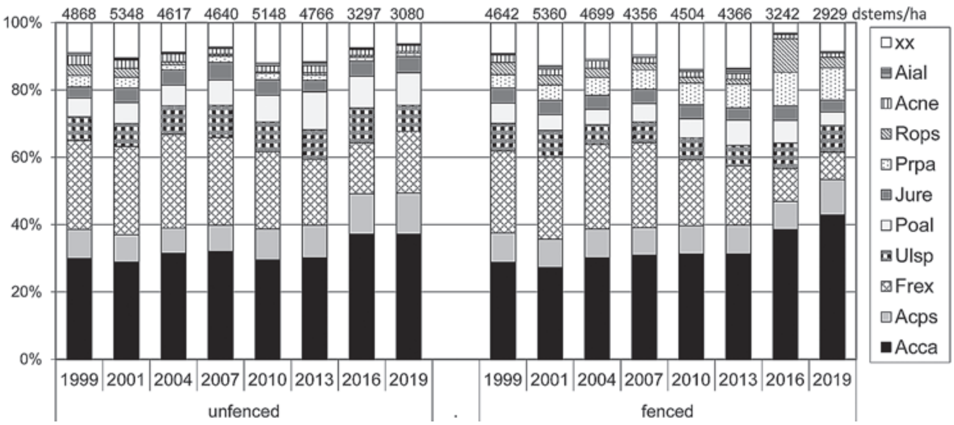

Fig. 4a: 1st series (1999–2019), **all height classes**. Tree species proportions (% of tree number) and UH-tree number per hectare (figures above columns); unfenced area (left) and fenced area (right). Acca=*Acer camp.*, Acps=*Acer pseudop.*, Frex=*Fraxinus exc.*, Ulsp=*Ulmus spp*, Poal=*Populus alba*, Jure=*Juglans regia*, Prpa=*Prunus padua*, Rops=*Robinia pseudoac.*, Acne=*Acer negundo*, Aial=*Ailanthus altissima*, Fram=*Fraxinus americ.*, xx=other tree species. – Abb. 4a: 1. Serie (1999–2019), **alle Höhenklassen.** Baumartenanteile (in %) und Oberhöhenstämmchen/ha (Ziffern oberhalb Säulen); ungezäunt (links) und gezäunt (rechts).

Constancy of tree species occurrence

1st series (1999–2019): In the last survey of the 1st comparison-area series (2019), field maple occurred in 76 % of the comparison pairs (Tab. 5). This tree species was the most frequently occurring species in the forest regeneration of the Donau-Auen National Park. Next frequent was ash with 46 %, followed by elm (41 %), sycamore maple (36 %), walnut (26 %), bird cherry (24 %), white poplar (21 %), crab apple (13 %), Norway maple and black locust (11 % each). The other tree species are found on less than 10 % of the comparison areas (Tab. 5). What is striking is the relatively high constancy of the occurrence of elm, walnut and bird cherry in comparison to their low proportion of tree numbers (<8 %). These tree species are therefore very scattered. On 7 areas (10 % of the comparison pairs) there was no young-tree growth, only shrubs were represented. In the first survey

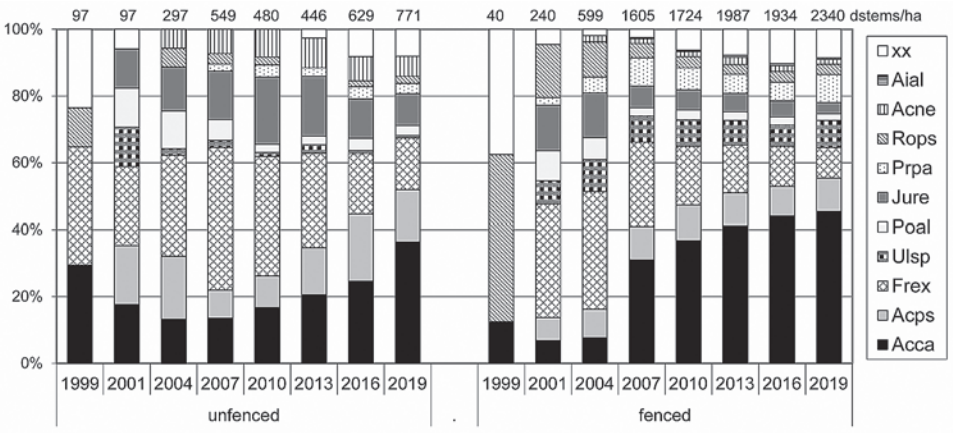

Fig. 4b: 1st series (1999–2019), **height classes >200cm**. Tree species proportions (% of tree number) and UH-tree number per hectare (figures above columns); unfenced area (left) and fenced area (right). Names of species see Fig. 4a. – Abb. 4b: 1. Serie (1999–2019), **Höhenklassen >200cm**, Baumartenanteile (in %) und Oberhöhenstämmchen/ha (Ziffern oberhalb Säulen); ungezäunt (links) und gezäunt (rechts). Baumarten siehe Abb. 4a.

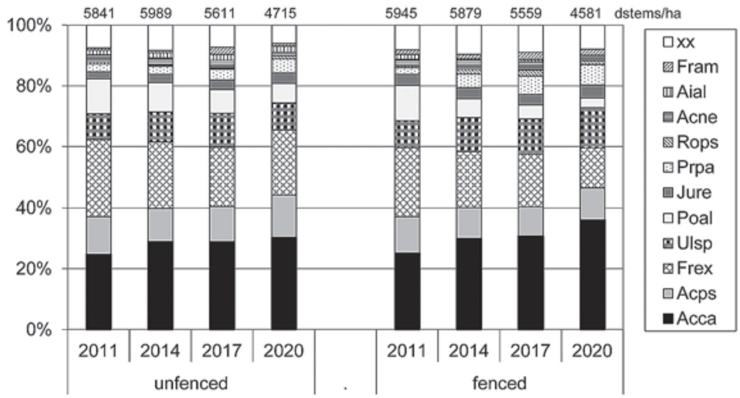

Fig. 5a: 2nd series (2011–2020), **all height classes.** Tree species proportions (% of tree number) and UH-tree number per hectare (dstems/ha; figures above columns); unfenced area (left), fenced area (right). Names of species see Fig. 4a. – Abb. 5a: 2. Serie (2011–2020), **alle Höhenklassen**, Baumartenanteile (in %) und Oberhöhenstämmchen/ha (Ziffern oberhalb Säulen); ungezäunt (links) und gezäunt (rechts). Baumarten siehe Abb. 4a.

(1999), 10 areas (14 % of the area pairs) were without young trees. In 1999 the constancy of field maple was much lower than in 2019, while the constancy of ash was much higher (Tab. 5). Tree species for which the impact of ungulates (U) showed clear advantages over ungulate exclusion (F) after 20 years were ash, white poplar, walnut and oak. Tree species for which the influence of ungulates (U) showed clear disadvantages compared to the exclusion of ungulates (F) were field maple, bird cherry, ashleaf maple, black locust and crab apple (Tab. 5). If ungulates are excluded by the fence, the trees are not browsed, but the lack of (selective) browsing and the faster height development of competitive tree species can result in disadvantages for less competitive tree species, mainly due to lack of light and competition for space.

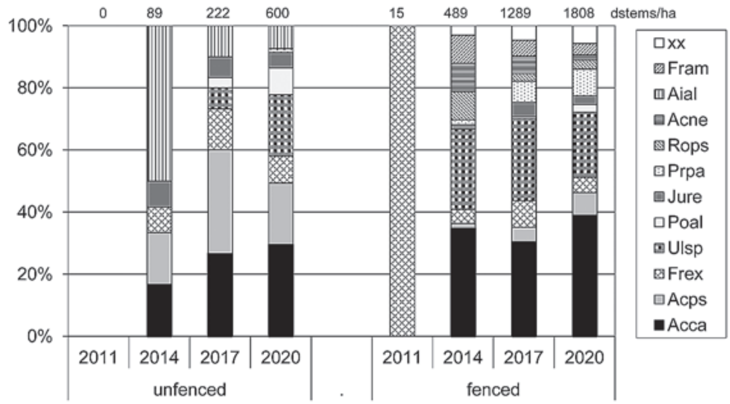

Fig. 5b: 2nd series (2011–2020), **height classes >200cm**. Tree species proportions (% of tree number) and UH-tree number per hectare (dstems/ha; figures above columns); unfenced area (left), fenced area (right). Names of species see Fig. 4a. – Abb. 5b: 2. Serie (2011–2020), **Höhenklassen >200cm**, Baumartenanteile (in %) und Oberhöhenstämmchen/ha (Ziffern oberhalb Säulen); ungezäunt (links) und gezäunt (rechts). Baumarten siehe Abb. 4a.

2nd series (1999–2019): In the last survey of the 2nd comparison-area series (2020) field maple occurred in 78 % of the comparison pairs (Tab. 5). This tree species was also the most frequently occurring species in the second series. In second place was the ash with 69 %, followed by elm (50 %), walnut (41 %), sycamore maple and bird cherry (39 % each), and white poplar (32 %), lime (13 %), and tree of heaven (11 %). The other tree species were found on less than 10 % of the comparison areas (Tab. 5). Also noticeable in the 2nd series was the relatively high constancy of the occurrence of walnut (41 %) and bird cherry (39 %) in comparison to their low proportion of tree numbers (<6 %, Tab. 4). These tree species are therefore very scattered. On one area (2 % of the comparison pairs) there was no young-tree growth, only shrubs were represented. In the first survey (2011), 2 areas (4 % of the area pairs) were without young trees. In 2011, the constancy of bird cherry and walnut was much lower than in 2020, while the constancy of ash, white poplar, Norway maple, ashleaf maple and hornbeam was much higher (Tab. 5). Tree species for which the influence of ungulates (U) showed clear advantages over ungulate exclusion (F) after 9 years were ash and white poplar, which also showed the same tendency in the first series, as well as tree of heaven. Tree species for which the influence of ungulates (U) showed significant disadvantages compared to ungulate exclusion (F) were up to now only the hornbeam (Tab. 5).

Browsing intensity on trees

To assess the browsing intensity, the terminal shoots of the 6 tallest trees of each species on the unfenced area are used. For the comparison of the development of the browsing pressure, trees under 11 cm high and over 130 cm are not taken into account in this evaluation step in order to determine the current browsing pressure in the preferred tree-height classes that are (still) reachable for top-twig browsing. The previous year's browsing (%), multiple browsing (%), and browsing index are used as indicators.

(i) Previous year browsing percentage (Bj) = proportion of trees (%) with browsing on the last leading shoot that was exposed to game for a whole year (annual browsing).

Tab. 5: Tree species constancy (% of the comparison areas with species occurrence), 1st series (70 area pairs), first survey 1999 and last survey 2019; as well as 2nd series (54 area pairs) first survey 2011 and last survey 2020; U = unfenced area, F = fenced area. – Tab. 5: Baumartenstetigkeit (% der Vergleichsflächen mit Vorkommen), 1. Serie (70 Flächenpaare), Ersterhebung 1999 und letzte Erhebung 2019; sowie 2. Serie (54 Flächenpaare), Ersterhebung 2011 und letzte Erhebung 2020.

Tree species	**1. Series**						**2. Series**					
	1. Survey **1999**			8. Survey **2019**			1. Survey **2011**			4. Survey **2020**		
	U	**F**	**Σ**	**U**	**F**	**Σ**	**U**	**F**	**Σ**	**U**	**F**	**Σ**
Field maple	66	61	*67*	66	69	*76*	74	78	*80*	70	74	*78*
Ash	63	63	*67*	39	29	*46*	74	74	*83*	61	43	*69*
Sycamore maple	29	24	*34*	27	26	*36*	33	35	*39*	33	32	*39*
Elm	31	29	*43*	27	27	*41*	35	35	*46*	33	37	*50*
White poplar	20	19	*24*	20	10	*21*	44	41	*48*	28	13	*32*
Bird cherry	13	21	*24*	4	24	*24*	13	24	*26*	19	32	*39*
Walnut	19	20	*24*	21	16	*26*	20	28	*35*	22	28	*41*
Norway maple	6	7	*9*	9	10	*11*	9	11	*13*	4	6	*6*
Oaks	3	3	*6*	3	0	*3*	4	7	*7*	6	9	*9*
Lime	6	4	*7*	4	4	*6*	9	6	*11*	9	4	*13*
American Ash				1	0	*1*	2	6	*6*	2	4	*4*
Ashleaf maple	11	7	*13*	4	4	*7*	15	11	*17*	6	6	*9*
Tree of heaven	4	4	*7*	3	3	*6*	4	6	*6*	9	2	*11*
Black locust	9	11	*13*	3	10	*11*	2	6	*6*	4	4	*7*
Crab apple	7	6	*10*	3	11	*13*	2	2	*4*	4	6	*7*
Hornbeam	3	6	*7*	3	1	*3*	9	7	*11*	2	4	*4*
Sweet cherry							4	4	*6*	2	4	*4*
Wild pear	1	3	*4*	1	0	*1*	0	2	*2*	2	2	*2*
Beech							2	2	*2*	2	2	*2*
Black poplar	3	3	*3*				4	2	*4*	2	0	*2*
Prunus sp.	6	6	*7*	4	1	*4*				0	2	*2*
Red pine	1	1	*1*							0	2	*2*
Black pine										0	2	*2*
Yew										0	2	*2*
Black walnut	0	1	*1*				2	0	*2*			
Chestnut				0	1	*1*						
Willow sp.	3	0	*3*									
Grey alder	0	1	*1*									

(ii) Multiple browsing percentage = proportion of trees (%) on which more than one leading shoot was browsed within the last 3 years.

(iii) Browsing index (BI) = multiple browsing percentage plus 50 % of the single browsing percentage (single browsing percentage = proportion of trees (%) with one leading shoot browsed within the last 3 years). The BI is used in the assessment of the impact of ungulates as an additional auxiliary indicator for the indicator of height increase, which can be expected to result in a lasting loss of height increase if browsing frequency remains constant (critical BI for deciduous tree species = 70, Tab. 2).

1st series (1999–2019): Taking into account the tree-height classes between 11 and 130 cm, the total annual browsing intensity (Bj) for all tree species was 55 % in the first survey (1999), as well as in the second survey (2001). Then it rose to 78 % (2004) and 80 %

(2007). Afterwards it decreased to 70 % (2010), further to 51 % (2013), 43 % (2016) and finally 11 % (2019). The browsing index (BI) showed a similar trend. The number of trees in the 11–130 cm height classes has recently decreased sharply because most trees were either taller after 20 years of growth or had already died due to competition in a lower height class (Tab. 6a).

2nd series (2011–2020: In the 2nd series of comparison areas, the two browsing indicators had a similar upward trend as in the 1st series up to the fourth survey; however, the browsing intensity was at a somewhat lower level (Tab. 6b).

In both series, field maple, Norway maple, ash, elm, oak and hornbeam were mostly much more browsed than sycamore maple, white poplar, walnut and lime (Tab. 6a, 6b).

When comparing the browsing intensity of foreign tree species (neophytes), which are undesirable in the national park, with that of the frequently occurring autochthonous tree species, it was noticeable that there was a selective preference for American ash and the ashleaf maple by the ungulates. The stronger browsing can result in competitive advantages for less intensely browsed tree species. In contrast, tree of heaven was not browsed, and black locust was little browsed, which can give these species competitive advantages over more intensely browsed tree species if no other growth-inhibiting factors (e.g., lack of light) are decisive.

For oak trees, which are characterizing species in the hardwood floodplain, it is interesting, that they are browsed intensely, and can be severely impaired in their height growth. But also without any browsing (fenced area) they have problems to develop, because of a stronger competition through other species (lack of light) within the fence. In the starting phase of regeneration, oaks seem to have an advantage from the ungulates due to their impact on the soil leading to better germinating acorns (cf. Tabs. 3a and b, 4a and b, 5).

Tab. 6a: 1st series. Annual browsing (Bj, tree-number %) and browsing index (BI) on upper-height trees 11–130 cm high on the unfenced area for the 8 surveys (1999–2019); n=number of trees recorded. – Tab. 6a: 1. Serie. Vorjahres-Verbissprozent (Bj) und Verbissindex (BI) an Oberhöhenbäumchen 11–130 cm Höhe auf ungezäunter Fläche für alle 8 Erhebungen (1999–2019); n=Anzahl erfasste Bäume.

Tree species	**1999**			**2001**		**2004**		**2007**		**2010**		**2013**		**2016**		**2019**		
	Bj	BI	*n*	B	BI	B	BI	B	BI	B	BI	B	BI	B	BI	B	BI	*n*
Field maple	64	51	*241*	64	58	87	79	90	89	78	80	64	63	51	52	19	17	*32*
Ash	59	48	*201*	61	53	89	80	88	87	72	73	63	64	49	50	11	11	*19*
White poplar	18	13	*45*	12	9	31	19	63	48	67	69	14	12	24	22	18	9	*17*
Elm	53	47	*58*	54	48	83	72	88	83	85	85	62	57	61	58	14	18	*14*
Sycamore maple	55	47	*71*	58	46	79	76	62	60	43	44	44	39	26	23	0	0	*9*
Walnut	60	54	*25*	10	15	21	19	56	69	24	32	30	25	33	28	0	0	*7*
Norway maple	77	53	*17*	80	80	100	83	73	64	74	68	26	37	14	7	0	0	*5*
Prunus sp.	80	60	*5*	67	50	58	54	100	100	100	100	100	100	0	0	0	0	*3*
Crab apple	50	58	*6*	62	62	40	30	13	13	69	70	64	63	0	0	0	0	*2*
Tree of heaven	0	0	*5*	0	0	0	0	0	0	25	25	0	0	0	0	0	0	*2*
Hornbeam	86	79	*7*	70	70	100	100	50	50	0	0	33	42	0	17	0	0	*1*
Oaks	100	75	*2*	30	25	50	25	67	67	33	46	57	36	0	25	0	0	*1*
Ashleaf maple	33	29	*24*	74	61	62	58	40	40	100	100	18	18	0	50	0	0	*1*
Bird cherry	48	46	*27*	52	44	75	63	100	96	77	69	64	73	33	33	0	0	*1*

Tree species	1999			2001		2004		2007		2010		2013		2016		2019		
	Bj	BI	*n*	B	BI	B	BI	B	BI	B	BI	B	BI	B	BI	B	BI	*n*
Lime	20	17	*15*	20	20	65	41	48	52	43	43	23	27	0	0			
Black locust	27	10	*15*	65	56	0	0	100	100	100	50	100	75					
Wild pear	100	50	*1*	100	83	100	100	0	0	100	50	100	50					
Black poplar	0	0	*6*	0	0													
Willow sp.	50	50	*2*															
TOTAL	55	45	*773*	55	49	78	69	80	78	70	71	51	50	43	43	11	10	*114*

Tab. 6b: 2nd series. Annual browsing (Bj, tree-number %) and browsing index (BI) on upper-height trees 11–130 cm high on the unfenced area for the 4 surveys (2011–2020); n=number of trees recorded. – Tab. 6b: 2. Serie. Vorjahres-Verbissprozent (Bj) und Verbissindex (BI) an Oberhöhenbäumchen 11–130 cm Höhe auf ungezäunter Fläche für alle 4 Erhebungen (2011–2020); n=Anzahl erfasste Bäume.

Tree species	2011			2014			2017			2020		
	Bj	BI	*n*	Bj	BI	*n*	Bj	BI	*n*	Bj	BI	*n*
Field maple	63	67	*188*	55	48	*213*	75	60	*195*	83	83	*138*
Ash	46	56	*192*	43	41	*161*	61	47	*137*	69	64	*119*
Sycamore maple	19	29	*98*	48	42	*79*	59	46	*69*	53	50	*60*
Elm	38	63	*58*	55	43	*69*	86	74	*65*	85	83	*33*
White poplar	18	28	*90*	27	17	*78*	70	65	*54*	64	61	*28*
Bird cherry	11	22	*18*	20	33	*20*	42	23	*26*	78	67	*23*
Walnut	6	9	*17*	5	8	*19*	13	9	*16*	15	8	*13*
Lime	17	42	*6*	0	33	*3*	33	50	*3*	75	63	*8*
Norway maple	21	18	*14*	32	34	*19*	63	18	*19*	50	75	*8*
Black locust	0	25	*4*	33	33	*3*	0	25	*2*	100	50	*7*
Beech	17	17	*6*	33	25	*6*	0	0	*6*	33	25	*6*
Ashleaf maple	53	71	*19*	63	55	*19*	90	63	*20*	100	83	*6*
American ash	83	83	*6*				42	21	*12*	100	92	*6*
Tree of heaven	0	0	*12*	0	0	*6*	0	0	*4*	0	0	*5*
Oaks	71	71	*7*	70	60	*10*	89	78	*9*	100	88	*4*
Crab apple	50	0	*2*	75	50	*4*	50	56	*8*	100	88	*4*
Sweet cherry	50	25	*2*	0	0	*2*	67	33	*3*	100	100	*2*
Hornbeam	55	41	*11*	58	38	*12*	67	83	*3*	100	50	*1*
Wild pear				0	0	*1*	100	50	*1*	100	100	*1*
Black walnut	0	0	*1*	0	0	*1*	0	0	*2*			
Black poplar	83	42	*6*									
TOTAL	40	49	*757*	45	39	*725*	66	52	*654*	71	68	*472*

Other impacts on young trees

Apart from browsing by ungulates, other inhibiting factors on forest regeneration were only noticed relatively rarely (a maximum of 13 % of the total number of trees, 2020, Fig. 6). Fraying by ungulates took place both in the 1st and in the 2nd series in the third survey, each around 4.0 %, which is much higher than in the first two surveys (Fig. 6). This is probably due to the already taller young trees with a higher fraying attractiveness. On the other hand, browsing by mice and hares was found mainly in the first surveys (smaller trees) and in years with an increased incidence of mice (Fig. 6). In 1999 (1st series), severe insect infestation was much more frequent than in the other surveys (Fig. 6). Clematis or hops were found to be inhibiting factors somewhat more often in the 1st series than in the 2nd series. Damage from frost was more pronounced in 2007 (Fig. 6). Ash dieback, which was only noticed in the 2nd series of comparison areas, was found in 5.7 % of the ash trees in 2014, 10.3 % in 2017 and 21.2 % in 2020. In the last three surveys of the 1st series (2013–2019), after a period of 14–20 years, other inhibiting factors were mainly dying trees due to a lack of light (stand-space competition in the thicket stage).

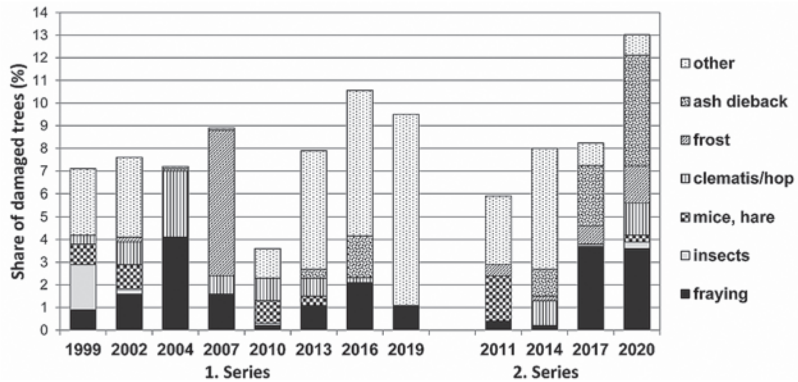

Fig. 6: Other inhibiting factors (tree-number %), 1st series (1999–2019) and 2nd series (2011–2020). – Abb. 6: Weitere Verjüngungshemmnisse (% Bäume), 1 Serie (1999–2019) und 2 Serie (2011–2020).

Impact of ungulates on shrub species

Constancy of shrub-species occurrence

In the 1st series of comparison area (1999–2019), 18 shrub species were found on the 70 pairs of comparison area in 2019; in 1999 there were 17 species (Tab. 7). Dewberry reached the greatest constancy of occurrence. In 2019 it occurred in 79 % of all pairs of comparison area (Tab. 7). Dogwood achieved 71 % constancy, followed by spindle (67 %) and hawthorn (49 %). In the 2nd series, beginning 12 years later (2011–2020), 18 shrub species were found on the 54 pairs of comparison areas in 2020, in 2011 there were 19 species (Tab. 7). The spindle achieved the greatest constancy in 2020 (80 %), followed by dewberry (72 %), hawthorn (65 %), and dogwood (63 %). In the 1st series there were shrubs on all pairs of comparison areas in both 1999 and 2019, in the 2nd series there were no shrubs on 2 pairs (4 %) at the beginning (2011), and in 2020 there were shrubs on all comparison areas.

When calculating the difference in constancy between unfenced and fenced areas (U-F) in the last survey and adjusting this difference by the initial difference in the first survey (see chapter 2.3) for the two comparison series, the following effects of the ungulate impact result (Tab. 7). The shrub species-promoting effects on the constancy of occurrence were found in both series for hazel (1st series +4 percentage points, and 2nd series +11pp), hawthorn (+3pp, +13pp and dewberry (+21pp +4pp), as well as for alder buckthorn (+6pp, only occurs in the 2nd series, Tab. 7). In contrast, the spread of the shrub species inhibited effects in both series resulted for ivy (–10pp, –11pp), spindle (–9pp, –13pp), elder (–4pp, –4pp) and wayfarer (–1pp, –2pp). For the other shrub species, the ungulate impact had an effect in different directions, depending on the series, or it had no effect on the constancy of occurrence (Tab. 7).

Tab. 7: Constancy of shrub-species occurrence (% of the comparison areas with species occurrence); 1st series (70 comparison pairs), first survey 1999 and last survey 2019; 2nd series (54 comparison pairs), first survey 2011 and last survey 2020. – Tab. 7: Stetigkeit des Strauchartenvorkommens (% der Flächenpaare mit Vorkommen der Art), 1. Serie (70 Vergleichsflächen), erste Erhebung 1999 und letzte Erhebung 2019; 2. Serie (54 Vergleichsflächen), erste Erhebung 2011 und letzte Erhebung 2020.

Shrub species	**1. Series**						**2. Series**					
	1999			2019			2011			2020		
	U	**F**	**Σ**	**U**	**F**	**Σ**	**U**	**F**	**Σ**	**U**	**F**	**Σ**
Dewberry, *Rubus caesius*	70	77	81	73	59	79	50	56	61	57	59	72
Spindle, *Euonymus europaeus*	49	66	70	39	64	67	69	70	78	56	70	80
Dogwood, *Cornus sanguinea*	49	46	61	59	61	71	44	48	57	50	54	63
Hawthorn, *Crataegus monogyna*	43	43	51	44	41	49	37	57	70	44	52	65
Elder, *Sambucus nigra*	31	30	44	23	26	39	37	35	44	31	33	46
Hazel, *Corylus avellana*	21	27	29	29	30	37	15	22	28	24	20	28
Privet, *Ligustrum vulgare*	14	16	21	20	17	24	24	17	26	22	17	28
Clematis, *Clematis vitalba*	13	16	20	7	16	19	7	11	13	28	31	39
Ivy, *Hedera helix*	13	14	20	16	27	31	2	2	2	11	22	26
Snowball, *Viburnum opulus*	7	10	11	0	3	3	4	6	7	0	2	2
Barberry, *Berberis vulgaris*	3	7	9	4	3	6	4	4	6	2	4	6
Dog rose, *Rosa canina*	3	7	9	3	0	3	2	2	2	4	6	9
Buckthorn, *Rhamnus cathartica*	3	1	3	1	1	3	2	2	2	2	4	6
Cornel, *Cornus mas*	1	1	3	1	4	4	2	2	2	2	4	6
Bladdernut, *Staphylea pinnata*	1	1	1	0	1	1	2	2	2	2	0	2
Honeysuckle, *Lonicera xylost.*	1	0	1	1	0	1						
Wayfarer, *Viburnum lantana*	1	0	1	1	1	3	4	0	4	4	2	4
Blackthorn, *Prunus spinosa*				0	3	3	0	2	2	4	6	6
Alder buckthorn, *Frangula alnus*							0	4	4	4	2	4
Currant, *Ribes sp.*							2	2	2			

Area coverage of shrub species

The highest overall arithmetic means of ground coverage (based on all comparison areas) were achieved in both series by dewberry and dogwood (Tab. 8). When calculating the difference in coverage between unfenced and fenced areas (U-F) in the last survey and adjusting this difference by the initial difference in the first survey (see chapter 2.3), following effects of ungulate impact result: Promoting effects on the coverage ratio were found in both series for dewberry (1st series +3.9 percentage points and 2nd series +3.6pp) and dog rose (+0.1pp, +0.2pp). On the other hand, inhibiting effects on the spread of shrub species in both series mainly resulted for spindle bush (–13.1pp, –6.5pp), ivy (–11.7pp, –5.0pp), elder (–1.6pp, –6.3pp), dogwood (–3.8pp, –3.0pp) and hawthorn (–1.6pp, –2.8pp). For the other shrub species, the ungulate impact had a predominantly inhibitory effect on the coverage ratio. Some species showed ambiguous effects, depending on the series (Tab. 8).

Height development of shrub species

The maximum heights of the shrub species on the comparison areas of their occurrence averaged between 12 cm and 150 cm in the first survey of the 1st series (1999), and between 5 cm and 155 cm in the first survey of the 2nd series (2011) (Tab. 8). When calculating the difference in the mean maximum heights between the unfenced area and the fenced area (U-F) in the last survey and adjusting this difference by the initial difference in the first survey (double difference B-A, see chapter 2.3), the following effects of ungulate impact result: In both series there were more or less inhibitory effects of the ungulates on the increase in height for all shrub species. In the 1st series (1999–2019), the mean loss in height, adjusted for the initial difference, on the unfenced area (compared to the fenced area) was greatest for spindle (–330 cm), followed by buckthorn (–285 cm), clematis (–262 cm), elder (–167 cm), dogwood (–164 cm) and hazel (–141 cm). In the 2nd series (2011–2020) the greatest difference in height was found in elder (–210 cm), followed by hazel (–207 cm), spindle (–204 cm) and dogwood (–111 cm).

Tab. 8: Mean ground coverage of shrub species (% - based on all areas), and average maximum height of shrub species (cm - based on the areas with occurrence of the concerned species, see Table 7) for the first and the last survey of both series; U=unfenced area, F=fenced area. – Tab. 8: Mittlerer Deckungsgrad der Straucharten (% - bezogen auf alle Fächen) und mittlere Maximalhöhe (bezogen auf die Flächen mit Vorkommen der betreffenden Art, sh. Tab 7) für die erste und letzte Erhebung beider Serien; U = ungzäunte Fläche, F = Zaunfläche.

Shrub species	1. Series								2. Series							
	Coverage (%)				Height (cm)				Coverage (%)				Height (cm)			
	1999		2019		1999		2019		2011		2020		2011		2020	
	U	F	U	F	U	F	U	F	U	F	U	F	U	F	U	F
Dewberry	13,8	13,6	16,7	12,6	55	57	48	56	8,4	11,8	19,4	19,3	38	37	46	50
Spindle bush	0,8	0,8	1,7	14,7	44	49	86	421	0,9	1,5	1,3	8,4	41	43	64	269
Dogwood	2,8	2,2	15,4	18,6	121	95	334	472	4,2	3,8	10,4	12,9	85	78	218	322
Hawthorn	1,7	1,1	5,6	6,6	71	86	211	283	0,8	1,0	1,0	4,1	59	57	123	177
Elder.	0,5	0,3	2,3	3,7	97	83	189	343	3,5	1,9	1,1	5,8	68	64	111	318
Hazel	0,2	0,5	3,8	5,6	66	87	263	425	0,4	0,8	1,0	1,8	155	75	189	316
Privet	0,7	0,4	2,7	3,0	66	91	135	240	0,8	0,8	2,4	2,0	63	83	142	182
Clematis	1,6	2,7	0,9	2,0	51	55	216	482	0,0	0,3	5,9	8,1	23	17	170	249
Ivy	1,2	1,4	1,5	13,4	12	12	8	21	0,7	0,7	0,1	5,2	5	5	8	9
Snowball	0,04	0,1	0,0	0,1	32	43	--	190	0,3	0,0	0,0	0,7	45	53	--	410
Barberry	0,05	0,04	0,5	0,3	90	78	170	190	0,0	0,02	0,01	0,1	60	93	40	165
Dog rose	0,01	0,04	0,1	0,0	30	45	145	--	0,01	0,0	0,3	0,1	70	50	130	223
Buckthorn	0,01	0,01	0,01	0,2	35	70	100	420	0,01	0,0	0,3	0,1	40	70	100	205
Cornel	0,2	0,01	0,01	0,3	150	120	400	390	0,0	0,01	0,1	0,1	70	40	80	330
Bladdernut	0,01	0,01	0,0	0,01	150	100	--	450	0,1	0,01	0,01	0,0	30	30	70	--
Honeysuckle	0,04	0,0	0,2	0,0	150	--	200	--								
Wayfarer	0,01	0,0	0,01	0,01	40	--	200	220	0,0	0,0	0,6	0,3	95	---	350	190
Blackthorn			0,0	0,2			--	240	0,0	0,01	0,3	0,4	---	90	200	150
Alder buckthorn									0,0	0,0	0,3	0,3	---	50	155	190
Currant									0,1	0,1			60	45	--	--

Browsing intensity on shrubs

To assess the browsing intensity for shrub and dwarf shrub species four browsing classes were built (estimate based on coverage of species): 0 - not browsed; 1 - up to 50 % of coverage browsed; 2–51–90 % browsed; more than 90 % browsed. The browsing from the past and the current year is considered as a common value. There is no browsing survey for *Rubus* species (raspberry, dewberry, etc.).

The mean total browsing on shrubs (all shrub species without dewberry; mean from browsing-percentage classes, browsing based on coverage ratio) was similarly high in both comparison series. In the 1st series at the beginning (1999) it was 31 %, then increased to

54 % by the fourth survey after 8 years (2007) and then decreased to 21 % by the seventh survey after 17 years (2016). In 2019, shrub browsing was no longer recorded. In the 2nd series, browsing was 48 % at the beginning (2011) and remained at about the same level until the fourth survey after 9 years (2020). The decrease of shrub browsing in the 1st series after 2007 is related to the longer duration of this series (20 years) and the advanced height development of the shrubs. Above all, spindle, elder and dogwood were severely browsed. In contrast, hawthorn, barberry and hazel were slightly browsed.

Impact of ungulates on the ground vegetation of the forest regeneration areas

The ground coverage of the various categories of ground vegetation was similar in both series of comparison areas, with the exception of the herbs, which in the 1st series showed a considerably higher coverage in the initial phase (Tab. 9).

1st series (1999–2019): If all plant species occurring on the respective regeneration areas are summarized (i.e. total ground vegetation up to 1.3 m height), the first survey (1999) resulted in an average coverage of 81 % on unfenced areas (U) and 82 % on the fenced areas (F); in the last survey (2019) the coverage on U was slightly lower (U 70 %, F 81 %; Tab. 9). Focused only on the woody vegetation (young trees, shrubs, dwarf shrubs and Rubus species), there was a clear increase from the first survey to the last survey. In the unfenced area (U) the coverage rose from 25 % to 49 %, in the fenced area (F) a little more from 26 % to 65 %. The influence of ungulates had a slightly positive effect on the coverage of herbs and grasses (Tab. 9). Mosses were only sparse, ferns were absent.

2nd series (2011–2020): For the categories "Total vegetation" and "Woody vegetation" there was a similar inhibiting effect of the ungulate impact as in the 1st series (double difference B-A, see chapter 2.3). In contrast to the 1st series, the influence of ungulates had an inhibiting effect on the area covered by herbs, and on grasses it had the same positive effect as in the 1st series (Tab. 9). Ferns and mosses were only sparse also in the 2nd series.

Tab. 9: Development of the mean coverage (area-%) for six categories of ground vegetation (up to 1.3 m in height) on unfenced (U) and fenced (F) areas; 1st and 2nd series of comparison area. – Tab. 9: Entwicklung des mittleren Deckungsgrades (Flächen-%) für sechs Kategorien der Bodenvegetation (bis 1,3 m Höhe) auf nicht eingezäunten (U) und eingezäunten (F) Flächen; 1. und 2. Serie der Vergleichsflächen.

Vegetation category	1. Series				2. Series			
	1999		2019		2011		2020	
	U	F	U	F	U	F	U	F
Total vegetation	81	82	70	81	73	73	75	85
Woody vegetation	25	26	49	65	31	31	58	73
Herbs	62	63	39	26	21	16	37	43
Grasses	16	16	13	7	16	16	22	16
Ferns	0	0	0	0	0	0	0	0,1
Mosses	4	6	3	2	9	12	6	8

Canopy density (light conditions for the forest regeneration)

1st series (1999–2019): At the beginning (1999), 63 % of all of comparison-area pairs were densely covered by the crowns of older trees (i.e., canopy cover >75 % of the related horizontal ground projection area). 20 % were moderately covered (51–75 %), 10 % slightly

(1–50 %), and 7 % were open area without canopy cover. Up to the last survey (2019), the canopy cover decreased considerably: 53 % were heavily covered, 26 % moderately, 13 % slightly, and 8 % had no canopy cover.

2nd series (2011–2020): At the beginning (2011), the light conditions were very similar to those at the beginning of the 1st series. 2011: 63 % were heavily covered, 20 % moderately, 9 % little, and 8 % were without canopy cover. Up to the last survey (2020) the canopy had increased somewhat in contrast to the 1st series: 61 % were heavily covered, 29 % moderately, 6 % little, and 4 % were without canopy cover.

Assessment of the ungulate impact based on the predefined benchmarks

The assessment of the ungulate impact on forest regeneration was carried out using a "benchmark–actual–comparison", whereby predefined benchmarks (BM), depending on the forest community, were compared with the current states of forest regeneration on each pair of the unfenced vs. fenced comparison areas (for the indicators and benchmarks see Tab. 2). Four assessment categories were distinguished: "Benchmark reached" (BM +), "Benchmark not achieved" (BM-), "Benchmarks partially achieved and partially not achieved" (BM±), "No influence on reaching benchmarks" (BM0).

BM+: Benchmark attainment was only possible through the influence of ungulates.
BM-: Benchmark not achieved due to ungulates.
BM±: Different impacts depending on the indicator.
BM0: No influence of ungulates on reaching benchmarks.

1. Series (1999–2019, Fig. 7a): In 2019, after a 20-year observation period, BM+ occurred on 13 % of the comparison areas, BM- on 39 %, BM± on 14 %, and BM0 on 34 %. The course over the survey intervals is shown in Fig. 7a: "BM+" 7, 7, 9, 6, 10, 11 and last (2019) 13 %; "BM-" 16, 33, 44, 39, 46, 46 and last 39 %. The balance of "BM +" minus "BM-" after 20 years of ungulate impact results in 26 % BM- (13–39 %).

2. Series (2011–2020, Fig. 7b): In 2019, after a 9-year observation period, BM+ occurred on 17 % of the comparison areas, BM- on 46 %, BM± on 4 %, and BM0 on 33 %. The course over the survey intervals is shown in Fig. 7b: "BM+" 15, 13, and last (2020) 17 %; "BM-" 26, 50, and last 46 %. The balance of "BM +" minus "BM-" after 9 years of ungulate impact results in 29 % BM- (17–46 %). Compared with the 1st series, in the 2nd series BM+ as well as BM- was somewhat higher, and BM± lower. Overall, both series showed a similar impact of ungulates on forest regeneration related to the benchmarks.

Forest communities (softwood and hardwood floodplain)

1st series (*1999–2019):* When evaluating the comparison plots according to the forest community, the result is a "BM+" to "BM-" ratio of 18 to 12 for softwood-floodplain sites, and 12 to 49 for hardwood-floodplain sites (Fig. 8). So in the softwood-floodplain there is a predominance of "BM+", in the hardwood-floodplain, however, of "BM-".

2nd series (*2011–2020):* For the 2nd series, the result is a "BM+" to "BM-" ratio of 23 to 15 for softwood-floodplain sites and 17 to 57 for hardwood-floodplain sites (Fig. 8). Same as in the 1st series, in the softwood-floodplain there is a minor predominance of "BM+", whereas in the hardwood floodplain "BM-" predominates considerably.

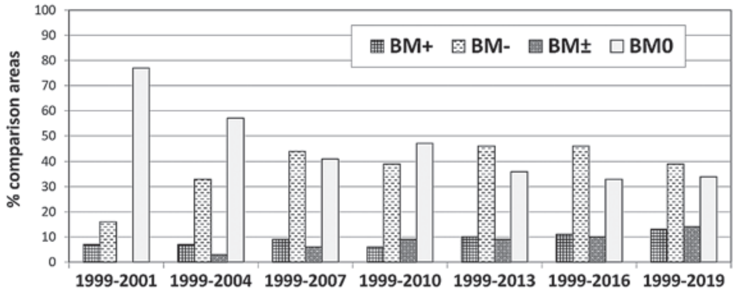

Fig. 7a: Assessment of the ungulate impact based on the predefined benchmarks after 2, 5, 8, 11, 14, 17 and 20 years (1st series, 1999–2019). Benchmark reached due to ungulate impact (BM+); benchmark not achieved due to ungulate impacts (BM-); benchmarks partially achieved and partially not achieved (BM±) = different ungulate impacts depending on the indicator; no influence of ungulates on reaching benchmarks (BM0). – Abb. 7a: Beurteilung des Huftiereinflusses aufgrund der vorgegebenen Richtwerte nach 2, 5, 8, 11, 14, 17 und 20 Jahren (1. Serie, 1999–2019).

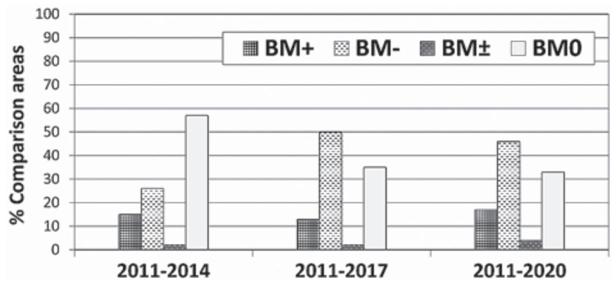

Fig. 7b: Assessment of the ungulate impact based on the predefined benchmarks after 3, 6 and 9 years (2nd series, 2011–2020). Benchmark reached due to ungulate impact (BM+); benchmark not achieved due to ungulate impacts (BM-); benchmarks partially achieved and partially not achieved (BM±) = different ungulate impacts depending on the indicator; no influence of ungulates on reaching benchmarks (BM0). – Abb. 7b: Beurteilung des Huftiereinflusses aufgrund der vorgegebenen Richtwerte nach 3, 6 und 9 Jahren (2. Serie, 2011–2020).

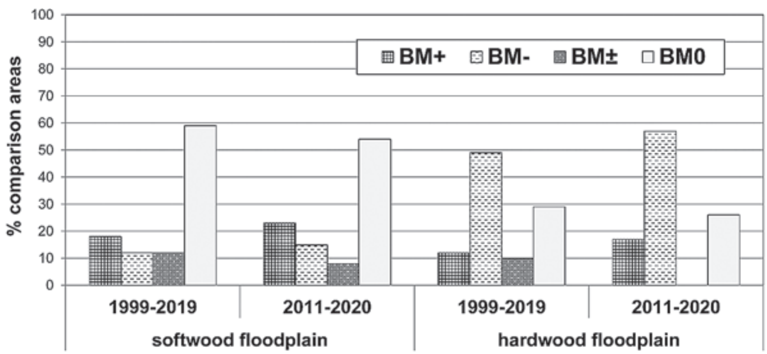

Fig. 8: Assessment of the ungulate impacts separated into softwood floodplain and hardwood floodplain; 1st series 1999–2019, 2nd series 2011–2020. Benchmark reached due to ungulate impact (BM+); benchmark not achieved due to ungulate impacts (BM-); benchmarks partially achieved and partially not achieved (BM±) = different ungulate impacts depending on the indicator; no influence of ungulates on reaching benchmarks (BM0). – Abb. 8: Beurteilung des Huftiereinflusses getrennt nach Weiche Au und Harte Au, jeweils für 1. Serie (1999–2019) und 2. Serie (2011–2020).

Individual indicators

1st series: Of the different indicators (cf. Tab. 2), in the 1st series (1999–2019, 20 years) for the occurrence of an undesirable impact (BM-), primarily the loss of tree-height increment was effective (44 % of cases), followed by the number of tree species (14 %) and the total tree density (13 %). For the occurrence of a desired effect (BM+), the number of tree species (16 %) was most effective, followed by additional tree-height increment (13 %) and total density of trees (9 %). The other criterions were not or only rarely decisive in the assessment of the impact of ungulates (Tab. 10).

2nd series: In the 2nd series (2011–2020, 9 years) for the occurrence of an undesirable impact (BM-), same as 1st series loss of tree-height increment was primarily effective (44 % of cases). For the occurrence of a desired effect (BM+), additional tree-height increment (15 %) was mostly effective (Tab. 10).

Tab. 10: Ungulate impact (% of cases) according to individual indicators (cf. Table 2); left 1st series (1999–2019), right 2nd series (2011–2020). Benchmark reached due to ungulate impact (BM+), Benchmark not achieved due to ungulate impact (BM-). – Tab. 10: Huftiereinfluss (% der Fälle) nach einzelnen Prüfkriterien (vgl. Tab. 2); links 1. Serie (1999–2019), rechts 2. Serie (2011–2020).

Individual indicators	1999–2019		2011–2020	
	BM-	BM+	BM-	BM+
Total regeneration density of trees	13	9	0	6
Mixture type of trees	0	0	0	0
Density of key-tree species	1	0	7	0
Total number of tree species	14	16	4	6
Height increment of key-tree species	44	13	44	15
Shrub volume index	0	0	4	0
Number of shrub species	0	1	4	0

Ungulate impact on the biodiversity of tree and shrub species

The impact of ungulates on the biodiversity of tree and shrub species after 20 years of exposure to ungulates (1st series of comparison areas) and after 9 years of exposure (2nd series) was represented using several biodiversity indices (richness, Shannon index, evenness, Gini-Simpson index) and calculating the mean values from the comparison areas. Unwanted neophytes (ashleaf maple, silver maple, black locust, tree of heaven, black walnut, American ash) were not taken into account. The development of the woody species inside and outside the fence was compared (difference U-Z at the time of the last survey), and this final difference was adjusted by the initial difference that was already present when the comparison areas were set up (calculation of the double difference, cf. chapter 2.3).

1st series of comparison pairs (1999–2019): For the entire comparison period (20 years), the ungulate impact on the four biodiversity indices can be classified as slightly negative for both tree and shrub species (Tab. 11). For woody species as a whole (trees + shrubs together) there was also a slightly negative impact (Richness –0.05, Shannon VI –0.24, Evenness VI –0.11, Gini-Simpson VI –0.10; Tab. 11).

2nd series of comparison pairs (2011–2020): For the 9-year study period of the 2nd series, overall (all indices) there was up to now no clear impact of ungulates on the biodiversity of tree species. Slightly positive values were obtained for the indicators Richness (+0.18), Shannon index SZ (+0.07) and Gini-Simpson index SZ (+0.02). In the case of the shrub species, the ungulate impact had a negative effect on all indices (Tab. 11). If tree and shrub species are combined, the result was a positive ungulate impact for Richness and a negative impact for the other indicators.

If the indices are not calculated as a mean value from the individual comparison area indices, but all comparison areas are taken as a total area and added up, then in the 1st series the biodiversity indices for tree species and trees plus shrubs together resulted mostly in positive effects due to the ungulate impact (Tab. 12).

Tab. 11: Impact of ungulates on the biodiversity of tree and shrub species based on various biodiversity indices (**mean values from the single pairs of comparison areas**), 1st and 2nd comparison series, duration of the exposure to ungulates 20 and 9 years, respectively; TN = tree number, AC = area coverage (shrubs), VI = volume index (TN or AC x height). – Tab. 11: Auswirkungen von Huftieren auf die Biodiversität von Baum- und Straucharten anhand verschiedener Biodiversitätsindizes (Mittelwerte aus den einzelnen Vergleichsflächenpaaren), 1. und 2. Vergleichsserie, Expositionsdauer gegenüber Huftieren 20 bzw. 9 Jahre; TN = Baumanzahl, AC = Flächendeckung (Sträucher), VI = Volumenindex (TN oder AC x Höhe).

Biodiversity index	**1. Series (1999 – 2019)**			**2. Series (2011 – 2020)**		
	Trees	**Shrubs**	**Trees + Shrubs**	**Trees**	**Shrubs**	**Trees + Shrubs**
Richness	–0,06	0,01	–0,05	0,18	–0,04	0,14
Shannon VI	–0,10	–0,10	–0,24	0,00	–0,18	–0,22
Shannon TN/AC	–0,03	–0,08		0,07	–0,22	
Evenness VI	–0,11	–0,09	–0,11	–0,07	–0,15	–0,13
Evenness TN/AC	0,01	–0,06		–0,03	–0,16	
Gini-Simpson VI	–0,06	–0,07	–0,10	–0,02	–0,09	–0,10
Gini-Simpson TN/AC	–0,01	–0,04		0,02	–0,12	

Tab. 12: Impact of ungulates on the biodiversity of tree and shrub species based on various biodiversity indices (**comparison areas summed up as one area**), 1st and 2nd comparison series, duration of the exposure to ungulates 20 and 9 years, respectively; TN = tree number, AC = area coverage (shrubs), VI = volume index (TN or AC x height). – Tab. 12: Auswirkungen von Huftieren auf die Biodiversität von Baum- und Straucharten anhand verschiedener Biodiversitätsindizes (Vergleichsflächen als eine Gesamtfläche betrachtet), 1. und 2. Vergleichsserie, Expositionsdauer gegenüber Huftieren 20 bzw. 9 Jahre; TN = Baumanzahl, AC = Flächendeckung (Sträucher), VI = Volumenindex (TN oder AC x Höhe).

Biodiversity index	**1. Series (1999–2019)**			**2. Series (2011–2020)**		
	Trees	**Shrubs**	**Trees + Shrubs**	**Trees**	**Shrubs**	**Trees + Shrubs**
Richness	3,00	–3,00	0,00	–2	1	–1
Shannon VI	0,37	–0,19	0,38	–0,16	–0,17	–0,17
Shannon TN/AC	0,02	–0,25		0,00	–0,29	
Evenness VI	0,09	–0,03	0,10	–0,04	–0,08	–0,05
Evenness TN/AC	–0,04	–0,03		0,01	–0,13	
Gini-Simpson VI	0,17	–0,07	0,17	0,02	–0,08	0,17
Gini-Simpson TN/AC	0,03	–0,04		0,03	–0,07	

Discussion and conclusion

In the present study, solely the impact of ungulates on the floodplain forest vegetation was investigated, depending on the specific impact intensity during the last 20 years. The consequences of this specific impact for the other parts of the ecosystem (small mammals, insects, soil, altering competition between ungulate species, etc.) and the total biodiversity are unknown yet. Particularly ruminating ungulates change the competitiveness of the plant species due to their selective browsing of certain plant species. The resulting change in plant species composition subsequently affects all other organisms that are dependent on plants, and the entire biocenosis. In the Swiss National Park (located in the mountains) the impact of the ungulates increased the diversity in all communities, the producers, primary consumers, secondary consumers, and the destructors (Schütz et al. 2020).

With their decisive influence on the interactions in plant communities, ungulates lead to "winners" and "losers" within the plant species. In general, if the preferred browsed species ("losers") are the dominant ones in the forest community and are still present despite the selective browsing, the winners are the rare species and the ungulate impact can increase the biodiversity. However, if seldom occurring species are browsed preferentially ("losers") and abundant trees become even more dominant, then the biodiversity decreases.

A further handicap for the detailed interpretation of the study results arises from the fact, that the species group "ungulates" is seen as a "black box", since it remains unknown which ungulate species contribute to which extent to the observed results and how interactions between species can alter the results. The effects of the occurring ungulates on vegetation and soil can vary depending on the ungulate species (and also its population density) and act in different directions. For example, wild boars have the characteristic of digging up the forest floor while looking for food, while ruminating ungulates concentrate more on the browsing of the shoots of trees and shrubs, whereby each species selects differently. In view of these complex and dynamic interactions in the ecosystem, numerous questions remain unanswered about the specific causes of ungulate-related dynamics in the national park, which can be further investigated step by step in the future.

National parks are well suited for long-term projects to investigate the factors influencing developments in forest ecosystems. In connection with the influence of wild ungulates on the ecosystem, the question arises whether there may be limits for the maximum ungulate impact on vegetation in a national park. The population dynamics of ungulates do not depend solely on the processes in a national park. Due to the mobility and the daily and seasonal change of location of the animals, the management in the surroundings of the protected area also plays an important role. This is particularly true of the Donau-Auen National Park, due to its narrow, elongated shape and the dominance of intensely managed agricultural landscape patches in the surroundings.

In a worldwide comparison of protected areas (particularly national parks), three basic types can be identified with regard to the ungulate impact tolerated by humans on forest vegetation (Reimoser 2001, 2002); impact of ungulates means effects such as seed dispersal, seed consumption, shoot browsing, tree fraying, bark peeling, trampling and soil digging that lead to changes in forest growth, biodiversity etc.:

a) Protected areas in which the independent development of ungulate populations has priority over the development of certain potential forest communities. There is no regulation of ungulate populations within the protected area in favor of certain plant communities (common in North America and Africa, in Europe e.g. the Swiss National Park).

b) Protected areas in which the development of certain forest communities has priority over the free development of ungulate populations. A regulation of ungulate populations within the protected area is mandatory (common e.g. in Germany).

c) Protected areas in which the development of ungulate populations and the development of certain forms of forest vegetation are basically equally important. Regulation of ungulate populations within the protected area is optional. The extent to which the population is regulated by shooting depends on the exceeding of certain tolerance limits for the impact of wild animals on vegetation (common e.g. in Austria).

For Austria, a uniform regulation on ungulate-browsing tolerance limits according to the third type of protected areas (equal importance for ungulates and forest vegetation) was proposed for national parks (Reimoser 2001, 2002). From this, benchmarks were derived for the Donau-Auen National Park, which, in contrast to the forestry guidelines in managed forests, allow the vegetation structure to be shaped by ungulates on parts of the national parks forest. However, this should not result in any unacceptable burdens in agriculture and forestry for the surroundings of the national park with which the ungulates are connected.

The evaluation of the investigations in the Donau-Auen National Park, which have been ongoing for 20 years, revealed clear differences in the development of young forests with the impact of ungulates (unfenced areas) compared with the development of forests with the exclusion of ungulates (fenced areas). However, the effects have so far been in an acceptable range for the national park. Most of the negative as well as positive effects caused by ungulates, measured against the various benchmarks, resulted from the influence on the increase in height of the tree species. An influence on the occurrence of tree species, in particular a sufficient number of key tree species, as well as on the required regeneration density, however, was only rarely effective.

With regard to the biodiversity of tree and shrub species (richness, Shannon index, evenness, Gini-Simpson index), overall (subsuming all indices) there has been no clear impact of ungulates on the biodiversity of tree species. In the case of the shrub species, the ungulate influence had a negative effect on almost all indices in both series.

Conclusion: According to the existing objectives of the national park, the influence of ungulate species on forest vegetation can be classified as compatible with the park for the period investigated. The authors are not aware of any serious damage caused by ungulates in the vicinity of the national park, which would require a reduction in the ungulate population. Differentiated according to softwood and hardwood floodplains, and according to parts of the park (north bank, south bank), distinct differences were found in the effects of ungulates on forest vegetation.

Outlook: In order to be able to continue to investigate the effects of the current impact of ungulates on forest regeneration, a new series of comparison areas was created in 2020 (64 pairs of comparison areas). The first results from this third series, which should depict the current influence of ungulates, are to be expected after the first repeat survey (2023).

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