CHAPTER 7

EFFECTS OF WEATHER VARIABILITY AND GEESE ON POPULATION DYNAMICS OF LARGE HERBIVORES CREATING OPPORTUNITIES FOR WOOD-PASTURE CYCLES.

Koen Kramer, Perry Cornelissen, Geert W.T.A. Groot Bruinderink, Loek Kuiters, Dennis Lammertsma, J. Theo Vulink, Sip E. van Wieren, Herbert H.T. Prins

Summary

Coexistence of large herbivores and vegetation heterogeneity is a challenge for managers of relatively small and homogeneous nature reserves in fragmented landscapes. A modelling analysis was performed to study if observed variability in weather conditions would be of sufficient magnitude to maintain long-term coexistence of large herbivore species, and to provide windows of opportunity for the establishment of thorny shrubs as predicted by the wood-pasture hypothesis. The study was applied to the Oostvaardersplassen nature reserve in the Netherlands, which has a large herbivore assemblage of Heck cattle, Konik horse and red deer. Owing to the fact that a large number of geese frequent the nature reserve, the effects of these small herbivores were taken into account in the model analyses. The results showed that weather variability increases population fluctuations and that geese reduce large herbivore numbers. The results also indicated that coexistence of the three large herbivore species is possible irrespective of weather variability and geese. However, the chances for the coexistence of cattle with the other large herbivores are reduced when weather is highly variable and geese numbers are high. If the management of large nature reserves aims at natural processes with assemblages of self-regulating large herbivore populations, our results show that weather variability and the presence of small competing herbivores may be essential factors in highly productive environments for the wood-pasture cycle creating a more heterogeneous landscape.

Introduction

Inspired by contemporary natural or near-natural grazing systems in Africa and North America as well as by past Pleistocene and Holocene ecosystems, (re-)introduction of wild large herbivores has recently gotten much attention (Caro and Sherman 2009; Jackson and Hobbs 2009; Huynh 2011; Navarro and Pereira 2012; Rey Benayas et al. 2009). The aim of this new management strategy is to restore historical ecosystems or increase biodiversity. In Western Europe, apart from wild herbivores, domestic cattle and horses as substitutes for their wild ancestors, are also introduced (WallisDeVries et al. 1998; Hodder and Bullock 2009). In our fragmented landscapes (Lindenmayer and Fisher 2006), these wild and domestic large herbivores are often introduced in relatively small reserves with fences to keep them inside and with large predators mostly absent. Under such conditions, the large herbivore populations are mainly regulated by food supply and winter conditions (Coulson et al. 2001). Although this management system is practiced the last 30 years in some European countries, little is known about population dynamics of the large herbivores and the effects on the environment in the long term (McCann 2007). In this paper we describe the possible long term population dynamics of large herbivores and effects on the environment by means of a process-based model. The model was applied to one of the first areas in Europe where a multi-species assemblage of large herbivores was introduced, the Oostvaardersplassen nature reserve in the Netherlands.

In the eutrophic wetland the Oostvaardersplassen (OVP), an assemblage of cattle, horses and red deer was introduced in the 1980s. The area is fenced and animal numbers are not controlled at fixed stocking rates, but individual large herbivores considered to have no chance of survival are culled in order to prevent unnecessary suffering. The large herbivores do not get supplementary feeding. Large predators are absent and the reserve is visited every year by thousands of geese. A few years after introduction, populations of the large herbivores grew exponentially and after these first years the growth rate levelled off and numbers reached a maximum. Corresponding with the increased herbivore population, the vegetation changed from a heterogeneous mixture of grasslands, tall herbs, reed, scrub and trees to a homogeneous vegetation dominated by grasslands (Cornelissen et al. 2014a). Over the last 10 years the population of cattle has decreased, whereas the populations of horses and red deer and also the total number of geese have increased. As the vegetation becomes more dominated by short grazed grasslands, competition among the different large herbivore species becomes more severe (Putman 1996; Menard et al. 2002). It can be envisaged that this competition would lead to exclusion of the less competitive species. In this case, cattle could be outcompeted by the other large herbivores and geese because cattle cannot graze on short swards as the other herbivores can (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Bos et al. 2005).

Even in situations with potential for competition there are possible mechanisms whereby the large herbivores involved may coexist (Putman 1996). In heterogeneous areas with abundant forage alternatives, resource partitioning may lead to the coexistence of competing species (De Boer and Prins 1990; Putman 1996; Stewart et al. 2002; Kleynhans et al. 2011) as one of the species can change its diet and habitat use towards the forage alternatives in other habitats. Another mechanism is based upon disturbances which can reduce the population numbers of all herbivores or of the dominant competitor(s), such as climatic variation, predation, pests and diseases (Coulson et al. 2001; Sinclair et al. 2003; Hopcraft et al. 2010). Reduction of large herbivore numbers will lead to an increase in the amount of forage per capita for all species, enabling the competing species to coexist.

A reduction of large herbivore numbers is also an essential component of the wood-pasture hypothesis (Vera 2000), which attributes a key-role to large herbivores. High numbers of large herbivores may assist the transition of woodland to grassland by browsing and bark stripping which causes mortality of shrubs and trees (Gill 2006). Simultaneously the large herbivores maintain short-grazed grasslands and therefore provide opportunities for the re-establishment of shrubs and trees in these natural 'pastures'. However, the (re-)establishment of thorny shrubs and eventually trees in these grasslands, require a temporary reduction of the herbivore densities for a sufficient duration (Cornelissen et al. 2014a; Smit et al. 2015).

In this study we are interested in the effects of long term weather variability and geese on large herbivores and vegetation development. For this purpose we used the model FORSPACE (see Model description) and long term weather data of the past. The questions addressed in this study are: A) Is the weather variability strong enough to disrupt population numbers of large herbivores so that they can coexist? B) Can geese reduce large herbivore numbers through competition, as they can graze the sward to even lower heights than the large herbivores? C) Does a temporary reduction in large herbivore numbers provide windows of opportunity for woody species to establish?

No analyses with respect to climate change was performed in the present study.

Material and Methods

Research area

The OVP-area (52°26' N, 5°19'E) is a eutrophic wetland of about 5,600 ha in Zuidelijk Flevoland polder in the Netherlands, reclaimed from lake IJsselmeer in 1968. As the area was a former lake, the bottom consists of soils with clay contents between 30-35%. Three habitat types can be distinguished in the research area: grasslands *(Poa trivialis* L.*, Lolium perenne* L.*, Trifolium repens* L. as dominant species), reed vegetation (*Phragmites australis* (Cav.) Steud.) and a semi-open mosaic vegetation of reed, tall herbs (*Urtica dioica* L.*, Cirsium* spp. Mill.), elder (*Sambucus nigra* L.) and willow (*Salix* spp.) (Jans and Drost 1995). Most of the willow species, predominantly white willow (*Salix alba* L.), established on the bare soil primarily in 1968/1969, after the water was pumped out of the polder and the surface area became dry. Elder established some years later and establishment occurred over a longer period from the early 1970s until the early 1990s. Elder produces *cyanogenic glucosides* (Atkinson and Atkinson 2002) which can be toxic or lethal (Majak and Hale 2001). Ruminants can counteract the effects of toxic compounds better than hindgut fermenters (Van Soest 1994), which was shown by Vulink (2001) for the Oostvaardersplassen.

Cattle, horses and red deer were introduced into the OVP-area in different years: 32 Heck cattle (*Bos taurus* L.) in 1983, 18 Konik horses (*Equus caballus* L.) in 1984, and 52 red deer (*Cervus elaphus* L.) in 1992. In January 2015, about 250 cattle, 1200 horses and 3200 red deer were present. The populations of the large herbivores were counted annually. The most important geese in the OVP-area are Greylag geese (*Anser anser* L.) and Barnacle geese (*Branta leucopsis* L.). Geese were counted every week along a fixed route along the grasslands. Annual average numbers of geese per observation day increased from about 3,000 in 1996 to about 10,000 in 2014. Both species are present throughout the year with maximum numbers during winter and spring.

Model description

We used the spatial-explicit and process-based model FORSPACE, which describes the feedbacks between vegetation development and herbivore density (Kramer et al. 2003; Kramer et al. 2006) (Fig. 1). In the model, plant populations are characterized by the density of plants, the weight of the different plant components, and their structural properties. These variables are calculated for each tree-, shrub-, herb- or grass species. Ungulate populations are described by the weight and number of both juvenile and adult cohorts for each ungulate species. The technical description of the model including sensitivity analyses and validation is presented Kramer (2001). The model is implemented in the dynamic GIS PC-Raster (Wesseling 1996).

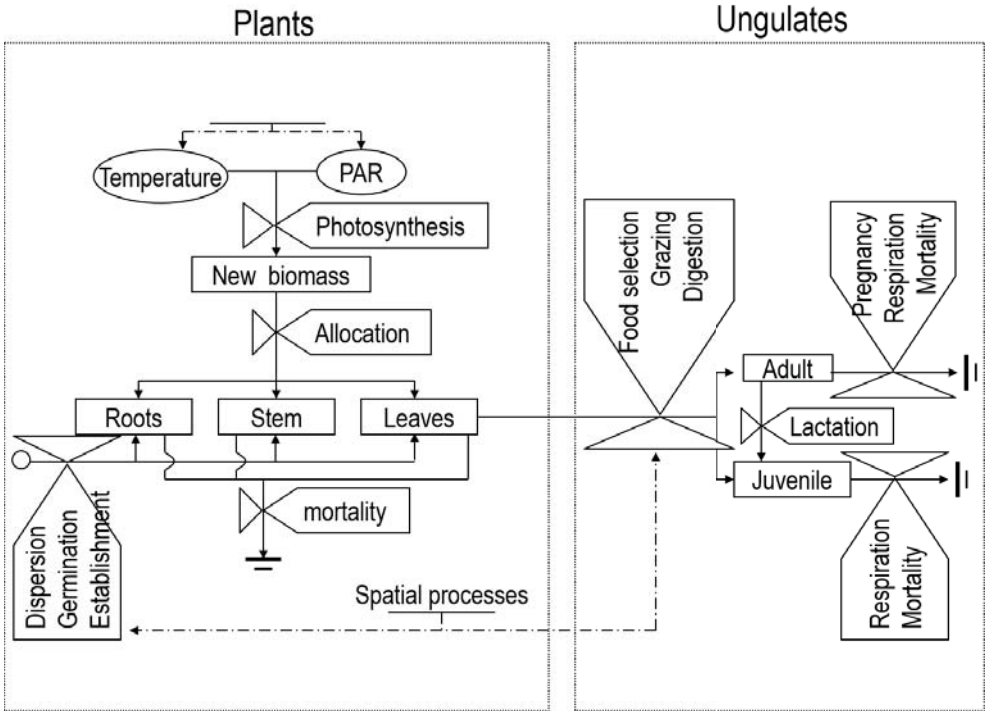

Fig. 1. Flow diagram showing the principal processes and flow of information between plants and ungulates in the model FORSPACE.

To apply the FORSPACE model to the OVP-area, it was necessary to make adjustments with respect to a number of processes that are specific for this area. The model adjustment considers the following issues: (*i*) observed meteorological time series of temperature, radiation, and snow cover were used instead of statistically generated time series of these meteorological variables used in the FORSPACE model. The weather data of the weather station De Bilt of the Royal Dutch Meteorological Institute (KNMI) in the Netherlands of the past 110 years was used as data collection started in 1901. This station is situated 38 km from the OVP-area. Snow cover is defined as the fraction of the month where the vegetation is covered with snow. It is assumed that the herbivores have no access to the plants as long as there is snow cover, even though we know that this is a rather narrow assumption. (*ii*) Large numbers of moulting and wintering geese visit the OVP-area year-round consuming a substantial part of the annual net primary production. The intake of the vegetation is described in the same way as that of the large herbivores. However, the population dynamics of the geese are not simulated because we assume that their population dynamics are largely determined by external factors such as the food availability outside the OVP-area (Van Eerden 1998). In the model analyses we compared two geese scenarios: no geese, and high geese densities. The high geese densities are comparable to the geese numbers that visited the OVP-area during the past five years. During days with snow cover or mean daily temperature below 0^{o} C, the number of visiting geese is set to zero as under such conditions the geese journey to warmer areas without snow cover. (*iii*) The parameter values of the woody species willow and elder were adjusted, using measurements of growth and development on these species at the OVP-area (Cornelissen et al. 2014 a, b). (*iv*) The plant functional type of 'thorny shrubs' was added, exemplified in the area by hawthorn (*Crataegus monogyna* Jacq). All large herbivores induce mortality of hawthorn by bark peeling. Bark peeling related mortality is a specific process that cannot be described generically. Therefore, an empirical approach for this particular process and species was taken, valid for this area only. This effect is brought in the model by an increased turnover of the number of individuals of hawthorn if the total herbivore numbers exceeds 800 animals. This number is comparable to the total number of large herbivores in 1996. Before this year new establishments of woody species were seen on aerial photographs (Cornelissen et al. 2014b) and after this year no new establishments were seen on photographs and no seedlings of woody species were found in the field (Cornelissen et al. 2014a, b). We define occurrence of thorny shrubs as the presence of hawthorn and of palatable shrubs as the presence of willow and elder exceeding 1.5 m in height. It is assumed in the model that from that height onward the large herbivores do not affect the height of the thorny shrubs. However, the height of the other shrubs can be reduced, until the plant exceeds the herbivore specific maximum browsing height. This difference between thorny shrubs and non-thorny, palatable shrubs was brought into the model because hawthorn can develop a shoot in the centre of the shrub that is beyond reach of animals even though the shrub itself is below the browsing height of the animal. That process of a central leader shoot escaping browsing is not present in the willow or elder considered. (*v*) The effect of winter temperature on survival of the large herbivores is simulated by an increase of maintenance cost of the large herbivores if the average monthly temperature drops below 0°C. There is little information available in the literature on the magnitude of the enhancement of maintenance respiration with decreasing freezing temperatures. Therefore, the model was calibrated assuming that each herbivore species in the model survived the most severe winter in the period 1901-2013. This assumption is based on the absence of evidence in the literature that wild herbivore populations got extinct due to severe winters in any large nature reserve in Northwest Europe during this period.

Validation

A model versus data comparison was performed between the observed and predicted number of herbivores over the period 1996-2013 based on the adjusted parameter values. We used 1996 as a starting point as from that year on the total area was grazed by cattle, horses and red deer. The actual number of geese and the observed weather data for this period were applied for this validation. The model results in a close match between observed and simulated numbers of the three large herbivore species, although Heck-cattle is over-estimated by the model whereas red deer is under-estimated (Fig. 2). The decrease in number of Heck cattle over time is most likely a result of competition among herbivores as the sward height of the grasslands of the OVP-area (Cornelissen et al. 2014c) decreased below minimum grazing height for cattle. In our model the minimum grazing height for cattle was set at 5 cm (Menard et al. 2002). Konik horse, red deer and geese can graze more efficiently on swards below 5 cm than cattle (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Durand et al. 2003; Bos et al. 2005; Cope et al. 2005). In the model the minimum grazing height for horses and red deer was set at 2 cm. For geese, a minimum grazing height was used of 1 cm (Durand et al. 2003; Cope et al. 2005). In the model, it is assumed that geese, as specialist grazers (e.g. Aerts et al. 1996; Owen 1979), only graze on grasses, not on any of the other plant species in the herb layer.

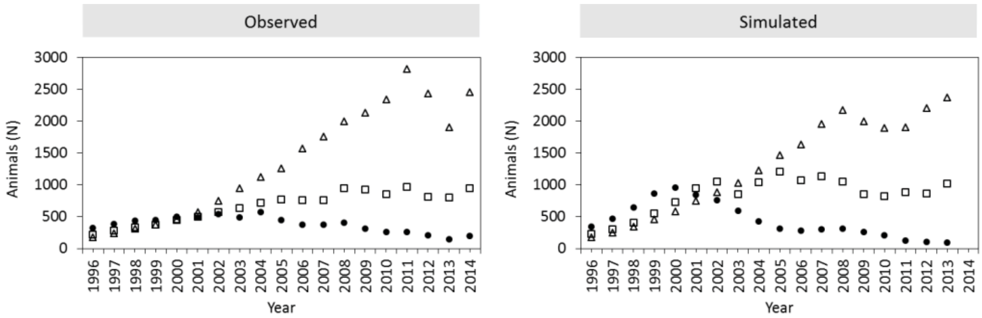

Fig. 2. Model versus data comparison with respect to dynamics in numbers of large herbivores. Left graph shows the observed numbers of animals of 1 year and older on May 1 of each year; right graph shows the results of the model. Black circles are Heck cattle; open squares are Konik horses; open triangles are Red deer.

Model runs
A number of scenario analyses was performed to answer the questions posed for this study. All combinations of these scenarios were evaluated with respect to: (i) Dynamics of the large herbivore populations; (ii) Effects of geese on large herbivore numbers; (iii) Opportunities for thorny or palatable shrubs to establish and grow to a size that prevents direct removal by the herbivores. These scenarios included:

a. Variable versus constant weather, to assess the effects of weather variability. The temperature series for the scenario with variable weather were based on weather time series for the period 1901–2013. For the scenario analyses with constant weather, monthly averages over the period 1901-2013 were used for: temperature, incoming radiation, snow cover, and the duration of the growing season, based on the variable weather series.
b. High geese density versus no geese, to assess the effects of the presence of geese. The high geese densities are comparable to the geese numbers that visited the OVP-area during the past five years.
c. All large herbivore species versus no large herbivore species, to assess the effects of large herbivores on the opportunities for woody species to establish and grow.

We used the animal numbers and the vegetation map of the year 1996 as a starting point for our model runs. From that year on, the whole area was grazed by the large herbivores.

Results

Animal numbers were affected by weather and geese (Fig. 3). Weather variability led to higher maximum and lower minimum population numbers and therefore increased fluctuations in animal numbers compared to the constant weather scenarios (Fig. 3). Reductions in animal numbers were closely associated with the occurrence of severe winters. Geese were responsible for decreased numbers of the large herbivores and the absolute fluctuations. The weather and geese also affected relative fluctuations (Fig. 4). The relative increase and decrease, i.e. the change of the population number over one year given as a percentage of the population number at the beginning of that year, were much greater in the variable weather scenarios. It was also greater in the scenarios with geese, but the effect of geese was less pronounced than that of the weather. The three large herbivores species continued to coexist in all weather and geese scenarios over a period of 110 years (Fig. 3). However, the number of Heck cattle occasionally became very low in the scenario with variable weather combined with high geese densities.

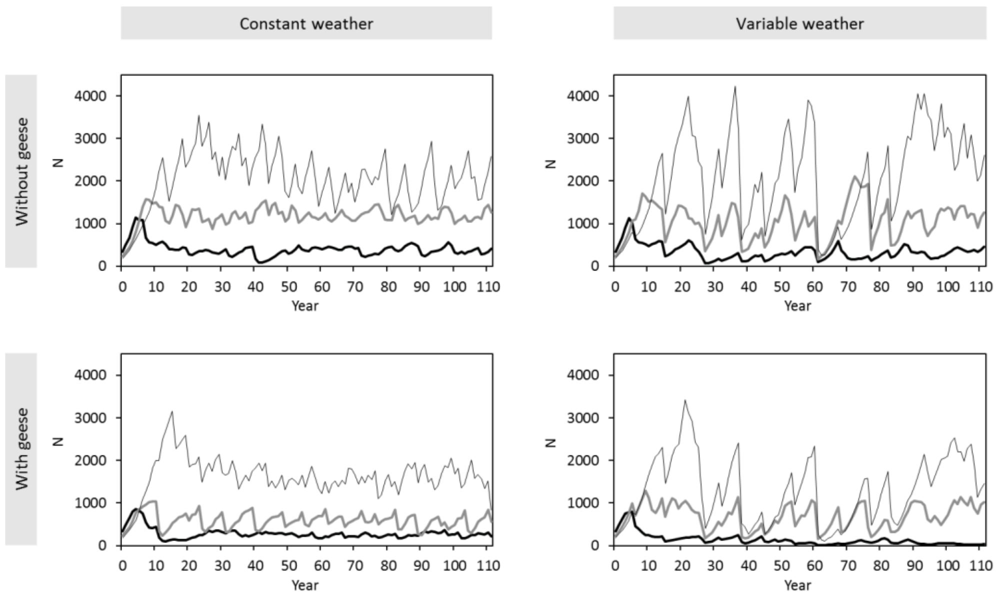

Fig. 3. Population dynamics in numbers of the populations of Heck cattle (thick black line), Konik horse (thick grey line) and Red deer (thin black line) in the scenarios with constant and variable weather, and without and with geese.

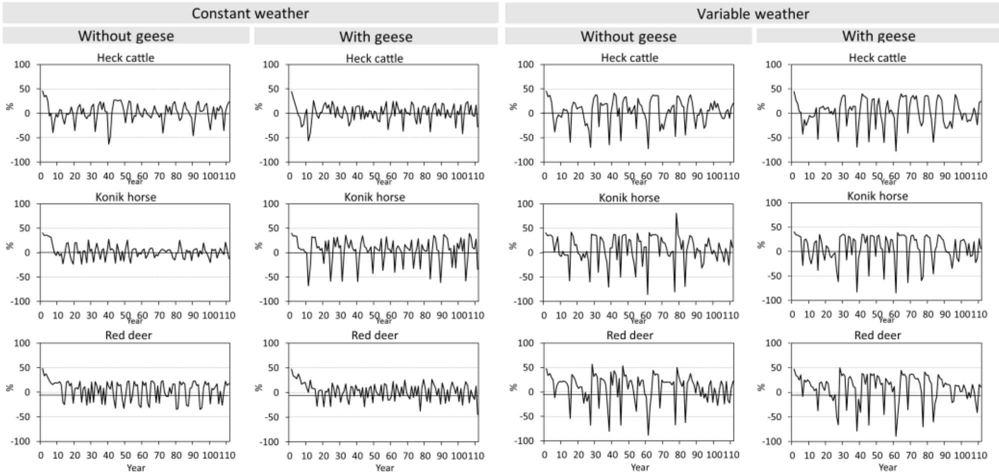

Fig. 4. Relative increase and decrease of the populations of Heck cattle, Konik horse and Red deer in the scenarios with constant and variable weather, and without and with geese. The increase or decrease is the change of the population number over one year given as a percentage of the population number at the beginning of that year.

Weather and geese directly and indirectly affected development of woody species (Fig. 5 and 6). The scenarios without large herbivores (Fig. 5) showed that weather variability and absence of geese led to slightly higher cover of woody species compared to scenarios with constant weather and presence of geese. In these scenarios without herbivores, the area was not covered totally by woody species. When large herbivores are absent, tall herbs and tall grasses start to dominate the vegetation, making it difficult for the woody species used in the model, to establish later on. As weather and geese affected large herbivore numbers (Fig. 3), both factors also indirectly influenced the development of woody species through the number of large herbivores. In general, the effects of the large herbivores on the development of woody species were much greater than the direct effects of weather and geese (Fig. 5 and 6). For the scenarios with all large herbivores (Fig. 6), the greatest opportunities for the establishment of woody species arose with variable weather and with geese and the smallest with constant weather and without geese. The thorny shrub hawthorn only established with variable weather and with geese, elder only with variable weather and willow established under all conditions. In the scenario with variable weather and with geese, hawthorn established twice (after two periods with the most severe winters), whereas the other two species established more frequently. But once established, hawthorn started to dominate the woody vegetation. The moments hawthorn established corresponded with a total large herbivore number of less than 800 animals which occurred for more than four years in a row (Fig. 3).

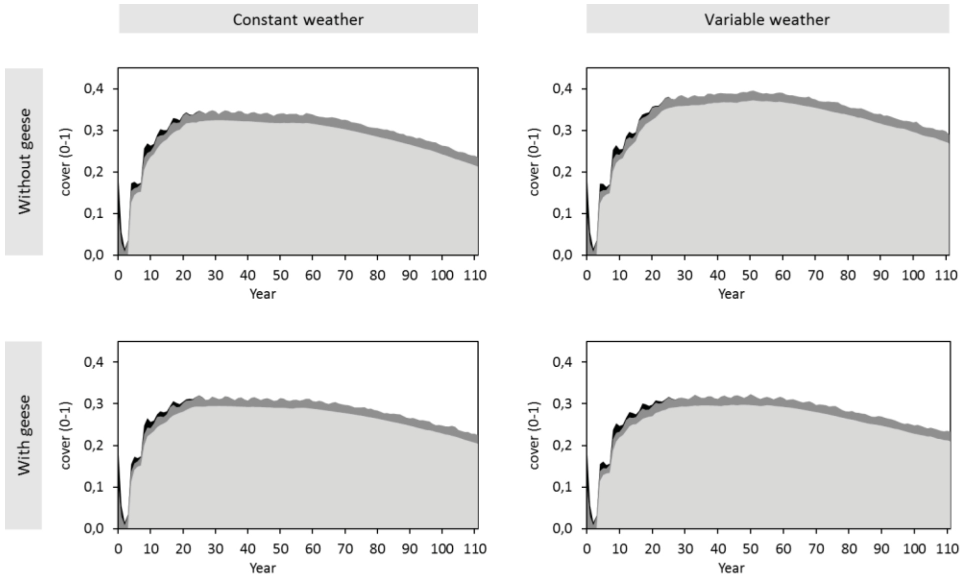

Fig. 5. Dynamics of hawthorn (light grey), willow (dark grey) and elder (black), exceeding 1.5m in height in the scenario without the assemblage of Heck cattle, Konik horses and Red deer, for constant and variable weather and without and with geese. Cover is presented as a proportion between 0-1.

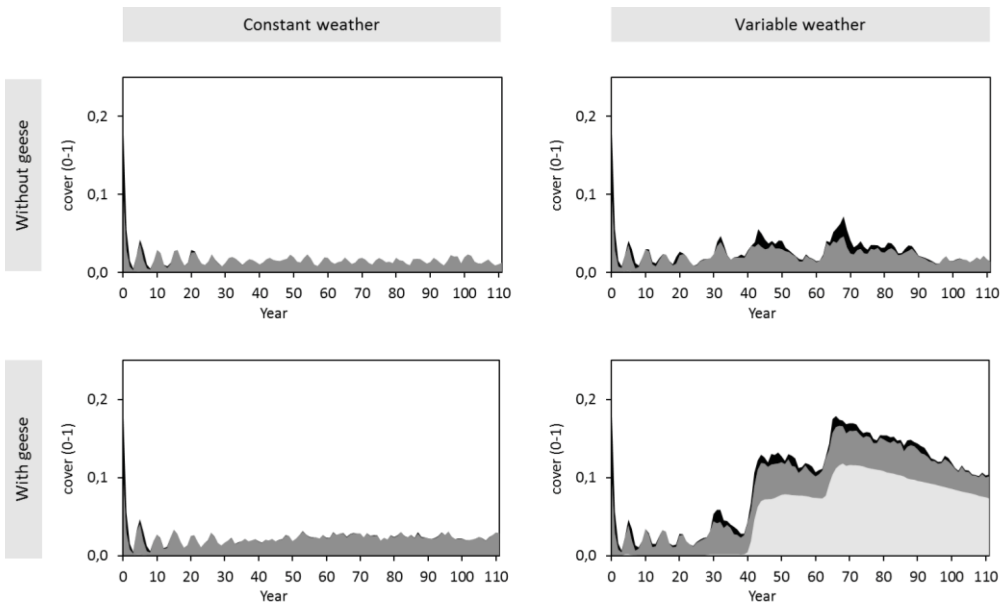

Fig. 6. Dynamics of hawthorn (light grey), willow (dark grey) and elder (black), exceeding 1.5 m in height in the scenario with the assemblage of Heck cattle, Konik horses and Red deer (see fig. 2), for constant and variable weather and without and with geese. Cover is presented as a proportion between 0-1.

Discussion

Few process-based models exist that are able to simulate the long-term dynamics of herbivore-vegetation interactions at a spatially explicit base (Bugmann 2003; Fontes et al. 2010). To understand those dynamics and how they are affected by weather variability and the presence of other herbivores such as geese, the model FORSPACE was applied for this purpose at the OVP-area (Groot Bruinderink et al. 1998). For this area a number of processes needed to be added to the general model, such as impact of geese, mortality of hawthorn due to bark peeling, and the impact of severe winters on maintenance requirements of the large herbivores. Empirical and area-specific data were taken for those processes. After adding these processes, we can conclude that the model represents the observed dynamics in herbivore numbers sufficiently well to allow model-based scenario analyses for a highly productive area as the OVP-area.

The model results showed that weather variability disrupts population numbers of large herbivores. As a result of these large decreases, food supply per capita increases. This creates opportunities for coexistence. However, coexistence was also possible in the scenarios with constant weather. In these scenarios it was expected that cattle, as the less competitive herbivore species, was not able to coexist with Konik horse, red deer and high numbers of geese. Under conditions where horses and red deer populations are not substantially reduced by severe winters, sward height of the grasslands will be too low for cattle. When the weather is constant, population numbers also fluctuate but much less than in the variable weather scenarios. The population fluctuations in the constant weather scenarios were caused by the consequences of the ever changing age distribution within the populations, which results in annual variation in mortality; and by the differences among the large herbivores with regard to years of increase and decrease of the populations, which causes differences in the strength of competition and therefore variable mortality and reproduction. Although fluctuations of animal numbers in the constant weather scenarios were much less than in the variable weather scenarios, these fluctuations might have been strong enough to create opportunities for the coexistence of the three large herbivores.

Geese substantially decreased large herbivore numbers (Fig 3). By closely harvesting the regrowth on the short grazed grasslands during winter and spring, they are strong competitors. During this period net primary production is still low and the thousands of geese can keep the sward very short (<2 cm). As cattle prefer sward heights between 9-16 cm (Menard et al. 2002) whereas horses, red deer and geese can efficiently graze on swards below 5 cm (Clutton-Brock et al. 1982; Illius and Gordon 1987; Vickery and Gill 1999; Menard et al. 2002; Durand et al. 2003; Bos et al. 2005; Cope et al. 2005), cattle will be the first species to experience the negative consequences of competition.

The model results showed that only variable weather and presence of high numbers of geese provides windows of opportunity for thorny shrubs to establish (Fig. 6). These two factors caused major decreases in large herbivore numbers needed for thorny shrub encroachment. Cornelissen et al. (2014a, b) showed that in the OVP-area the large herbivores can transform woody vegetation into grasslands, whereas woody species only established at low herbivore densities (<0.5 animals ha^{-1}). Smit et al. (2015) conclude that large herbivores can create wood-pasture landscapes as long as grazing refuges are present. However, if the large herbivore numbers are high, the grazing refuges will not be present (Cornelissen et al. 2014b). Negative effects of high herbivore numbers on the establishment of woody species are also reported in many other studies (see Gill 2006). Our results agree with these findings that effectively no wood-pasture cycling is possible when large herbivore species are present in high numbers without periods with very low animal densities due to fluctuations in weather conditions, diseases or other factors. However, apart from the effects of weather, high numbers of geese are also a prerequisite for the low numbers of large herbivores needed. Small herbivores also affect establishment of woody species (e.g. Kuiters and Slim 2003; Bakker et al. 2004), but these are all direct effects of the small herbivores on the woody species through browsing or debarking. In our study the effect of the geese on the establishment of woody species is not direct but indirect through competition. Geese will damage young and small seedlings in the very short grazed grasslands. However, in the highly productive OVP-area, the geese cannot keep the swards short without the large herbivores and the height of the vegetation will increase. Vulink (2001) showed that geese prefer to feed on intensively grazed, highly nutritious, short swards. As higher swards are less nutritious than shorter ones, these swards become less attractive to geese and they are eventually avoided. It is during this temporary (in our model at least 4 years) reduction of large herbivores numbers that chances increase for woody species to establish and grow. The model shows that this window of opportunity for thorny woody species only happened twice during a period of 110 years, resulting in distinct cohorts of plants as was also described by Prins and Van der Jeugd (1993) for Acacia in Lake Manyara National Park in Tanzania.

In our model, geese play a key role in the dry zone of the eutrophic wetland the OVP-area with regard to wood encroachment and the creation of a heterogeneous landscape. Apart from their key role in the dry zone, geese also play an important key role in the marsh zone of the OVP-area (Vulink and Van Eerden 1998). Moulting greylag geese have a great impact on the development of the reed vegetation in the marsh creating a diverse habitat, benefiting many other animal species. However, geese cannot fulfil their key role within the eutrophic wetland without the presence of two important factors. Within the marsh it is the water level dynamics that is necessary for the recovery of the grazed reed vegetation (see Vulink and Van Eerden 1998 for a detailed description). Within the dry zone it is the populations of large herbivores which facilitate the geese by creating large scale short grazed grasslands.

Although coexistence of the three large herbivores occurred in all scenarios, the chances for cattle in a highly productive homogeneous area are reduced with increasing weather variability and when geese numbers are high. A strong decrease in a small population has a greater impact on the survival of a large herbivore species than in a large population. A strong decrease in a small population can lower the numbers to such an extent that the population cannot reproduce anymore as for example all males die. In sexual dimorphic species, such as cattle and red deer, mortality of males is greater than of females (Clutton-Brock et al. 1982; Georgiadis 1985) especially when food becomes limited (Toïgo and Gaillard 2003) or winters are more severe (Clutton-Brock et al. 1982). As mortality of male cattle and red deer of the OVP-area is also higher than female mortality (unpublished data), this possibility is likely to occur when populations of cattle or red deer become small. This means that the size or the productivity of an area (i.e. the fenced nature reserve) are important factors in the survival of a population as smaller or less productive areas can contain fewer animals. In our modified landscapes with habitat sub-division, degradation and loss (Fischer and Lindenmayer 2007) resulting in small fragmented areas for nature conservation, coexistence of large (introduced) herbivores in these small, isolated and less heterogeneous areas can become difficult. Apart from temporal variation in environmental factors such as weather, resource partitioning may also be a possible mechanism whereby the large herbivores involved may coexist (De Boer and Prins 1990; Putman 1996; Stewart et al. 2002; Kleynhans et al. 2011). Increasing heterogeneity in homogenous areas such as the OVP-area, resulting in abundant forage alternatives, may lead to resource partitioning. Increasing heterogeneity can be achieved by carrying out measures such as planting shrubs and trees, or creating wet areas with reed vegetation. Another option is to increase the area of the homogenous nature reserve using adjacent areas with other habitat types, or to create corridors to other areas with other habitat types further away (Gilbert-Norton et al. 2010). As an extension of the homogenous nature reserve may lead to an increase in total heterogeneity (and therefore resource partitioning), distribution of the large herbivores over the area may alter. This could change the chances for the establishment and survival of shrubs and trees in the original, homogenous nature reserve, benefitting the wood-pasture cycle and enhancing the overall heterogeneity. Enlarging and connecting nature reserves to create better opportunities for large herbivores and wood-pasture cycles, also benefits biodiversity to a great extent as landscape modification and habitat fragmentation are key drivers of global species loss (Hanski 2005; Fischer and Lindenmayer 2007).

References

Aerts, B.A., Esselink, P., Helder, G.J.F. 1996. Habitat selection and diet composition of Greylag Geese Anser anser and Barnacle geese Branta leucopsis during fall and spring staging in relation to management in the tidal marshes of the Dollard. Zeitschrift für Ökologie und Naturschutz, 5, 65-75.

Atkinson, M.D., Atkinson, E. 2002. Sambucus nigra L. Journal of Ecology, 90, 895-923.

Bakker, E.S., Olff, H., VandenBerghe, C., De Maeyer, K., Smit, R. Gleichman, J.M., Vera, F.W.M. 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. Journal of Applied Ecology, 41, 571-582.

Bos, D., Loonen, M.J.J.E., Stock, M., Hofeditz, F., Van der Graaf, A.J., Bakker, J.P. 2005. Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. Journal for Nature Conservation, 13, 1-15.

Bugmann, H.P.J.W., Weisberg, P.J. 2003. Forest-Ungulate Interactions: Monitoring, Modeling and Management. Journal of Nature Conservation, 10, 193-201

Caro, T., Sherman, P. 2009. Rewilding can cause rather than solve ecological problems. Nature, 462, 985.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. 1982. Red deer. Behavior and Ecology of two sexes. The University of Chicago Press, Chicago.

Cope, D.R., Loonen, M.J.J.E., Rowcliffe, J.M., Pettifor, R.A. 2005. Large barnacle geese (Branta leucopsis) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. Journal of the Zoological Society of Londen, 265, 37-42.

Cornelissen, P., Bokdam, J., Sykora, K., Berendse, F. 2014a. Effects of large herbivores on wood pasture dynamics in a European wetland system. Basic and Applied Ecology, 15, 396-406.

Cornelissen, P., Gresnigt, M.C., Vermeulen, R.A., Bokdam, J., Smit, R. 2014b. Transition of a Sambucus nigra L. dominated woody vegetation into grassland by a multi-species herbivore assemblage. Journal for Nature Conservation, 22, 84-92.

Cornelissen, P., Kuipers, J., Dekker, J., Beemster, N. 2014c. Vegetatie, grote herbivoren, vogels en recreatie in de Oostvaardersplassen. Monitoring mei 2013 – apr 2014. Staatsbosbeheer, Deventer, The Netherlands.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M. Clutton-Brock. T.H., Crawley, M.J., Grenfell, B.T. 2001. Age, sex, density, winter weather, and populations crashes in Soay sheep. Science, 292, 1528-1531.

De Boer, W.F., Prins, H.H.T. 1990. Large herbivores that strive mightily but eat and drink as friends. Oecologia, 82, 264-274.

Durant, D., Fritz, H., Blais, S., Duncan, P. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. Journal of Animal Ecology, 72, 220-231.

Fischer, J., Lindenmayer, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography, 16, 265-280.

Fontes, L.,Bontemps, J.D., Bugmann, H.,Van Oijen, M., Gracia, C., Kramer, K., Lindner, M., Rötzer, T., Skovsgaard, J.P. 2010. Models for supporting forest management in a changing environment. Forest Systems, 3, 8-29.

Georgiadis, N. 1985. Growth patterns, sexual dimorphism and reproduction in African ruminants. African Journal of Ecology, 23, 75-87.

Gilbert-Norton, L., Wilson, R., Stevens, J.R., Beard, K.H. 2010. A meta-analytic review of corridor effectiveness. Conservation Biology, 24, 660-668

Gill, R. 2006. The influence of large herbivores on tree recruitment and forest dynamics. Large herbivore ecology, ecosytem dynamics and conservation (eds J. Danell, R. Bergström, P. Duncan & J. Pastor), pp. 170-202. Cambridge UK. Cambridge University Press.

Groot Bruinderink, G.W.T.A., Lammertsma, D.R., Kramer, K., Baveco, J.M., Kuiters, A.T., Cornelissen, P., Vulink, J.T., Prins, H.H.T., Van Wieren, S.E., De Roder, F.E., Wigbels, V. 1998. Draagkracht van de Oostvaardersplassen voor grote herbivoren. Deel 1 Concept en beschrijving van het model. Intern rapport IBN-DLO, Wageningen.

Hanski, I. 2005. Landscape fragmentation, biodiversity loss and the societal response. EMBO reports 6, 388-392.

Hodder, K.H., Buckland, P.C., Kirby K.J., Bullock, J.M. (2009) Can the pre-Neolithic provide suitable models for re-wilding the landscape in Britain? British Wildlife, 20, 4-15.

Hodder, K.H., Bullock. J.M. 2009. Really wild? Naturalistic grazing in modern landscapes. British Wildlife, 20, 37-43.

Hopcraft, J.G.C., Olff, H., Sinclair, A.R.E. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution, 25, 119-128.

Huynh, H.M. 2011. Pleistocene re-wilding is unsound conservation practice. Bioessays, 33, 100-102.

Illius, A.W., Gordon, I.J. 1987. The allometry of food intake in grazing ruminants. Journal of Applied Ecology, 56, 989-999.

Jackson, S.T., R.J. Hobbs. 2009. Ecological restoration in the light of ecological history. Science. 325:567-569.

Jans, L., Drost, H.J. 1995. De Oostvaardersplassen. 25 jaar vegetatieonderzoek. Flevobericht nr. 382. Rijkswaterstaat Directie IJsselmeergebied, Lelystad The Netherlands.

Kleynhans, E.J., Jolles. A.E., Bos, M.R.E., Olff, H. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. Oikos, 120, 591-600.
Kramer, K., Groen, T.A., Van Wieren, S.E. 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. Forest Ecology and Management, 181, 205-222.
Kramer, K., Groot Bruinderink, G.W.T.A., Prins, H.H.T. 2006. Spatial interactions between ungulate herbivory and forest management. Forest Ecology and Management, 226, 238-247.
Kramer, K., Baveco, H., Bijlsma, R.J., Clerkx, A.P.P.M., Dam, J., Van Goethem, J., Groen, T.A., Groot Bruinderink, G.W.T.A., Jorritsma, I.T.M., Kalkhoven, J., Kuiters, A.T., Lammertsma, D., Prins, R.A., Sanders, M., Wegman, R., Van Wieren. S.E., Wijdeven, S., Van der Wijngaart, R. 2001. Landscape forming processes and diversity of forested landscapes: description and application of the model FORSPACE. Alterra, Wageningen, The Netherlands. http://library.wur.nl/WebQuery/wurpubs/fulltext/17351.
Kuiters, A.T., Slim, P.A. .2003. Tree colonisation of abandoned arable land after 27 years of horse-grazing: the role of bramble as a facilitator of oak wood regeneration. Forest Ecology and Management, 181, 239-251.
Lindenmayer, D.B., Fischer, J. 2006. Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press, Washington USA.
Majak, W., Hale, M. 2001. Toxic glycosides in rangeland and pasture forages: What they are and what they do. Anti-quality facotrs in rangeland and pature land forages (ed K. Launchback) pp. 48-53. USDA Natural Resouces Conservation Service, University of Idaho.
McCann, K. 2007. Protecting biostructure. Nature, 446, 29-29.
Menard, C., Duncan, P., Fleurance, G., Georges, J-Y., Lila, M. 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. Journal of Applied Ecology, 39, 120-133.
Navarro, L.M., Pereira, H.M. 2012. Rewilding abandoned landscapes in Europe. Ecosystems, 15, 900-912.
Owen, M. (1978) Food selection in Geese. Verhandlungen der Ornitologischen Gesellschaft Bayern, 23, 169-176.
Prins, H.H.T., Van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. Journal of Ecology, 81, 305-314.
Putman, R.J. 1996. Competition & resource partitioning in temperate ungulate assemblies. Chapman & Hall, London.
Rey Benayas, J.M., Newton, A.C., Diaz, A., Bullock, J.M. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science, 325, 1121-1124.
Sinclair, A.R.E., Mduma, S., Brashares, J.S. 2003. Patterns of predation in a diverse predator-prey system. Nature, 425, 288-290.
Smit, C., Ruifrok, J.L., Van Klink, R., Olff, H. .2015. Rewilding with large herbivores: The importance of grazing refuges for sapling establishment and wood-pasture formation. Biological Conservation, 182, 134-142.
Stewart, K.M., Bowyer, R.T., Kie, J.G., Cimon, N.J., Johnson, B.K. 2002. Temporal distribution of elk, mule deer and cattle: resource partitioning and competitive displacement. Journal of Mammalogy, 83, 229-244.

Toïgo, C., Gaillard, J.M. 2003. Causes of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? Oikos, 101, 376-384.
Vera, F.W.M. 2000. Grazing ecology and forest history. CAB International, Oxford, UK.
Vickery, J.A., Gill, J.A. 1999. Managing grassland for wild geesei n Britain: a review. Biological Conservation, 89, 93-106.
Van Eerden, M.R. 1998. Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. PhD thesis, University of Groningen, Groningen, The Netherlands.
Van Soest, P.J. 1994. Nutritional ecology of the rumiant (2nd ed.). Ithaca, New York. Cornell University Press.
Van Wieren, S.E. 1991. The management of populations of large mammals. The scientific management of temperate communities for conservation. (eds I.F. Spellerberg, F.B. Goldsmith & M.G. Morris), pp. 103-127. Blackwell. Oxford, UK.
Vulink, J.T. 2001. Hungry herds. Management of temperate lowland wetlands by grazing. PhD thesis University of Groningen, Groningen, The Netherlands.
Vulink, J.T., Van Eerden, M.R. 1998. Hydrological conditions and herbivory as key operators for ecosystem development in Dutch artificial wetlands. Grazing and conservation managment (eds M.F. WallisDeVries, J.P. Bakker & S.E. Van Wieren), pp 217-252. Kluwer Academic Publishers, Dordrecht The Netherlands.
WallisDeVries, M.F., Bakker, J.P., S.E. Van Wieren 1998. Grazing and conservation management. Kluwer Academic Publishers, Dordrecht The Netherlands.
Wesseling, C.G., Karssenberg, D., Van Deursen, W.P.A., Burrough, P.A. 1996. Integrating dynamic environmental models in GIS: the development of a Dynamic Modelling language. Transactions in GIS, 1, 40-48.