MSC ECOLOGY & CONSERVATION RESEARCH PROJECT REPORT

Modelling and visualizing the effects of grazing by large herbivores on landscape heterogeneity in grassland ecosystems.

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Abstract

Controlled grazing is a widely used management tactic, that can be used to reduce biodiversity loss. It is thought that (re-)introduction of self-regulating populations of herbivores can create heterogeneous and biodiverse landscapes through their grazing preferences in so-called rewilding projects. But such (re-)introductions can have unforeseen ecological and social consequences, which can limit the success of rewilding projects. Thus, there is a need for innovative techniques to study rewilding itself and to convince the public. I investigated and visualized how grazing pressure and population dynamics of a population of large grazers affected landscape heterogeneity of grazing landscapes. To do this, I created a discrete spatial vegetation model, described by partial differential equations for vegetation growth, grazed by individually modelled grazers. I found that, under intermediate grazing pressure, stable grazer populations created a stable two-phase vegetation mosaic, consisting of grazing lawns and woodland. When grazer populations were dynamic, the vegetation mosaic alternated between a two-phase mosaic and a three-phase mosaic (with the third phase being tall grasses), thus creating more heterogeneous landscapes. There was also a clear coarsening effect visible. I then processed the model output to create a virtual 3D landscape, which can be used to convey the ideas and benefits of rewilding to the public. To explore what people thought of the modelled landscapes, I held a short online survey. In general, respondents of the online questionnaire were very enthusiastic about the use of 3D visualizations. Based on these results, I recommend the use of dynamic herbivore populations in rewilding projects, and to convince the public of the benefits of this management method using 3D computer graphics.

Introduction

Biodiversity provides the foundation for human existence and welfare. Humans have altered over half of the earth's land surface, damaging and destroying ecosystems in the process (Singh 2002). A growing body of evidence indicates that, as a result, we are entering a sixth, human-induced mass extinction event (Ceballos et al. 2015). The largest contributor to this massive biodiversity loss is the agricultural sector, through conversion of natural habitats to intensively managed, polluting farmland (Dudley and Alexander 2017). But the increasing abandonment of (especially European) marginal farmland provides opportunities to stem biodiversity losses (Queiroz et al. 2014, Corlett 2016). Grazing by free ranging herbivores in such areas can promote vegetation biodiversity through trampling (creating germination gaps), consumption of vegetation, redistribution of nutrients through faeces and urine, the compaction of soil, and the dispersal of seeds (Ruifrok et al. 2014). Moreover, grazing enhances or maintains biodiversity by preventing domination of competitive grassland species, and by reducing encroachment of brush and woodland (Tallowin et al. 2005, Tälle et al. 2016, van Klink et al. 2016). Grazers are often under careful management, with regular human intervention (Török et al. 2011).

In recent years, there has been a growing interest in, and application of grazing in rewilding projects. The general aim of rewilding projects is to restore natural ecosystem processes with minimal (long term) human intervention (Navarro and Pereira 2012). In some rewilding projects, the late Pleistocene (11.000 B.C.) is used as a historical baseline (Corlett 2016). It is suggested that Europe's primeval landscape consisted of an open, park-like landscape, where grazing by (now extinct) megafauna created a mosaic woodland pasture (Vera 1997, 2000, Olff et al. 1999, Vera et al. 2006). This view is not unchallenged, however, and there is both evidence for (e.g. Sandom et al. 2014) and against (e.g. Mitchell 2005) the theory. Nevertheless, from an ecological standpoint, it would be interesting to recreate such mosaic landscapes by functionally replacing extinct, self-regulating Pleistocene herbivore communities. Besides restoring ecosystem functioning, reducing management costs, and providing a visually and culturally interesting landscape (Olff et al. 1999), the high variety in vegetation types and landscape heterogeneity in such landscapes is associated with considerable biodiversity (Benton et al. 2003, Vera et al. 2006, Hovick et al. 2014).

Selective grazing from (reintroduced) free-ranging large grazers can facilitate the creation of these mosaic landscapes. Generally speaking, grazers will prefer short vegetation over tall vegetation (McNaughton 1984, Fryxell 1991, van de Koppel et al. 1996, Augustine and McNaughton 1998). This can be explained by a variety of mechanisms. For example, taller vegetation has a lower nutritional value compared to shorter vegetation due to the relatively high amount of structural tissue required to support their architecture (Fryxell 1991, Augustine and McNaughton 1998, Ruifrok et al. 2015). Other factors include grazers having to be more vigilant in dense vegetation (e.g. Lagory 1986, Laundre et al. 2010), and the simple fact that taller vegetation may be harder to consume (van de Koppel et al. 1996). This focused grazing on short vegetation leads to asymmetry in grazing pressure within the landscape, giving rise to swards of high-quality, low biomass vegetation that are kept open through continuous grazing. Meanwhile, less palatable patches of vegetation remain relatively undisturbed. Unpalatable shrubs, such as bramble or blackthorn, get a chance to settle in such patches, and their chemical or physical defences will protect saplings of more palatable tree species, a process called associational resistance (Vera et al. 2006, Barbosa et al. 2009, Cornelissen et al. 2013, 2014). These protected saplings will eventually grow into mature trees, overshadowing and outcompeting their nurse plants, forming patches of woodland (Vera et al. 2006).

At first glance, the (re)introduction of a self-regulating population of free-ranging large grazers thus seems a simple, yet promising management method. However, the (re)introduction of novel species into an ecosystem can have unforeseen, and often undesirable consequences. In practice, the formation of a mosaic landscape is a complex process that is dependent on many different aspects. Variables include, but are not limited to, soil fertility, vegetation species, and grazer species (Vera 1997, Olff et al. 1999, Vera et al. 2006, Cromsigt et al. 2018). In fact, scientific evidence supporting rewilding theories as a whole is limited (Nogués-Bravo et al. 2016, Pettorelli et al. 2018). As a result, carefully planned introductions can have severe unintended consequences (Nogués-Bravo et al. 2016, Pettorelli et al. 2018). In turn, this can lead to societal conflict. An example of this is The Oostvaardersplassen, one of the oldest European rewilding locations. A small (mostly) self-regulating population of large grazers were introduced into the area on the 1980s and early 1990s. A lack of natural predators caused the grazer population to flourish. The resulting overgrazing threatened both biodiversity and animal welfare, and required mass shooting of animals to prevent widespread starvation. This sparked a heated public debate. Management strategies in The Oostvaarderplassen were criticized by scientists, conservation practitioners, and the public (Kopnina et al. 2019). New policy required more active grazer management, bringing an end to an almost 40-year long period of self-regulating natural grazing.

So, besides a lack of clear evidence that can be used in decision-making (Pettorelli et al. 2018), political dynamics involving the public opinion on the success of rewilding projects may also limit the feasibility of these projects. Hence, there is a need for innovative approaches that not only study rewilding itself, but also convey the goals and possible outcomes of rewilding to the general public. Management interventions such as those in The Oostvaardersplassen, as well as the large timescale of the complex underlying processes, make it difficult to study this physically. The use of mathematical models can provide an outcome here. Mathematical models can simulate the effects of grazing on the landscape, without the risk of damaging actual ecosystems, and without time-scale limitations. Such models can also be used to show the impact of changing conditions, making it possible to predict the effects of, for example, different grazing regimes. It is then possible to communicate the model outputs to the public through 3D computer graphics, making it easy to grasp complex model outcomes at a glance. Demonstrating what a landscape could look like under natural circumstances (i.e. minimal human intervention; rewilding) will raise public awareness of shifting perceptions of what is 'natural' or 'normal'. This may reduce tensions between nature managers, policy makers and the public, and can shift the public opinion in favour of rewilding projects, leading to public enthusiasm and political support for rewilding and even nature conservation in general.

In this study, I aim to provide more insight into the effects of different grazer management tactics on the natural landscape by answering the question: how does grazing pressure and the dynamics of grazer populations affect the heterogeneity of grazing landscapes? I expect that intermediate grazing pressure creates a cascade of pattern formation that creates a heterogeneous mosaic landscape. To investigate this, I constructed a spatially explicit vegetation model consisting of partial differential equations for eutrophic temperate grasslands, grazed by individually modelled large grazers. To investigate the effects of different management tactics on the landscape, I compared landscape heterogeneity for different fixed grazer populations, and a dynamic population. I then processed the resulting data using a so-called pipeline to create a data-based 3D visualization. While there are plenty of studies that use (grazing) models (e.g. Rietkerk and van de Koppel 1997, Adler et al. 2001, Ruifrok et al. 2015, DeAngelis and Yurek 2017) or computer graphics (e.g. Prusinkiewicz and Lindenmayer 1990, Deussen et al. 1998, Smelik et al. 2014), these two are rarely, if ever, combined.

Methods

I constructed an individual based grazer model, combined with a discrete spatial partial differential equation vegetation model, with a discrete number of timesteps. The model (Figure 1) describes a eutrophic temperate European grassland ecosystem, where an individually modelled grazer community H grazes from a spatially explicit grassy (g) and woody (w) vegetation grid (Figure 2). The grassy vegetation community represents fast growing grassy or herbaceous grassland vegetation (grasses, forbs, etc.), while the woody community represents the slower growing woody vegetation (shrubs, trees, etc.). Incorporated in the model is the grazer's preference for short, grassy vegetation and avoidance of unpalatable shrubs. With this model, I investigate the effects of different grazing intensities and population dynamics, representing different management techniques, on landscape heterogeneity. The general vegetation-grazing system can be described as:

$$\frac{\Delta N}{\Delta t} = G(N) - L(N, H) + D(N), \tag{1}$$

Where Δ describes the use of a discrete spatial model with $\Delta t > 0$, N is grazable biomass of a vegetation community, function G(N) describes the vegetation growth, L(N, H) describes the loss of this vegetation biomass through consumption and mortality, and D(N) describes the spatial dispersal of the vegetation.



Figure 1: Overview of the grazer model. Managers determine what grazers species can graze in the landscape, and can control their population size. Grazing preferences determine where grazers prefer to forage and how much they consume, decreasing vegetation biomass. Vegetation biomass can influence vegetation type through competition. Vegetation biomass and type in turn influence grazing behaviour, based on the herbivore's preferences. This can lead to an asymmetry in (local) grazing pressure, which leads to vegetation pattern formation and landscape heterogeneity.

Vegetation growth

Vegetation growth is based on a logistic population growth model, which describes how the initial exponential growth of a population declines as per capita intrinsic growth rate r ultimately becomes limited by resource availability, until growth becomes zero, and the population reaches its carrying capacity K:

$$G(N) = rN\left(1 - \frac{N}{K}\right).$$
(2)

This model contains two distinct vegetation communities, each with their own carrying capacity and intrinsic growth rate, which will be competing for space and resources. Given two vegetation communities, the competitive Lotka-Volterra equations (Volterra 1928, Lotka 1932) add an additional term, describing the competitive interaction between the two groups:

$$G(N_i, N_j) = r_i N_i \left(1 - \frac{N_i + a_{ij} N_j}{K_i} \right), \qquad (3)$$

where, a_{ij} represents the negative competitive effect of vegetation community j on (the growth of) vegetation community i. Increasing population densities will thus lead to increased competition between species, lowering growth rates.

Aboveground, grazable leaves only make up a portion of a full plant's biomass, as the rest can be found belowground in the form of the root system. Excess nutrients are stored inside these (often) ungrazable roots, which allows plants to regrow, even without leaves to photosynthesize (Owen-Smith 2008). I assumed this ungrazable reserve effect to be relevant for grassy vegetation community Ng only, as it has been shown that severe browsing and debarking (i.e. when grazable biomass approaches or reaches zero) of woody vegetation by large grazers leads shrub and tree mortality (Cornelissen et al. 2013). For the sake of simplicity, I also assumed that all grassy vegetation always has an ungrazable reserve available. I implemented this ungrazable reserve effect by simply adding the fixed growth term b to the grass growth equation. Because this model includes competition between grassy and woody vegetation, the fixed growth term b for grassy vegetation should decrease with increasing competition from woody vegetation w. Thus, I defined b as $b = b_{max} \left(1 - \frac{a_{gw}N_w}{K_w}\right)$, where b_{max} is the maximum value for the fixed growth term b (i.e. without any competition from woody vegetation). We thus end up with the following equations for grassy (Ng) and woody (Nw) vegetation growth:

$$G_g(N_g, N_w) = (r_g N_g + b) \left(1 - \frac{N_g + a_{gw} N_w}{K_g} \right),$$

$$G_w(N_w, N_g) = r_w N_w \left(1 - \frac{N_w + a_{wg} N_g}{K_w} \right)$$
(4)

Initially, the model also included a seasonal growth effect, in the form of a simple sine wave which either decreases or increases intrinsic vegetation growth based on the season. However, after running the model, the modelled seasonal differences only caused yearly fluctuations that did not appear to have any long-term effects on the landscape. Such yearly fluctuations would have consequences for the food availability for grazer population, but since I did not explicitly model grazer population growth (see grazing pressure and population dynamics), I have decided to omit seasonality from the model to keep the model as simple as possible.

Diffusion

I have modelled the dispersal to of vegetation by adding a diffusion function D(N), as used by (Klausmeier 1999) and (Rietkerk et al. 2002), to the model, where D(N) is a Laplace operator with diffusion coefficient *d*:

$$D(N) = d\left(\frac{\delta^2 N}{\delta x^2} + \frac{\delta^2 N}{\delta y^2}\right).$$
(5)

Grazing behaviour

Large grazers have preferences for certain vegetation types over others, and when given the choice, grazers will graze vegetation in order of preference. This selective grazing leads to relative overgrazing of palatable vegetation, and relative undergrazing of unpalatable vegetation. These unpalatable, undergrazed patches protect vulnerable tree and shrub saplings, which will grow into thickets and woodland, giving rise to a heterogeneous mosaic landscape. I have translated selective grazing into the model through grazer movement and consumed biomass, based on local conditions.

Grazer movement

Movement of individual grazers (Figure 2) is described by a random walk, with a random angle and a stepsize based on local conditions. The length of stepsize S is determined by a grazer's preference for high quality grass G and the avoidance of unpalatable or hard to traverse woody vegetation W:

$$S(N_g, N_w) = G(N_g) + W(N_w).$$
(6)

Short grass has a high nutrient concentration, but low amounts grazable biomass. As grasses grow taller, they have to invest more resources into vertical structures, which leads to a decrease in nutritional value, but an increase in grazable biomass (McNaughton 1984, Fryxell 1991, van de Koppel et al. 1996, Augustine and McNaughton 1998, Ruifrok et al. 2015). The increase in rumination requirements of these tall, low quality grasses lead to a decrease in available grazing time, and thus energy intake, offsetting the benefits of increased food availability (Gibb et al. 1997). Large grazers will thus generally prefer vegetation of intermediate height, where sufficient biomass of decent quality is available (Gibb et al. 1997). In this model, I used biomass as a proxy for vegetation height. I have implemented the preference for intermediate height grass with a simple convex parabola shaped grazer movement curve, where grazers lower their walking speed when grazing grassy vegetation of intermediate biomass, and gradually increase their speed when biomass deviates from their preference:

$$G(N_g) = \alpha_g N_g^2 + \beta_g N_g + \gamma_g, \tag{7}$$

where α_{g} , β_{g} , and γ_{g} are constants describing the shape of the parabola.

Grazers prefer eating grasses over browses, such as forbs, shrub leaves and stems (Searle and Shipley 1970, Shipley 2001). Moreover, dense thickets of unpalatable (e.g. thorny) shrubs will be harder to traverse for large animals, forming a natural barrier (Vera et al. 2006, Smit et al. 2015). To maximize forage intake, grazers will want to avoid unpalatable and hard to traverse woody vegetation, and search for patches of grass instead. I assumed that woody vegetation is the most avoided when biomass is intermediate, as it is then dominated by a dense thicket of mature and unpalatable nurse shrubs, making it both hard to traverse and difficult to consume. When biomass is lower, the thicket may be less dense or less mature (and thus more palatable) (Vera et al. 2006), which makes foraging easier. When biomass is higher, nursed species will start overshadowing their nurse plants, which results in a change in species composition from unpalatable nurse shrubs to tall and more palatable trees, which leads to more favourable grazing conditions. Again, I used biomass as a proxy for vegetation height, and implemented avoidance of unpalatable or hard to traverse shrubs in the model as a concave parabola shaped curve, where grazers avoid woody vegetation of intermediate biomass, and decrease their stepsize again as biomass deviates from this intermediate biomass:

$$W(N_w) = \alpha_w N_w^2 + \beta_w N_w + \gamma_w, \tag{8}$$



where α_{w} , β_{w} , and γ_{w} are again constants describing the shape of the parabola.

Figure 2: Example of the model. The model consists of two vegetation grids (grassy on the left, woody on the right) that occupy the same space. Individual grazers (white dots) move across the landscape in search of suitable foraging locations, causing them to aggregate in certain areas. Colour represents vegetation biomass (g/m²).

Vegetation consumption

Grazing pressure determines how much vegetation is actually consumed by large grazers at every time step. Overall grazing pressure is determined by population size (see grazing pressure and population dynamics), while local grazing pressure is determined by a combination of grazer movement and vegetation consumption. As previously mentioned, grazers can forage optimally at intermediate grass heights, and grazing pressure will have to be adjusted accordingly. I have chosen to use a simplified dome-shaped Holling IV functional response (Sokol and Howell 1981, Fryxell 1991, Huang and Xiao 2004, Ruifrok et al. 2015), which describes how vegetation consumption C by a single grazer rapidly increases with increasing vegetation biomass in a cell (increase in food availability), up to a maximum,

from which consumption gradually declines due to the inhibitory effect tall vegetation on grazing (such as increased rumination times, vigilance, difficulties with grazing high vegetation, etc.):

$$C(N) = I_{max} \left(\frac{\mu N}{\lambda + N^2} \right), \tag{9}$$

where I_{max} is maximum intake rate, μ and λ constants that describe the shape of the consumption curve, and λ also describes for what value of N consumption is optimal. For the sake of simplicity, I assumed that this grazing curve was identical for consumption of both herbaceous and woody vegetation. To incorporate both preference for grassy over woody vegetation, and proportions of available grassy/woody biomass in a given cell, I included a weighted proportion factor, where constant p is the preference of grassy vegetation over woody vegetation. Furthermore, since the function C(N) describes the vegetation consumption of a single herbivore, C(N) is multiplied by the number of herbivores H that are present within a vegetation grid cell:

$$C_g(N_g, N_w, H) = H * I_{max} \left(\frac{pN_g}{pN_g + N_w}\right) \frac{\mu N_g}{\lambda + N_g^2},$$

$$C_w(N_w, N_g, H) = H * I_{max} \left(1 - \frac{pN_g}{pN_g + N_w}\right) \frac{\mu N_w}{\lambda + N_w^2}.$$
(10)

Vegetation Mortality

I experimented with using grazing-related mortality, where woody vegetation had a higher chance to die when grazed, and age-related mortality, where woody vegetation had a higher chance to die with increasing age. However, I could not successfully implement this into the model. So, for the sake of simplicity and time, I have added woody biomass loss through a random mortality factor M for woody vegetation, where every cell has a chance m to have its woody biomass set to 0 at every timestep. I assumed mortality to only be relevant for woody vegetation, as the death of a single large tree is much more impactful on the overall landscape than the death of individual tufts of grass.

Thus, combined with consumption, we end up with the following formula for vegetation biomass loss:

$$L_g(N_g, N_w, H) = C_g(N_g, N_w, H),$$

$$L_w(N_w, N_g, H) = C_w(N_w, N_g, H) + M.$$
(11)

Grazing pressure and population dynamics

Herbivore population size determines overall grazing pressure, and can have a large impact on the landscape. High stocking density can result in overgrazing, which prevents regeneration of woody species (Cornelissen et al. 2013, Smit et al. 2015). Overgrazing is also associated with reduced soil quality, decreased (endemic) diversity and increased invasion of undesirable plant species (Metera et

al. 2010). However, undergrazing may have equally harmful effects as overgrazing, such as the succession of undesirable plant communities (Metera et al. 2010).

Herbivore population growth can be modelled in great detail; in reality, individual survival and population growth will be dependent on many factors, including age, sex, body size, digestive processes (e.g. type of digestive system, mean retention time, stomach capacity), vegetation intake rate and vegetation fibre content (Duncan et al. 1990, Ruifrok et al. 2015). However, I am not specifically interested in the fine details of grazer population growth. Instead, I am more interested in the effects of broad grazer population dynamics in itself on the vegetation community. Therefore, I opted not to use (often complicated) herbivore population growth equations which take the previously mentioned factors into account. Instead, I simplified grazer population dynamics by assuming that a managed grazer populations (like in the OVP) remains constant, and that a self-regulating grazer population follows a sinusoid curve, where ω determines the amplitude of a fluctuation, H₀ is the baseline number of herbivores, φ is the frequency of cycles, and t is time:

$$H = \omega H_0 \sin(\varphi t) + H_0. \tag{12}$$

Model parameters

Model parameters (Table 1) were chosen from literature when possible, and where calibrated or estimated otherwise. I have chosen a value of $500g/m^2$ for K_g , as used by Ruifrok et al. (2015), and (Owen Smith 2002) in similar (though non-spatial) grassland models. Finding a value for K_w was difficult, as values were often species-specific, and often did not include all grazable biomass, such as understory growth or bark and twigs (Duliere and Malaisse 1994, Kantor et al. 2009, Katona et al. 2011). I opted to set K_w to double the value of K_g . Intrinsic growth rate r was calibrated so that, when undisturbed, grassy vegetation grew to K_g in approximately one year, and woody vegetation grew to K_w in approximately fifteen years. Competition, diffusion, mortality constants (a, d, and m) and the extra growth term b_{max} were all estimated (Table 1). Grazer movement variables were calibrated so that for grassy vegetation, grazers moved 0.1m per time step under optimal grazing conditions $(0.5K_g)$, and 4m under the most unfavourable grazing conditions (0 or K_g). For woody vegetation, variables were calibrated so that movement was not affected at optimal conditions (0 or K_w), and 8m per time step at the most unfavourable grazing conditions $(0.5K_w)$. Initially, these values may seem on the low side, but keep in mind that grazers are always active (no sleep or rumination breaks). I chose the European bison as model grazer, the largest European herbivore. Adult European bison consume around 23kg to 32kg of biomass a day (Pucek et al. 2004), so I set maximum intake rate Imax to 27.4 kg/day. I calibrated vegetation consumption variables μ and λ so that both grassy and woody vegetation are optimally foraged at a biomass value of 250 g/m², while I estimated the grass preference variable p to be 4. Population dynamics were chosen so that during the runtime of the model, the population would undergo four cycles, where the most extreme values deviated a factor 0.5 from the baseline.

Model setup and initial conditions

The model was created in Spyder 4.1.5, using Python version 3.8.5, with the numpy, matplotlib and math libraries. Both vegetation communities (grassy and woody) were modelled on a vegetation grid, with a size of 256×256 square cells, where each cell has a length of 10 meters, giving an area of

approximately 6.55 km². Initial vegetation biomass was normally distributed on the vegetation grid, with $\mu = 250g/m^2$, $\sigma = 50g/m^2$ for grassy vegetation and $\mu = 100g/m^2$, $\sigma = 25g/m^2$ for woody vegetation, representing recently abandoned farmland with relatively tall grasses and freshly established saplings. Grazers were randomly distributed across the vegetation grid. Grazers move individually, and can freely move across the landscape, where movement is based on a random angle and a stepsize (see Grazer Movement). Grazers cannot move outside of the vegetation grid, as they will be moved back into the domain using periodic boundary conditions. All grazers occupy a single grid cell, and will graze from this cell until they move to another cell. I ran the simulations for five million timesteps, where 100000 timesteps represent a single year, for a total of fifty years.

With this model, I investigated the effects of grazing intensity and dynamics on landscape heterogeneity, a measure for biodiversity. I compared landscape heterogeneity for a no-grazing control (no grazers), a low grazing intensity (100 grazers, 0.15 grazers/ha), medium grazing intensity (400 grazers, 0.61 grazers/ha), high intensity grazing (800 grazers, 1.22 grazers/ha), and dynamic grazing (200-600 grazers, 0.31-0.92 grazers/ha), representing different grazer management tactics. These differences in grazer management tactics can lead to temporal changes in vegetation biomass (Figure 3).

Variable	Meaning	Grassy	Woody	Unit
Vegetation growth				
r	Intrinsic growth rate	0.000035	0.0000075	$g m^{-2} \Delta t$
b _{max}	Extra growth term	0.0005	-	$\mathrm{g}~\mathrm{m}^{-2}~\Delta \mathrm{t}$
Κ	Carrying capacity	500	1000	g m ⁻²
a	Competition constant	0.35	0.50	-
d	Diffusion coefficient	0.0000010	0.0000010	$m^2 \Delta t^{-1}$
Μ	Mortality chance	-	0.0000005	Δt^{-1}
Grazer movement				
α	Constant	0.000064	0.000032	$m^5 g^{-2}$
β	Constant	-0.032	0.032	$m^{3} g^{-1}$
γ	Constant	4.1	0	m
Vegetation loss				
μ	Constant	62500	62500	-
λ	Constant	500	500	-
р	Preference variable	4	-	-
Ι	Maximum intake rate	100	100	$g m^{-2} \Delta t$
Population dynamics				
ω	Fluctuation amplitude	0.5		-
φ	Fluctuation frequency	0.000005		-

Table 1: Parameters used in the model simulation. Variables ω and φ used in calculating population dynamics belong neither to the "grassy" or "woody" column, but were included in this table to provide a convenient overview for all variables in a single table.



Figure 3: Line plots showing average vegetation biomass (g/m^2) for two types of vegetation under a stable population (left) and dynamic population (right) over time. While for a stable population the average vegetation biomass tends to converge to an equilibrium, average vegetation biomass fluctuates with time for dynamic populations.

Pipeline and Blender

Visualizing the model outputs may be helpful in generating both public and political support for rewilding projects, as 3D pictures of a landscape are likely to be more interesting and/or convincing to the general public compared to regular model outputs (Ijsselsteijn 2004, Seuntiëns et al. 2005). I visualized the model outputs using Blender v2.91, a free and open-source 3D computer software programme. The raw model output first has to be processed through a so-called pipeline, to make it suitable for use in Blender (Figure 4). Here, 2D vegetation biomass data is split up into four categories (short and tall for both grassy and woody vegetation, with the cut-off value at half the carrying capacity of the respective vegetation type) and normalized. In Blender, these four 2D vegetation biomass maps are used to place individual plants into the landscape, where cells with higher biomass values get assigned more plants. This is done using a method called instancing, where a large number of duplicates is rendered that are copies of a single object (for example, a single 3D tree model). The maximum number of duplicates of a vegetation type that can be placed in the landscape scales with the number of cells that are present in the respective vegetation map. For example, when the number of cells from the model vegetation grid that contain tall grassy vegetation doubles, the number of tall grass plants that can be placed in the 3D landscape also doubles. I used a relatively small selection of plants due to computational limitations. Grazers were placed in the landscape using a manually defined polygon. The number of grazers put into the landscape was also scaled with the number of grazers used in the simulation. I scaled down the landscape constructed in Blender by a factor ten for computational feasibility, meaning that every square meter in the 3D landscape, represents a 10 x 10m cell in the model.

To investigate the value of data-based 3D computer graphics over more traditional media, I sent a short, exploratory survey (supplementary material) to staff and students from the Conservation Ecology group

from the University of Groningen, student peers studying at various (vocational) universities, as well as staff with a modelling and/or visualizing background from the Royal Netherlands institute for Sea Research and the Computer Graphics & Visualization Group from the Delft University of Technology. I received a total of 29 anonymous responses. Since the questions were open-ended, I interpreted and classified responses into different categories. Due to fairly small sample size, frequent unclear answers to the open-ended questions, and non-random sampling of the respondents, I chose not to perform a statistical analysis on the data.



Figure 4: Overview of the data processing required to create 3D visualizations from 2D model output. First, the model output (A) is processed to create various vegetation maps (in this case trees, B). These vegetation maps are then used to place individual plants in Blender (C). By combining various vegetation maps, it is possible to create a virtual 3D landscape.

Results

My results highlight that grazing intensity is an important landscape shaping factor. As shown in Figure 5 and 6, grazing under various grazing scenarios creates widely different landscapes: closed canopy woodland develops when grazing is absent or with a low grazing pressure. Short-grazed, monotonous swards (grazing lawns) develop under high grazing pressure. A vegetation mosaic consisting of high biomass patches alternating with short grazing lawns emerge under intermediate and dynamic grazing pressure. When grazing intensity was low, grazers did not exert enough grazing pressure to form grazing lawns. Grassy vegetation quickly grew near carrying capacity, followed by a decline in grassy biomass as shrubs and trees began to outcompete grasses. Since the resulting landscape is very homogeneous, grazers move practically randomly across the landscape, grazing as they move. As a result of this constant but low intensity grazing, the growth of woody vegetation was supressed, and overall biomass was lowered compared to the no-grazing control (Figure 5). While there is patchiness visible within the woodland, the formation of these patterns is mortality driven, as these patterns were also visible in the no-grazing control. When increasing grazing pressure, a well-defined two-phase mosaic emerged (Figure 5), consisting of bare grazing lawns without woody vegetation and low grasses, and woodland with higher grasses and high woody vegetation biomass. There was also a small "halo" of tall grassy vegetation present around woodland edges. When further increasing grazing intensity, woody vegetation did not get a chance to properly establish, practically turning the entire landscape into a homogenous grazing lawn. So, intermediate grazing intensities created more landscape heterogeneity compared to low and high intensities.

Population dynamics played a major role in amplifying landscape heterogeneity. The dynamic grazer populations created a mosaic of grassland and woodland, similar to the fixed intermediate grazer



Figure 5: Model output (left) and histogram (right) of combined grassy and woody biomass of the simulated landscape (2.56 x 2.56 km) after 50 years under different grazing conditions. In the control, no grazers were present. Under low, intermediate and high grazing intensity, there were 100, 400, and 800 grazers present respectively. Under the dynamic grazing regime, grazer numbers fluctuated between 200 and 600 grazers, following a sine wave, with cycles lasting 12.5 years. Colour indicates combined grassy and woody vegetation biomass in g/m². Intermediate constant grazing led to the formation of a two-phase vegetation mosaic, while intermediate dynamic grazing led to the formation of three-phase vegetation mosaics.

population (Figure 5). But as seen in Figure 6 the changes in grazing pressure over time produced oscillations in vegetation cover. When grazing pressure was low, a three-phase vegetation mosaic was created in the landscape (Figure 5, 6); besides grazing lawns and woodland, patches of tall grass were present in the landscape. These tall grass patches are mostly located on grazing lawns near unpalatable, relatively undergrazed woodland edges The dynamic grazer population recovered sufficiently fast, so that woody species did not get a chance to settle, turning the tall patches of grass into grazing lawns once more. So dynamic grazing seemed to lead to a multitude of patch types occurring at multiple spatial scales: a large-scale mosaic of woodland and grazing lawns, tall grassy vegetation patches near woodland edges (depending on grazing pressure), and a temporal pattern in vegetation cover and biomass.

There was also a clear coarsening effect visible in the landscape. Initially, the landscape was very finegrained, but as time went on, the landscape became coarser, with smaller patches disappearing, and large patches that keep growing (Appendix A, also see videos in supplementary material). Given enough time, these coarsening effects will result in a landscape consisting of a small number of very large patches, which would decrease (smaller scale) landscape heterogeneity.

Visualizations

The 3D computer graphics (Figure 7) were perceived very positively by the questionnaire respondents. While the visualizations were considered to look quite realistic, the respondents mentioned that visualizations could be improved by, among other things, using a more realistic vegetation species composition, by adding (more) animals into the landscape (especially large herbivores), by using larger tree models, and also by improving tree model resolution. Respondents did not appear to have a clear preference of 3D panoramas over the model output (Figure 8), but instead mentioned that both have their own strengths and weaknesses. Generally speaking, the model output was considered to be more informative, while the 3D panoramas were easier to interpret. Most respondents also preferred a combination of 2D (such as the model output, but also real-life pictures or artist impressions) and 3D pictures (such as the 3D panorama) (Figure 8), with the 3D panoramas being more convincing, but 2D pictures (like artist's impressions) being more eve-catching and/or aesthetically pleasing. However, many others also preferred the 3D panoramas over other pictures, especially emotional interpretations of reality like artist's impressions, as the 3D panoramas were model-based and therefore more scientifically accurate. Moreover, the possibility to look around in 3D panoramas was perceived very positively, but some respondents mentioned that (camera) movement still felt fairly restricted. Overall, the vast majority of respondents thought the 3D panoramas could help in convincing the public on the benefits of rewilding (Figure 8). There do not appear to be any clear differences between the different groups, except for a slight preference of people unfamiliar for the panoramas, and a slight preference of people familiar with rewilding for a combination of model output and panorama (Figure 8).



Figure 6: Line plots demonstrating showing cover for grazing lawns (blue, combined vegetation biomass < 300 g/m²), woodland (yellow, combined vegetation biomass \geq 700 g/m²) and tall vegetation (red, combined vegetation biomass \geq 300 g/m² and < 700 g/m²) for an intermediate stable population (left, 400 grazers) and a dynamic population (right, 200-600 grazers) over 50 years. While vegetation cover stabilizes and tall vegetation quickly disappears from the landscape grazed by the stable population, vegetation cover in the landscape grazed by the dynamic population oscillates instead, creating alternating periods of two-phase and three-phase vegetation mosaics.



Figure 7: Model output (left) and the corresponding 3D virtual landscape (right) of combined grassy and woody biomass of the simulated landscape (2.56 x 2.56 km) after 50 years under different grazing conditions. In the control, no grazers were present. Under low, intermediate and high grazing intensity, there were 100, 400, and 800 grazers present respectively. Under the dynamic grazing regime, grazer numbers fluctuated between 200 and 600 grazers, following a sine wave, with cycles lasting 12.5 years. Colour indicates combined grassy and woody vegetation biomass in g/m^2 . When grazing pressure is low or absent (control), the landscape is dominated by woody species. When grazing pressure is high, the landscape is transformed into a large grazing lawn. Intermediate grazing intensity created either a two-phase (stable grazer population) or a three-phase (dynamic grazer population) vegetation mosaic.



Figure 8: Barplots showing the results of the anonymous online questionnaire (n = 29). Colour represents familiarity with rewilding. "Unknown" indicates empty or unclear response.

Discussion

The results of the modelling study presented in this paper highlight that grazing by selective herbivores that focus on short-grazed vegetation can lead to a strongly patterned landscape. The model shows that intermediate amounts of selective grazing led to the formation of a two-phase vegetation mosaic consisting of short grazing laws and bush and woodland patches where grazing is limited. My results are in line with previous research that has shown that herbivores can create mosaics of intensively grazed short vegetation, and tall patches of lightly grazed vegetation (McNaughton 1984, Adler et al. 2001), forming heterogeneous landscapes. My results show that a grazing intensity threshold may exist for these patterns to form, as they were not formed under lower grazing intensities. This threshold will likely depend on grazing preferences, as less selective herbivores will have more difficulty forming grazing lawns than more selective grazers due to more evenly distributed grazing pressure. If managers wish to recreate such patterned and heterogeneous landscapes through grazing, they should thus take grazing preferences and herbivore population size into account.

Two-phase mosaics, and pattern formations in general, are found all over the natural world. Pattern formation in response to differentiated grazing has been found in a large number of grazing systems, such as heathlands (Bakker et al. 1984), moorlands (Fraser et al. 2009), salt marshes (Berg et al. 1997), semi-arid grasslands (Wan et al. 2015), wetlands (Cornelissen et al. 2013, 2014) and savannahs (McNaughton 1984). Self-organized patterning resulting from ecosystem interactions have furthermore been found in a wide range of ecosystems, ranging from self-organizing mussel beds (Koppel et al. 2005, van de Koppel et al. 2008, Liu et al. 2016) to positive feedback between water infiltration and plant density leading to vegetation patterns in (semi-) arid ecosystems (Rietkerk and van de Koppel 1997, Augustine and McNaughton 1998, Klausmeier 1999). Heterogeneity and patterns often positively affect ecosystem functioning and stability (Liu et al. 2014, Bonachela et al. 2015) and biodiversity (Benton et al. 2003, Winqvist et al. 2011, Katayama et al. 2014, Ruifrok et al. 2015). Understanding of the mechanisms of pattern formation, and more specifically the two- or three-phase mosaics is thus crucial for successful management of natural ecosystems.

My study also highlights that herbivore population dynamics are an important landscape shaping factor. I found that dynamic herbivore populations created more dynamic and heterogeneous landscapes than stable populations through alternating cycles of two- and three-phase vegetation mosaics, the third phase being tall grasses. Not only are these landscapes more dynamic, with vegetation cover changing over time, but these landscapes are also more heterogeneous because they contain patches types not seen in other conditions (neither ungrazed or grazed by stable herbivore populations). Like mentioned previously, such heterogeneity (in this case both spatial and temporal) is associated with high biodiversity (Benton et al. 2003, Winqvist et al. 2011, Katayama et al. 2014, Ruifrok et al. 2015).

Similar processes have been observed in the Serengeti ecosystems, where large dense herds of grazers quickly deplete local resources, which leads to the constant relocation of herds, leading to continually changing grazing pressure over time (Hopcraft et al. 2010). These behaviours create ever-changing mosaics of vegetation (McNaughton 1984, Cromsigt and Olff 2008). In more temperate climates, it is hypothesized that temporary fluctuations in grazing pressure may provide a window of opportunity for woody species to settle (Olff et al. 1999, Mysterud 2006, Cornelissen et al. 2013). In semi-arid ecosystems, trampling by (most likely managed, and thus non-dynamic) livestock also created three-phase mosaic of woody vegetation patches, interpatch space and trampling routes (Stavi et al. 2012). How vegetation mosaics are affected by population dynamics will most likely depend on the severity and frequency of grazing intensity fluctuations, which could make for an interesting topic for future research. I conclude that, in order to maximise biodiversity, landscapes should be grazed by dynamic herbivore populations.

The model also showed a clear coarsening effect, a process in which large patches merge and grow, at the expense of smaller patches (Ratke and Voorhees 2002). Coarsening is found all over the natural world, ranging from molecular (Ratke and Voorhees 2002, Bray 2003) to landscape scale (Bautista et al. 2007). These effects are also found in grazing ecosystems (Berg et al. 1997, Dumont et al. 2012, Ge and Liu 2021). For example, Berg et al. (1997) showed that sheep grazing in a German salt marsh led to the merging of tall patches of *Festuca rubra*. Coarsening effectively leads to a simplification of the landscape, decreasing heterogeneity. It has been shown that such landscape homogenisations can decrease species richness, plant cover and bird abundance (Winqvist et al. 2011). Furthermore, the growth of large patches and the disappearance of small patches leads to a loss of habitat edges, which are often associated with high biodiversity, species richness and abundance (Magura 2002, Kark 2017). Since coarsening leads to the creation of fairly simple landscape with a small number of very large patches, there may be a need to "break up" larger patches to increase landscape heterogeneity to maximize biodiversity in the long term. In rewilding projects, this can be achieved without any human intervention through, for example, weather fluctuations (Berg et al. 1997) or forest fires (Malamud et al. 1998, Pascual and Guichard 2005).

The model has a few shortcomings. First of all, I modelled grazer movement individually, while in reality herbivores tend to form herds (e.g. McNaughton 1984). While not the focus of this study, herd behaviour (including herd migrations) is known to create spatial patterning in the landscape (Augustine and McNaughton 1998, Hopcraft et al. 2010, Liu et al. 2016). Investigating the effects of a combination of selective grazing and aggregating behaviours could lead to novel insights in pattern formation in grazed ecosystems, and may thus be an interesting avenue for future research. Second, I included only one herbivore species into the system. The addition of other herbivores with different foraging behaviours and/or predators can have major consequences for the landscape, including cyclical vegetation succession (Ruifrok et al. 2015) and, in the case of predators, landscapes of fear, where herbivores avoid areas with a high predation risk (Laundre et al. 2010). Third, consumption of established (i.e. high biomass) woody vegetation leads to a decrease in palatability, producing a

negative feedback loop which creates extraordinarily stable patches of woodland. For future work on this model, I would advise to split up the woody vegetation community into two distinct communities (unpalatable nurse shrubs, and palatable woody species each with their own palatability) and investigate how this affects temporal landscape heterogeneity.

Through the use of a pipeline, I created model-based 3D visualizations of my grazing ecosystem. Model-based 3D computer graphics appear to be a promising tool in convincing and teaching the public about the goals and benefits of rewilding. The 3D computer graphics created from the mathematical model were well perceived by respondents of the questionnaire. The large majority of respondents preferred either a combination of 2D and 3D or images, or just 3D images, and mentioned that the 3D images could help in shaping their opinions on rewilding projects. Respondents did not have a clear preference for the model output or the 3D panoramas, but it should be noted that the large majority of respondents have a background in science, making them more skilled in reading and interpreting schematics such as the model output. It was mentioned that graphical realism could be improved through a variety of ways. However, care should be taken as to not turn the model-based visualizations into 3D artist's impressions, and to strike a balance between aesthetics and science. While more realistic visualizations may be more aesthetically pleasing or convincing, the model is not supposed to be a perfect representation of reality, and beautifying visualizations can take away from the scientific foundation.

3D computer graphics may have benefits over more traditional forms of media (Ijsselsteijn 2004, Seuntiëns et al. 2005). The use of immersive virtual reality may help in conveying the concepts and advantages of rewilding to the general audience, as virtual reality increases the user's engagement and motivation, and increases the variety of learning styles that can be used (Freina and Ott 2015). Another option is the use of so-called serious games, which are games that are built with (for example) education or training as a primary focus, instead of entertainment (Gloria et al. 2014). Providing the player with the freedom to interact with a realistic virtual environment, without spatial or temporal barriers, can help with learning as the user is encouraged to explore different situations (Gloria et al. 2014). In the context of this project this could, for example, be achieved by letting the user freely walk around in the landscape and letting them change some simple model parameters (e.g., herbivore species, stocking density, rewilding management or not, etc.) so they may experience for themselves how the landscape changes under different management conditions. Landscape dynamics may be best shown using an animation of the 3D landscape over time, since it may difficult to show changes over time using only static images.

A more tailored combination of innovative visual methods and more traditional types of media (artist's impressions, model outputs, photographs, etc.) is likely to reach and engage a wide variety of audiences, allowing scientists to communicate the ideas and benefits of rewilding to the general public, policy makers, and nature managers. In a broader perspective, these approaches can also be useful in combating the phenomenon of shifting baselines: changing perceptions what is considered "normal" or "natural" (Papworth et al. 2009). By showing the public what landscapes looked like in the past compared to how they look now, people can be made aware of the nature and ecosystems we have lost over time. This may not only increase their enthusiasm for and understanding of the value of rewilding, but for nature conservation in general as well.

Based on all the previous results, I would advise to reconsider management practices in the OVP. Current management for the OVP is to cull the herbivore populations whenever they grow beyond a fixed artificial carrying capacity. As a result, herbivore populations will most likely remain very stable over time. While reducing overall grazing pressure may be useful for allowing the landscape to recover from its overgrazed state (e.g. Cornelissen et al. 2013), my model suggests that such stable populations cannot create dynamic three-phase vegetation mosaics. This would lead to a loss of potential landscape heterogeneity and all of its associated benefits. Managers should thus aim to restore herbivore populations dynamics.

Since the OVP is a relatively small site (56 km²), and there are no plans to expand the park in the foreseeable future, there will not be enough space for herbivores to migrate, or to reintroduce predators like wolves (Arts et al. 2016). This means that, assuming a rewilding approach, population dynamics will have to be determined through factors like the weather, disease and food availability. Since public outrage concerning this type of population dynamics was the reason initial hands-off management has changed, it is necessary to convince the public first. Through a combination of one-time management interventions to improve animal welfare and protect biodiversity (such as creating grazing refuges to facilitate sapling establishment (Smit et al. 2015)), and innovative use of 3D computer graphics discussed previously to convince the public, I think it is possible to turn the OVP into a visually appealing and biodiverse rewilding site, that can be enjoyed by everyone.

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Appendix A



Appendix A: An overview of combined grassy and woody biomass of the simulated landscape (2.56 x 2.56 km) over 50 years under different grazing conditions. In the control, no grazers were present. Under low, intermediate and high grazing intensity, there were 100, 400, and 800 grazers present respectively. Under the dynamic grazing regime, grazer numbers fluctuated between 200 and 600 grazers, following a sine wave, with cycles lasting 12.5 years. Colour indicates combined grassy and woody vegetation biomass in g/m2. Red patches indicate grazing lawns, while yellow/green patches are woodland. The orange patches that are visible in year 10 and 50 under a dynamic grazing regime are patches of high grass that overtook grazing lawns due to a temporary decrease in grazing pressure. Note that patches become coarser over time, with large patches that keep growing at the expense of smaller patches.