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Loss of spatial structure after temporary herbivore absence in a high-productivity reed marsh

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Abstract

1. Grazing can significantly impact spatial heterogeneity and conservation value of ecosystems. Earlier work revealed that overgrazing may stimulate persistent vegetation collapse in low-productivity environments where vegetation survives by concentrating scarce resources within its local environment. However, it remains unclear whether grazer fluctuations may cause persistent vegetation changes in high-productivity systems where dense stands facilitate their own survival by hampering grazer access.

2. Here, we experimentally tested how the release from grazing by greylag geese (*Anser anser*) affects spatial vegetation structure in a highly productive, brackish marsh in which dense reed (*Phragmites australis*) stands and bare roosting areas coexist. Next, we assessed the resilience of the change in vegetation patterning by reintroducing the geese after a 2-year exclosure period.

3. During herbivore exclusion, vegetation rapidly colonized the bare areas, while reintroduction of herbivores generated a clear species-specific response. Specifically, the pioneer species, *Bolboschoenus maritimus*, was immediately eradicated, while the dense and high structure of *P. australis* facilitated its own persistence by limiting grazer access. Surface accretion (~1 cm/year) during herbivore exclusion further amplified this herbivore-inhibiting feedback, because greylag geese primarily rely on waterlogged conditions for grubbing.

4. *Synthesis and applications.* Our results indicate that temporary reductions in herbivore numbers may induce persistent unfavourable changes in the spatial structure of a high-productivity system. It is therefore important to first assess whether vegetation changes are naturally reversible or persistent. If state shifts are indeed persistent, sufficiently high grazer densities must be maintained to warrant the favourable heterogeneous system. If changes in vegetation structure negatively impact grazer densities, active management such as sod cutting or mowing may be required to restore ecosystem structure and functions.

1 | INTRODUCTION

High spatial heterogeneity is often desired by ecosystem managers as it typically stimulates ecosystem-level productivity, biodiversity and resilience (Pringle, Doak, Brody, Jocqué, & Palmer, 2010; Stein, Gerstner, & Kreft, 2014; van Nes & Scheffer, 2005). Such patchiness, in the form of alternating bare and vegetated patches, or patches of multiple species, can result from underlying abiotic heterogeneity, but can also arise in rather homogenous abiotic environments due to ecological interactions (Rietkerk, Dekker, De Ruiter, & van de Koppel, 2004; Sheffer, Hardenberg, Yizhaq, Shachak, & Meron, 2013). Top-down (e.g. plant–herbivore) interactions have been found to independently, or in synergism with bottom-up (e.g. plant–soil) interactions, control the spatial structure and functioning of many terrestrial, freshwater and marine ecosystems (Adler, Raff, & Lauenroth, 2001; Bakker et al., 2016; Cromsigt & Olff, 2008; Kerbes, Kotanen, & Jefferies, 1990; Olff et al., 1999; van de Koppel, Rietkerk, & Weissing, 1997; van der Heide et al., 2012). However, when these interactions are self-promoting, for instance by stimulating vegetation growth in vegetated patches and inhibiting vegetation development in bare patches, they may theoretically lead to nonlinear ecosystem dynamics and even multiple stable states if such feedbacks are strong enough (Rietkerk & van de Koppel, 1997; Scheffer, Carpenter, Foley, Folke, & Walker, 2001; van de Koppel et al., 1997). In such cases, structural changes in vegetation patchiness as a result of herbivore fluctuations may persist and management strategies aimed at restoring original herbivore numbers may be insufficient (Abraham, Jefferies, & Alisauskas, 2005; Jefferies, Jano, & Abraham, 2006; Peterson, 2002).

In harsh environments, such as arid ecosystems or artic saltmarshes – where plant growth is limited and overall ecosystem productivity is low – overgrazing has been shown to decrease the number of vegetated patches and provoke desertification (Jefferies, 1988; Kéfi et al., 2007; Rietkerk & van de Koppel, 1997). In these low-productivity systems, grazing can interact with plant–soil feedbacks in which vegetation patches facilitate themselves by preventing soil erosion and retaining water to stimulate plant growth (HilleRisLambers, Rietkerk, van den Bosch, Prins, & de Kroon, 2001). By removing vegetation biomass to levels below the critical threshold at which the patches can sustain themselves, grazing may disrupt these self-maintaining feedbacks and further reduce plant growth, resulting in more bare soil. The unfavourable edaphic conditions of the bare state – e.g. high soil salinities and low moisture content – inhibit vegetation re-establishment and the bare state may persist

for decades (Jefferies et al., 2006; Rietkerk et al., 2002; Srivastava & Jefferies, 1996). In contrast, in more benign environmental conditions, where overall ecosystem productivity is high, grazing may induce spatial patterning when it interacts with self-reinforcing feedbacks in which plant species hamper grazer access by modifying the abiotic environment. An intertidal seagrass landscape of alternating hummocks and hollows, for instance, has been shown to be maintained by geese that selectively graze on young, sparse vegetation in the hollows, while dense vegetation traps sediment to form hummocks that reduce grazer access (van der Heide et al., 2012).

Although multiple studies highlighted that an increase in grazing may induce persistent vegetation collapse in feedback-driven, harsh and low-productivity systems, it remains unclear whether grazer fluctuations may cause persistent vegetation changes in feedback-mediated, high-productivity systems. Yet, if vegetation changes feed back on grazing pressure by hampering grazer access or by reducing herbivore numbers, theory suggests that the ecosystem may change permanently following a temporary change in grazing pressure (Allen et al., 2016; Johnstone et al., 2016; Peterson, 2002). If this is indeed true, it is of utmost importance to know whether such feedbacks exist in the system, whether they are important drivers of vegetation structure, and whether they are strong enough to cause persistent, non-desired changes if not properly managed.

Here, we examine (a) the role of herbivory by greylag geese (*Anser anser*) in maintaining a spatial mosaic of common reed (*Phragmites australis*) and bare patches in a high-productivity brackish wetland and (b) the persistence of changes due to herbivore exclusion after grazing pressure has been restored. Similar to lesser snow geese (*Chen caerulescens caerulescens*) along the US Atlantic coast, greylag geese along the European Atlantic coast have dramatically increased and moved up the latitudinal range, negatively impacting agricultural lands, and pressurizing conservation of important wetlands (Abraham et al., 2005; Bakker et al., 2016; Esselink, Helder, Aerts, & Gerdes, 1997; Fox & Madsen, 2017; Gauthier, Giroux, Reed, Bechet, & Bélanger, 2005; Klok et al., 2010; Ostendorp, 1989). We hypothesize that in reed-dominated brackish marshes, self-facilitation by reed and grazing by geese create opposing feedbacks to form a patchy, heterogeneous landscape in which reed-dominated, and grazed, bare, roosting areas co-occur. By grazing on young emerging shoots and by grubbing on below-ground storage organs in waterlogged soils, geese hamper vegetation expansion (Esselink et al., 1997; van den Wyngaert, Wienk, Sollie, Bobbink, & Verhoeven, 2003). Conversely, the dense vegetation structure of *Phragmites* may limit grazer access. Furthermore, organic matter accumulation may further stimulate this grazer-inhibiting effect

by raising the marsh surface above the water-table, thereby preventing future grubbing (Elschot et al., 2017; Esselink et al., 1997; Rooth, Stevenson, & Cornwell, 2003). As a consequence, we suggest that in these highly productive marshes, temporary herbivore absence could lead to unfavourable persistent shifts in the spatial structures of the landscape as it would allow reed to rapidly expand and exclude future geese foraging required to maintain the bare roosting areas (see Figure S1 for a graphical representation of our hypothesis).

To test our hypothesis, we conducted a field experiment in which we studied the vegetation development and resulting surface accretion in plots that either allowed or excluded herbivores for two consecutive years. Next, to assess the persistence of the vegetation changes in the system due to herbivore exclusion we reintroduced herbivores after 2 years and studied the resulting development. We demonstrate that a temporary reduction of herbivory may provoke long-lasting changes, as it allows the vegetation to exert self-reinforcing feedbacks that exclude herbivores.

2 | MATERIALS AND METHODS

2.1 | Study site description

The experiment was carried out in a ~120 ha brackish back-barrier marsh on the Wadden Sea island of Schiermonnikoog, the Netherlands (53°29′51″N, 6°13′10.6″E). After the construction of a sand-drift dike in the late 1950s, the area was protected from the North Sea, which accelerated vegetation development. Heavy storms in the beginning of the 1970s, however, created a large 200-m gap in the man-made dike, which is still present. Only during storms surges that rise beyond 2.80 m above mean water level (MWL) does seawater enter the area through this gap (on average once per 2 years) (Dillingh, 2013). Any incoming seawater is prevented from flowing back to the sea, because the elevation of the marsh is relatively low in relation to the 2.80 m MWL threshold at the entrance. As a result, both the water-table and salinity levels fluctuate strongly throughout the year (Olff, Huisman, & Van Tooren, 1993) (Figure S2c).

The above-mentioned artificial stabilization caused a rapid transition of the system from a low-productivity beach plain to a high-productivity brackish marsh, as also reflected in porewater nutrient levels (Figure S2a,b). The transition from a beach plain to a brackish marsh coincided with the arrival of high numbers (700–900) of greylag geese (*A. anser)* to the island in the early 1990s that used the brackish marsh as a staging area (Bakker, van der Wal, Esselink, & Siepel, 1999). At present, the marsh consists of a patchy mosaic formed by dense vegetation stands dominated by reed, alternated with open gaps (patch cross-sections ~10–100 m). As a consequence, the marsh now functions as a vital roosting, foraging and breeding area for many species of waterbird, including spoonbills, little egrets, mallards, tufted ducks, common shellducks, common eiders and greylag geese (Mooser & van Loon, 2017, personal camera observations). This makes the heterogeneous structure of the marsh an important management target. Since the early 2000s, greylag geese have started to use the area as a breeding ground with their numbers still expanding (±3.3 individuals/100 ha in 2013 to 10.22 individuals/100 ha in 2017) (Kleefstra, 2017).

2.2 | Experimental setup

To test our hypothesis that geese grazing controls reed expansion, we first set up 18-m^2 rectangular (6 × 3 m) control (C) and exclosure [X] plots over the patch borders such that they covered: bare area (from 0 to 2 m), sparse vegetation (2–3 m) and the fully vegetated *Phragmites*-dominated part of the plot (3–6 m) (see Figure S3 for an aerial photograph of the experimental setup). Next, to test the hypothesis that dense reed stands can prevent grazer access, yielding lasting changes in vegetation patchiness, we removed the exclosures again after 2 years.

In total, six exclosures and control plots were constructed on the marsh in October 2014. At the start of the experiment (December 2014), the *Phragmites* edge was at the middle of the plot at 3.0 ± 0.2 m with no significant difference between treatment levels ($t_{8,8}$ = 1.1; p = 0.29; Figure S4). We constructed the exclosures by attaching 60 cm tall 5-cm mesh on the side poles of the plots, and wire on top of the exclosures prevented the geese from flying in. The exclosures were taken down in October 2016 and thereafter monitored throughout one more year to evaluate the effect of reintroduction of geese foraging.

2.3 | Vegetation biomass and herbivore pressure

The vegetation biomass and composition of each plot was measured each year at the end of the growing season (September 2015, August 2016, 2017) at 0.5-m intervals along the gradient from bare to dense vegetation (see Figure S3 for detailed pictures on plot position and gradient). Using quadrats (15 cm × 15 cm), we estimated standing biomass on each point along the plot gradient (from 0.5 to 6 m, yielding 12 sampling points per plot) using a non-destructive method by counting and measuring the height of all *Phragmites* and *Bolboschoenus* individuals within the quadrat (Catchpole & Wheeler, 1992; Thursby, Chintala, Stetson, Wigand, & Champlin, 2002). The dry weight of both species was calculated using species-specific calibration curves that were made by harvesting shoots of differing heights and weighing them after drying at 60°C to constant weight (N = 69; R^2 = 0.93 for *Phragmites* and N = 36; R^2 = 0.94 for *Bolboschoenus*; Figure S5).

We used footage recorded by a camera trap (Reconyx XR6) installed on a fixed position in front of one of the control plots to have an indication of the numbers of greylag geese foraging in our experimental control plots (from May 2015 until May 2016). From the camera footage, seven randomly chosen days per month (e.g. the 1th, 5th, 10th, 15th, 20th, 25th and the 30th of each month) were analysed to assess the average number of greylag geese/day visiting the plot.

2.4 | Surface elevation

To evaluate the effect of standing biomass on marsh accretion, we measured the surface elevation of each plot at the start of the experiment (year 1: December 2014), after the exclosure period (year 2: October 2016) and 1 year after the exclosures had been removed (year 3: October 2017). Surface elevation was measured over the same plot gradient as vegetation biomass. Starting at 0.5 m from the first plot pole, we measured the elevation at 0.5-m intervals until the final plot pole at 6 m, using an optical levelling instrument (Spectra Precision® Laser LL500 and Spectra Precision® Laser HL700 laser receiver by Trimble) with an accuracy of <0.5 cm, calibrated to a fixed point of which the height was determined using RTK-GPS (Real Time Kinematic Global Positioning System, Topcon GRS-1 RTK rover).

2.5 | Data analyses

The effect of herbivore exclusion on vegetation biomass and surface elevation was analysed over the plot gradient as this enabled us to analyse the marsh expansion over time. To test for statistical differences in vegetation development and the associated surface elevation between exclosure treatment levels (C vs. X), we compared the fit of a single regression on the combined data of both exclosure treatments with separate regressions per treatment level. Specifically, we followed the following procedure: we first tested whether the response variable (biomass or surface elevation) was best described by a linear or a nonlinear regression over the plot gradient based on Akaike's information criterion (AIC). Next, if both treatment levels were best described by a nonlinear function, we compared the AIC value of a single global regression with two separate nonlinear regressions. If, however, both treatments levels were best described by a linear function, we tested whether the slope and intercept were significantly different using a two-tailed F-test. Finally, if one treatment was best described by a nonlinear function, whereas the other was best described by a linear function, we performed a linear regression on both treatment levels and tested whether slope and intercept were significantly differently using a two-tailed F-test.

For the nonlinear regression used in our statistical analyses, we fitted a four-parameter sigmoid Hill function that allows for extrapolating ecologically relevant parameter values such as the maximum biomass and the spatial extent of the vegetation:

$$y(x) = y_{min} + \frac{y_{max} - y_{min}}{1 + 10^{\log k - \log x \cdot H}} \tag{1}$$

with $y(x)$ being the standing biomass or surface elevation at a certain point x along the plot gradient. Maximum and minimum values are represented by y_{max} and y_{min}, respectively, and k indicates the point x where the S curve is halfway between y_{max} and y_{min}. Finally, H represents the Hillslope, i.e. the steepness of the curve. Parameter values were estimated numerically by minimizing the sum-of-squares over 1,000 iterations, with y_{min} and y_{max}

constrained between lowest and highest value of the dataset, and k constrained to the extent of our plot (0–6 m). Statistical differences between two nonlinear functions were reported as differences in AIC value (dAIC) between a global, single regression versus different regressions per treatment level. For the linear functions, we report the F-value with the regression degrees of freedom and residual degrees of freedom in subscript. All data analyses were performed using the software programs R (version 3.4.0, R Development Core Team, 2017) and Graphpad Prism 6 (Graphpad software, San Diego, CA, USA).

3 | RESULTS

3.1 | Herbivory effect on standing biomass

Camera trap observations revealed the highest number of greylag geese visiting the experimental plots (~3 geese/day) during the breeding season (March to June) (Figure S6). After the first growing season, the vegetation development over the plot gradient in both the exclosures and the control plots was best described by nonlinear functions (Table S2). However, the two treatment levels differed (dAIC = 36.72) with a higher standing biomass in the exclosure plots compared to the controls. This biomass enhancement in the exclosures was primarily the result of an increase of *Phragmites* biomass in the standing vegetation (y_{max} total: 2,152 g/m^2; y_{max} *Phragmites*: 1,668 g/m^2 [X] vs. y_{max} total: 1,261 g/m^2; y_{max} *Phragmites*: 975 g/m^2 (C); Figure 1a,b). After the second growing season, total standing vegetation biomass in the former bare areas (~0–3 m) was strongly enhanced in exclosures compared to the control plots (Figure 1b). This caused the previous sigmoid response of total standing biomass over the plot gradient to be replaced by a linear response with a high offset and a weak slope (Table S2). In fact, the fitted equation (slope: 28 g m^{-2} m^{-1}) did not significantly diverge from a flat line at 2,308 g/m^2 ($F_{1,70}$ = 1.8; p = 0.668). *Phragmites* development in the exclosures continued to differ significantly from the control plots (dAIC: 67.48). However, the much higher biomass at the lower end of our exclosure plots (~0–2 m of the plot gradient) compared to controls was caused by a sevenfold higher *Bolboschoenus* biomass in this section (mean: 1,695 g/m^2 [X] vs. 230 g/m^2 (C); Figure S7b).

After the exclosures had been removed, vegetation response over the plot gradient in the exclosures was best described by a four-parameter Hill equation, whereas the vegetation response of the controls was now better described by a linear function (Table S2, Figure 1c). By fitting a linear function to both treatment levels (C vs. X), we found the vegetation biomass to remain higher over the full plot gradient in the former exclosures than in the control plots, but to show no significant differences in relative response over the plot gradient (mean slope: 231 g m^{-2} m^{-1} (X & C); $F_{1,140}$ = 1.96; p = 0.164; intercept: 370 g/m^2 [X] vs. −448 g/m^2 (C); $F_{1,141}$ = 24.25; p < 0.001). Furthermore, we found the effect of herbivore reintroduction in the exclosures to be far larger on *Bolboschoenus* than on *Phragmites*, as the biomass response of *Phragmites* in the third year was not significantly different from
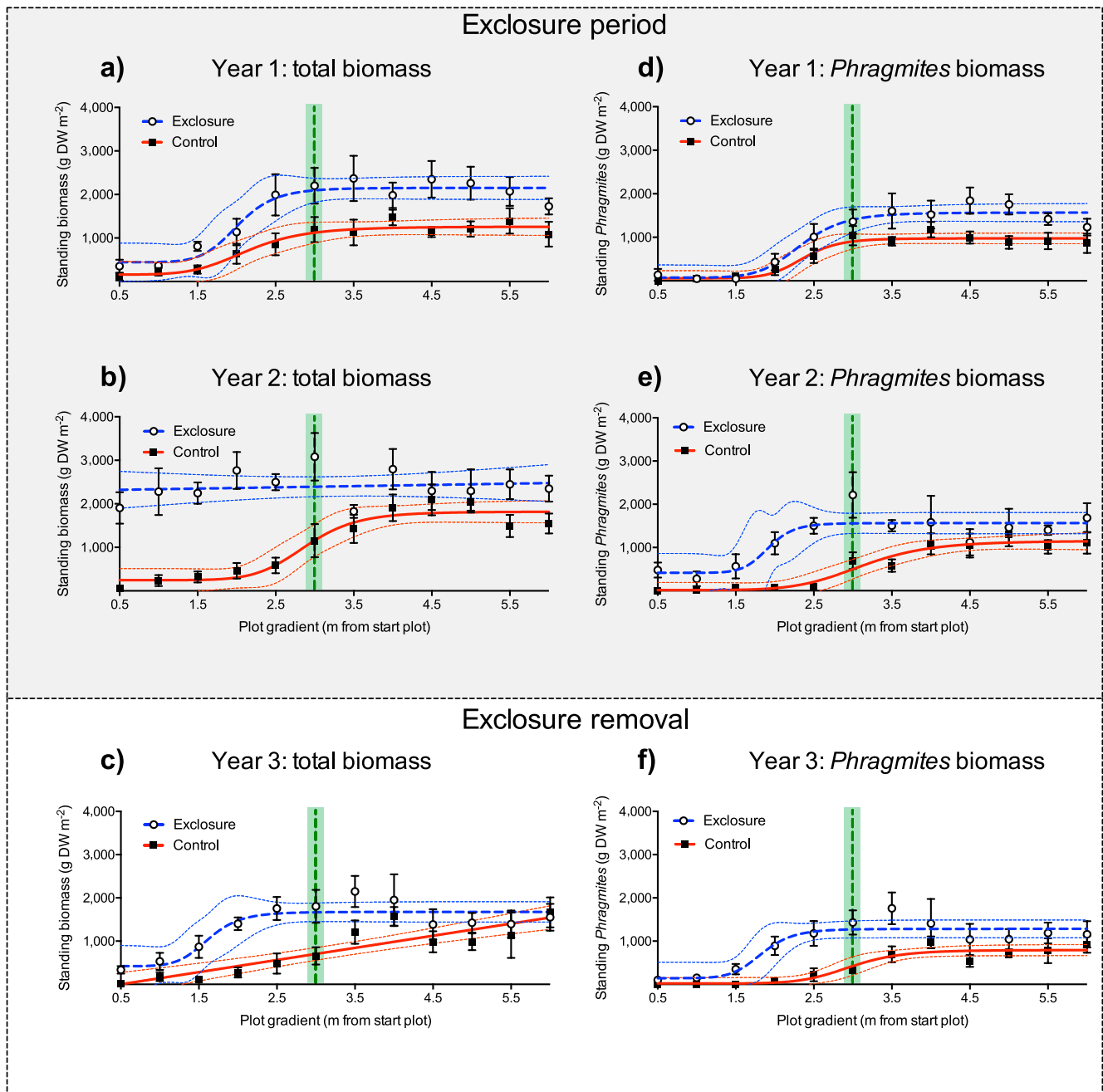
FIGURE 1 Average standing total biomass (a–c) and standing *Phragmites* biomass (d–f) in grazed (control, C; red lines) and ungrazed (exclosure, X; blue dashed lines) plots (*N* = 6) over the plot gradient from bare (0.5 m) to dense vegetation (6 m) after each growing season (see Figure S3 for visual plot description). Years 1 and 2 (upper panels: a, b & d, e) depict the exclosure period, in the third year of the experiment (lower panels: c & f), the exclosures were removed. The green dashed vertical line indicates the position of the reed edge (mean ± *SE*) at the start of the experiment (December 2014) (see Figure S4 for analyses on the *Phragmites* edge over consecutive years). Red and blue lines represent the linear and nonlinear regressions and 95% confidence bands (see Table S2 for the parameter values). Points represent the mean ± *SE*

the *Phragmites* biomass in the exclosure plots in the second year (dAIC: −4.15; Figure 1e,f; Table S2). One year after the exclosures had been removed, the expansion of *Phragmites* into the bare areas was halted, but it did also not retreat back to its former extent as indicated by the *k* exponent (*k*: 1.92 m [$X_{year\ 2}$] vs. 1.83 m [$X_{year\ 3}$]; Figure 1e,f and Figure S4 for additional analyses).

3.2 | Surface elevation

At the start of the experiment, before the first growing season, surface elevation over the plot gradient was best described by a single linear regression to the combined data of both treatment levels (dAIC: −3.79; Figure 2a). At the end of the exclosure period, however,
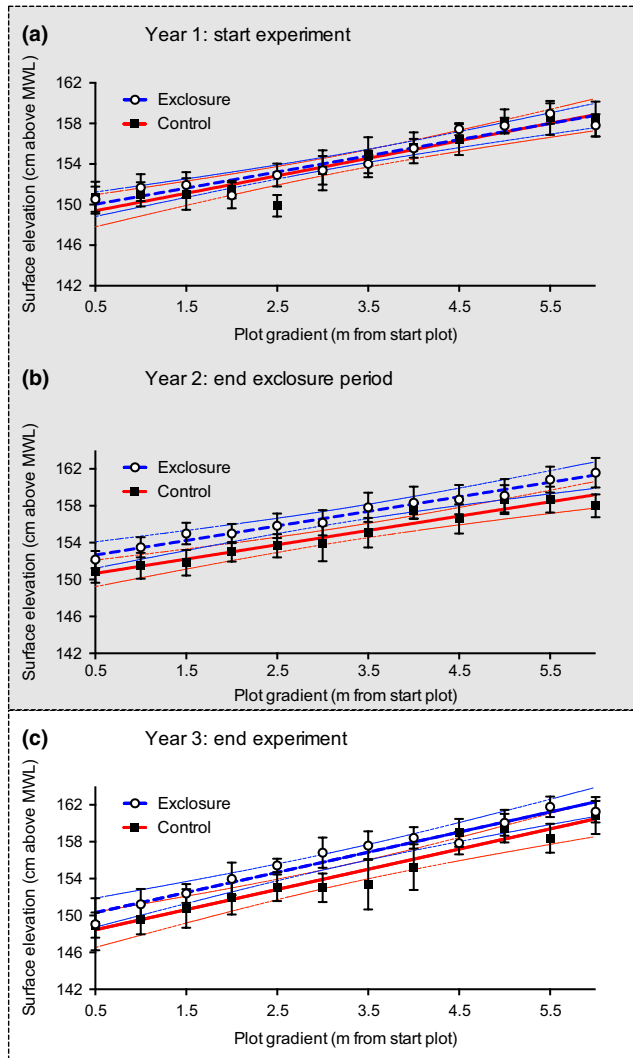
FIGURE 2 Average surface elevation (cm above mean water level, MWL) in grazed (control) and ungrazed (exclosure) plots over the gradient from bare (0.5 m) to dense vegetation (6 m) after each growing season. Years 1 and 2 (a, b) depict the exclosures period, in the third year of the experiment (c), the exclosures were removed. Lines represent the linear regressions and 95% confidence bands (see Table S2 for the parameter values). Error bars represent ±*SE*

it was better described by separate linear regressions per treatment (dAIC: 9.86; Figure 2b). Enhanced surface accretion in the exclosure plots was apparent over the full gradient, with the slopes of the fitted linear equations not being significantly affected, while the intercepts differed per treatment (mean slope: 1.6 cm/m; $F_{1,140} = 0.01$; $p = 0.931$; intercept: 150 cm [X] vs. 148 cm [C]; $F_{1,141} = 14.61$; $p < 0.001$; Figure 2b). After the exclosures were removed, surface elevation of the exclosure plots remained significantly higher compared to the control plots (mean slope: 2.2 cm/m; $F_{1,140} = 0.001$; $p = 0.992$; intercept: 147 cm [X] vs. 145 cm [C]; $F_{1,141} = 7.87$; $p = 0.006$, Figure 2c). Moreover, the surface elevation response of the exclosures did not change after the exclosures were removed (X year 3 vs. X year 2: mean slope: 1.9 cm/m, $F_{1,140} = 3.39$; $p = 0.07$; mean intercept: 150.5 cm, $F_{1,141} = 1.42$; $p = 0.235$; Figure 2b,c).

4 | DISCUSSION

Previous work has shown that grazing may induce state shifts in ecosystem structure and functioning, especially when it interacts with growth-inhibiting feedbacks in harsh, low-productivity environments (Jefferies et al., 2006; van de Koppel et al., 1997). Here, we experimentally demonstrate that in high-productivity environments, ecosystem structure and functioning is created and maintained by herbivores in interaction with self-reinforcing feedbacks of the dominant plant species that inhibit grazing at high standing biomass. Specifically, we found that in the absence of grazing, vegetation rapidly colonized the bare area of the marsh that functions as a roosting site for many waterbird species including greylag geese (Bakker et al., 1999) (Figure 1a,b). Next, following herbivore reintroduction, we found the two dominant species in our study system to vary greatly in their resilience to grazing (Figure 1c). *Bolboschoenus maritimus*, first colonized the bare areas, but was immediately removed once the geese were reintroduced. The dominant species of our study system, *P. australis*, on the other hand, more gradually expanded into the bare area during the exclosure period to form dense stands and did not show any sign of retreat upon geese reintroduction (Figure 1f, Figure S4). Given our observation that the geese do not significantly graze on dense, over 1-year-old reed stands in both exclosure and control plots, our findings suggest that the observed expansion is rather persistent in nature. Earlier model simulations on low-productivity systems suggest that overgrazing can induce state shifts in ecosystem structure that are notoriously difficult to reverse (Box 1a,b). By contrast, our experimental results imply that in high-productivity ecosystems dominated by vegetation that exerts grazing-inhibiting feedbacks, continuous grazing is required to maintain ecosystem heterogeneity (Box 1c,d). Consequently, temporary herbivore reductions may induce a state shift to a homogeneous fully vegetated state that prevents future grazing. From the management perspective of productive grazed ecosystems, it is therefore important to assess whether changes in vegetation structure are naturally reversible or persistent, as short-term changes in grazing pressure may have long-term consequences. Next, if state shifts are indeed persistent, it is vital to maintain grazer densities at levels high enough to prevent vegetation encroachment to preserve the desired heterogeneous ecosystem state.

4.1 | Species-specific growth strategies determine response to herbivore reappearance

The global increase in goose populations has exposed natural wetlands world-wide to increased grazing intensity (Esselink et al., 1997; Gauthier et al., 2005; Jefferies et al., 2006; Van Eerden, Drent, Stahl, & Bakker, 2005). However, the impact of geese on the spatial structure or vegetation composition of a natural wetland may differ depending on locally prevailing conditions. In contrast to the large bare areas created by grubbing geese in artic saltmarshes that remain empty for years to come (Abraham et al., 2005; McLaren & Jefferies, 2004), recolonization of bare patches by vegetation was not impeded in our highly productive brackish system. In fact, we

Box 1 NaN Spatial heterogeneity in low- and high-productivity grazing systems

(a)

(b)

(c)

(d)
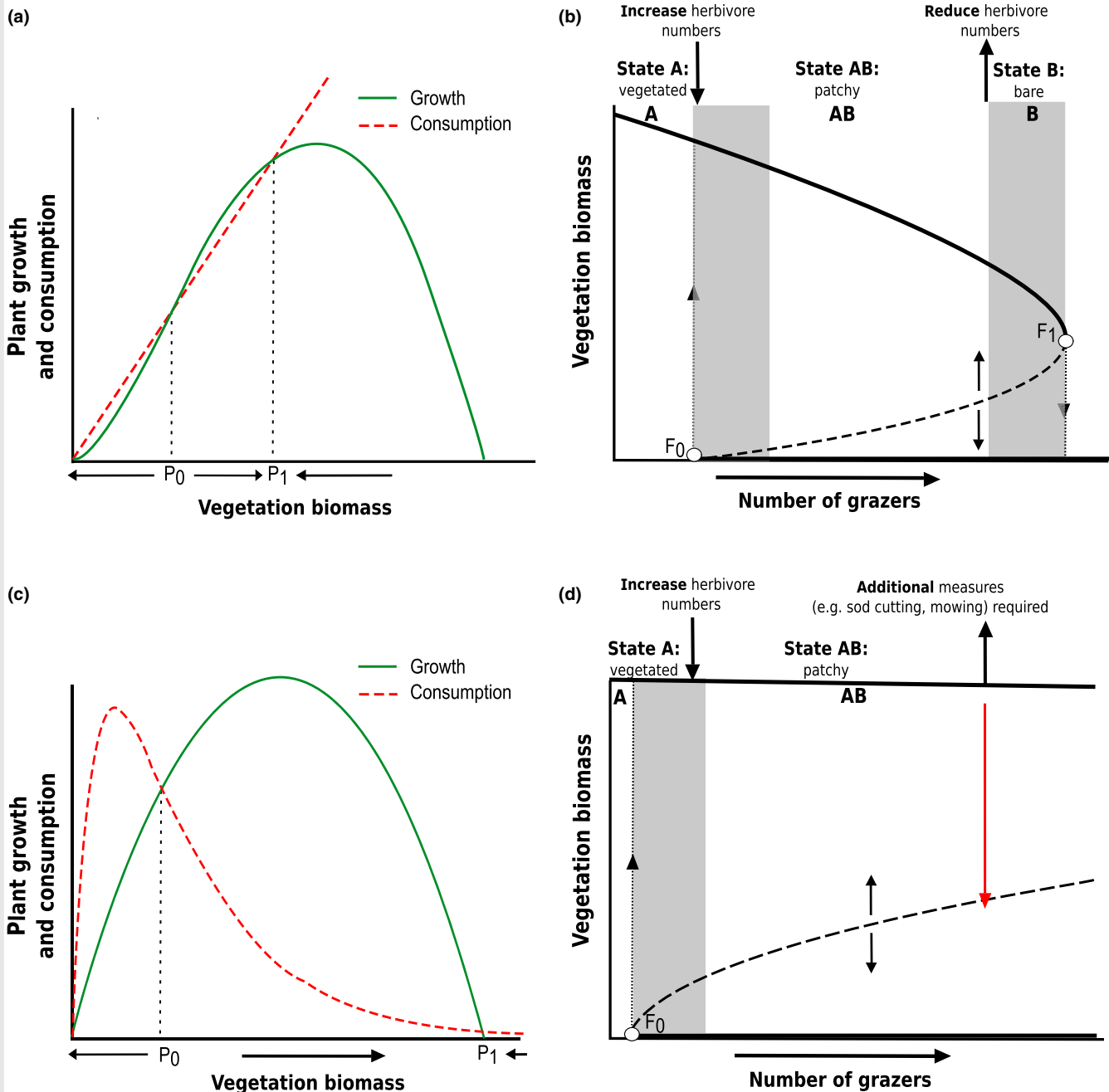
We constructed two simple mathematical models to illustrate how the dynamics of two contrasting types of heterogeneous grazed ecosystems differ in response to grazing and management decisions (for model specifications see Appendix S2). Model 1 (a, b) simulates low-productivity environments (e.g. arid ecosystems, arctic salt marshes) where soil degradation reduces growth (a, green line) at low standing biomass (a, left of P_0) (van de Koppel et al., 1997). Consequently, vegetation cannot persist when grazing exceeds a critical intensity (F_1 in b). To preserve heterogeneity, management can either reduce (b, right grey square) or increase (b, left grey square) the numbers of grazers depending on initial conditions. Model 2 (c, d) symbolizes high-productivity grazed systems (e.g. reed marshes and intertidal seagrass meadows) where vegetation inhibits grazing (c, red dashed line) at high standing biomass (c, right of P_0). As a consequence, herbivores will maintain the heterogeneous state by removing all vegetation below the critical biomass threshold (P_0 in c). However, once established, vegetation persists irrespective of herbivore numbers (note the absence of F_1 in d). To preserve heterogeneity, management should be aimed at keeping herbivore numbers high enough. To restore open areas, measures such as sod cutting (Figure S8) or mowing (d, red arrow) will be required to lower vegetation biomass beyond the unstable equilibrium (d, dashed black line).

found that after 2 years of herbivore exclusion, vegetation biomass in the former bare area was equal to the biomass in the already vegetated area (Figure 1b). However, vegetation composition was dissimilar as *Bolboschoenus maritimus* rapidly colonized and dominated the former bare areas (0–2 m of plot gradient), whereas the dominant species of the standing marsh vegetation, *P. australis*, more gradually expanded its range (Figure 2b,e). After exclosure removal, the reintroduced geese immediately recreated bare patches at the lower end of the plots by grazing on *Bolboschoenus* (Elschot et al., 2017; Esselink et al., 1997). The slower expanding reed vegetation in the middle part of the plots, however, remained stable and showed little response to herbivore reintroduction (Figure 1f, Figure S4). Although, our experiment only lasted three growing seasons, we observed an overall expansion of *Phragmites* of 1.4 m from the original edge (3 m) (Figure S4), whereas the edges in the control plots showed year-to-year fluctuations but remained relatively stable at 3 m. Most likely, the dense and tall *Phragmites* stands prevent the geese from feeding on young emerging shoots in spring (van den Wyngaert et al., 2003). This self-facilitative effect was further stimulated by ~2 cm accretion of the substrate in the former exclosure plots over a 2-year period (Figure 2b), which promotes growth of *Phragmites* (Elschot et al., 2017). Moreover, since geese foraging predominantly occurs under waterlogged conditions, surface accretion can greatly hamper the grazing activities by greylag geese when it prevents water logging or shortens its duration.

4.2 | Ecological functioning of spatially heterogeneous wetlands

Spatial heterogeneity is considered to be important for the functioning of most ecosystems, because it can increase ecosystem resilience, enhance primary productivity and promote overall biodiversity (Adler et al., 2001; Eriksson et al., 2010; Hovick, Elmore, Fuhlendorf, Engle, & Hamilton, 2015; van de Koppel et al., 2005). In our system, both waterbirds and vegetation ultimately benefit from such a heterogeneous state. The geese, for example, use the bare, wet areas as a roosting area and profit from the vegetation to conceal their nests from potential predators, while they simultaneously feed on the young colonizing plants at the marsh edges (Barton & Koricheva, 2010; Boege & Marquis, 2005; Elschot et al., 2017; Kristiansen, 1998). In this way, they hamper the further expansion of the marsh' climax species *Phragmites*, thereby maintaining the open structure and valuable roosting function of the marsh. This in turn, prevents terrestrialization by allowing the transport of accumulated litter during storm surges beyond the marsh interior (Hackney & Bishop, 1981). *Phragmites* generally grows at the land–water interface, and as its expansion progresses, the landwards stands increasingly accumulate litter which can eventually reduce growth (Clevering, 1997; van den Wyngaert et al., 2003; van der Putten, Peters, & Van Den Berg, 1997). Hence, a heterogeneous landscape in which both bare and vegetated areas co-occur likely enhances overall productivity and allows the coexistence of multiple ecosystem functions in these reed-dominated brackish marshes.

4.3 | Management implications

The global goose expansion and their increasing reliance on agricultural resources, and wetlands increasingly raises conflict with farmers and nature managers, leading to the formulation of management strategies to reduce geese numbers (Abraham et al., 2005; Bakker et al., 2016; Bauer, Lisovski, Eikelenboom-Kil, Shariati, & Nolet, 2018; Castelijns & Jacobusse, 2010; Dokter et al., 2018; Esselink et al., 1997; Fox & Madsen, 2017; Jefferies et al., 2006; Klok et al., 2010; Ostendorp, 1989; Simonsen, Madsen, Tombre, & Nabe-Nielsen, 2016). However, whereas most studies report on negative impacts of geese on wetlands, our study highlights that in high-productivity reed marshes, geese can positively affect ecosystem functionality (in our case roosting and nesting habitat) by maintaining patchiness. Moreover, we experimentally demonstrate that a temporary reduction in geese grazing may induce lasting changes in vegetation patchiness that are difficult to reverse naturally. Specifically, our findings imply that once open patches become fully vegetated, they can become highly resistant to grazing, irrespective of the number of geese in the system (Box 1b). Hence, even temporal decreases in geese numbers may induce a sudden, and potentially persistent expansion of the reed patches, shrinking bare areas required for roosting. For ecosystems controlled by such mechanisms, we suggest that management strategies may need to actively compensate sudden dips in grazing pressure, for instance by mowing or sod cutting (see Figure S8).

Overall, our findings suggest that when plant species exclude grazing beyond certain critical vegetation thresholds – e.g. density, biomass or age – the long-term spatial structure and conservation value of an ecosystem can be significantly altered by herbivore fluctuations. In seagrass meadows, habitat heterogeneity may be lowered by temporary herbivore absence, because it allows previously grazed seagrass hollows to accumulate sediment, thereby excluding future grazers and homogenizing the system (van der Heide et al., 2012). In wood pastures, on the other hand, temporary herbivore absence can increase habitat diversity by allowing establishment of shrubs that are able to persist after herbivore reappearance (Smit, Bakker, Apol, & Olff, 2010). Although temporary absence or exclusion of grazers may stimulate patchiness when the initial system state is bare or dominated by grazing-tolerant vegetation, our findings emphasize the need to timely restore grazing when the goal is to maintain a heterogeneous mosaic. This illustrates that, depending on the initial state, the desired management outcome, and the current state of the ecosystem, managers should either stimulate or discourage herbivore fluctuations. Finally, our work overall highlights that not only direct and immediate effects but also indirect and long-term consequences of herbivore perturbations should be understood for the successful long-term conservation of heterogeneous grazed ecosystems.

AUTHORS' CONTRIBUTIONS

V.C.R., T.v.d.H., L.P.M.L. and H.O. designed the study; V.C.R., P.M.J.M.C., S.C.S.H., J.H.T.H. and M.v.d.A. conducted the practical work; J.v.d.K. performed model simulations; V.C.R. analysed the data; V.C.R. wrote the first draft of the manuscript. All authors contributed substantially to revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Data Archiving and Networked Services (DANS) EASY https://doi.org/10.17026/dans-2xd-67qj (Reijers et al., 2019).

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