

# Vegetation patch dynamics in rangelands: How feedbacks between large herbivores, vegetation and soil fauna alter patches over space and through time

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## Abstract

**Aim:** Large herbivore grazing is a popular conservation management tool to promote vegetation structural diversity of rangelands. However, vegetation patch dynamics, that is, how patches of grazing-defended tall vegetation and grazer-preferred short lawns shift over space and time, is poorly understood. Here, we describe a new conceptual framework for patch dynamics within rangelands, combining theories of classical cyclical succession, self-organization and multitrophic feedbacks between grazers, vegetation and bioturbating soil fauna.

**Location:** We use the cattle-grazed salt marsh of the island Schiermonnikoog, The Netherlands, as a model system. The grazed salt marsh is characterized by distinct tall vegetation patches dominated by the grazing-defended rush *Juncus maritimus* and grazing-intolerant grass *Elytrigia atherica*, surrounded by a matrix of grazing lawn (dominated by *Festuca rubra*).

**The Framework:** Based on previous observational and experimental studies, we propose a cyclical patch dynamic where plant species composition and structure transitions through four phases: patch initiation (a) occurs when the grazing-defended rush *J. maritimus* establishes in the grazed lawn. Patch establishment (b) follows when the grazing-intolerant grass *E. atherica* establishes in the patch due to associational defence by *J. maritimus* and produces a large amount of litter that attracts the key bioturbating amphipod *Orchestia gammarellus*. Patch expansion (c) occurs when *O. gammarellus* activities improve soil properties of the patch, which favours *E. atherica* growth, leading to *E. atherica* competitively displacing *J. maritimus* in the centre of the patch. Patch degeneration (d) follows when cattle enter the enlarged patch to consume *E. atherica* in the centre, trample the soil, displace *O. gammarellus* and decrease vegetation cover, opening space for grazing-lawn species to invade. The cycle restarts when remnants of the rush *J. maritimus* in the degenerated patches (or individuals recently established from seed dispersal) initiate new patches in the grazing lawn.

Christian Smit and Isabelle P. R. Buyens contributed equally as first author.

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**Synthesis:** Our proposed patch-dynamic model provides a means to describe the mechanisms driving vegetation patch dynamics and serves as a foundation for further experimental and observational exploration, not only for this specific system, but more generally for grazed systems worldwide that show patches of typical grazing-defended and grazer-preferred vegetation.

**KEYWORDS**

bioturbation, *Elytrigia atherica*, facilitation, grazing, herbivory, *Juncus maritimus*, *Orchestia gammarellus*, positive feedbacks, salt marsh, vegetation patch dynamics

## 1 | INTRODUCTION

Grazing by large herbivores is commonly used in conservation and restoration management with the objective of maintaining or increasing biodiversity (Van Wieren & Bakker, 2008; Smit & Putman, 2011; van Klink et al., 2016). Indeed, large grazers can have broadscale impacts on the diversity of plant species and vegetation structure through various trophic and non-trophic effects (Adler et al., 2001; Bakker et al., 2020). These effects include impacts on vegetation structure and composition by trampling and consuming plant material, and through compacting the soil (Tuomi et al., 2021; Zhang et al., 2022), as well as impacts on vegetation through changes in soil nutrient cycles via dung and urine deposits (Day & Detling, 1990; Zhang et al., 2022), on soil-dwelling organisms (e.g. small mammals and soil arthropods – Lagendijk et al., 2019; Tuomi et al., 2021), and by altering plant–plant interactions (Smit et al., 2009; Kelemen et al., 2019).

A globally observed outcome of these effects of large herbivores are mosaic or ‘patchy’ vegetation types (Belsky, 1986; Frank et al., 1998; Olf et al., 1999; Howison et al., 2017), where the heterogeneous vegetation structure comprises discrete aggregates of tall grazing-defended plants (e.g. chemically or physically defended) in a matrix of shorter grazer-preferred plants (e.g. high forage quality or palatability). While our understanding of the mechanisms underlying vegetation mosaics under grazing by large herbivores has increased over the last decades, and has even led to better predictions of the required combination of abiotic conditions to form patchy landscapes (Howison et al., 2017), we still know relatively little about the processes that drive the shifts in vegetation patches over space and time. From a conservation point of view, dynamic patch shifting is considered more favourable to biodiversity, stability and resilience than a static system that lacks shifting vegetation patches (Holling, 1973; Folke et al., 2004). At present, however, it remains unclear what drives the processes of vegetation patch formation and dynamics in rangelands (see also Veldhuis et al., 2018), with rangelands defined as land carrying natural or semi-natural vegetation which provides a habitat suitable for herds of wild or domestic ungulates (Pratt et al., 1966), thus including a wide range of grazed grasslands such as prairies, steppes, desert shrublands, tundras, and salt marshes. Here, we describe several key theories on vegetation pattern formation and combine them to come to a new conceptual

framework for an improved mechanistic understanding of vegetation patch dynamics in rangelands.

## 2 | VEGETATION PATCH FORMATION IN RANGELANDS

Watt (1947) was the first to propose a generalized explanation for the cyclic nature of successional changes in plant composition of vegetation patches. This classical cyclic succession model proposes a successional cycle consisting of an upgrade, downgrade and gap phase (Watt, 1947). The upgrade cycle comprises the creation of a suitable patch habitat where the dominant interaction is positive and productivity increases, whereas the downgrade phase describes the disintegration of the components and productivity decreases. The gap phase is a time-limited interval at the end of the upgrade phase where the cover of the dominant species has started to decrease and other plant species can establish, a concept incorporated into the theory of gap phase dynamics of forests succession (for review, see Yamamoto, 2000). Watt's classical cyclic succession model is suitable in describing the general successional changes of vegetation structure of patches through time, but it neither describes how multiple successional stages co-exist within patches nor specifically includes the role of other trophic-level organisms such as large grazers.

A second important theory that seeks to explain vegetation patchiness focuses on the process of spatial self-organisation, that is, global patterns that emerge only from interactions between lower trophic levels, with important effects on primary productivity and ecosystem resilience (Rietkerk & van de Koppel, 2008; Verwijmeren et al., 2012, 2019; Siero et al., 2019). In rangelands, spatial self-organization processes play an important role, as plants interact with each other at small spatial scales through both competition and facilitation. Plant species can facilitate each other by protecting against grazing (Hay, 1986; Smit et al., 2005, 2007), while also competing locally for abiotic resources and light. However, they also indirectly interact with each other at larger spatial scales by means of the grazers that exert grazing pressure over the landscape. Grazing pressure can locally vary as the grazing animals select the most profitable (that is, less defended, more palatable) patches, often amplifying heterogeneity in vegetation composition (Ruifrok et al., 2014), and generating a landscape

where biodiversity is closely linked to patch dynamics. Spatial self-organization has been shown to be very useful to explain critical transitions in various ecosystems (Rietkerk & van de Koppel, 2008; van Wesenbeeck et al., 2008; Liu et al., 2014; Rietkerk et al., 2022), for example from a healthy (vegetated) to a degraded (bare) state, typically preceded by a rapid drop in the number and size of vegetated patches (Kefi et al., 2007; Berdugo et al., 2017; van Belzen et al., 2017). Such critical transitions are generally hard to reverse, and early detection is of crucial importance for timely conservation management interventions (Kefi et al., 2007; Nijp et al., 2019). Spatial self-organization is regularly applied to describe dynamics of patchy (semi-)arid systems with mixed vegetated and bare patches. However, the theory is not commonly used to explain patch dynamics in more fertile grazed systems characterized by multispecies communities, despite that vegetation patch dynamics are a governing and characterizing feature in these landscapes (Nolte et al., 2014; Howison et al., 2017; Bakker et al., 2020).

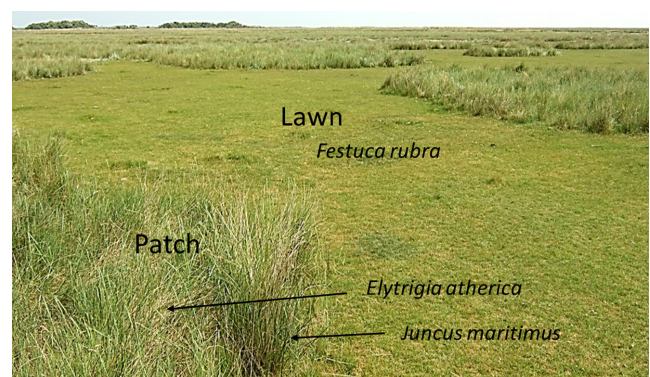
A third group of conceptual models incorporates the impacts of large grazers at the landscape level. Olf et al. (1999) proposed that large free-ranging grazers initiate and perpetuate a cyclic succession of the diverse mosaic of grassland, thicket and trees in grazed woodlands: grazing-defended (spiny) shrubs provide associational defence and facilitate the establishment of palatable tree species. Over time the palatable trees outcompete the shrubs by shading and, as a result, no longer receive the benefits of associational resistance, with grasses re-establishing after the death of the trees (Olf et al., 1999). Conceptually, the idea resembles a Rock-Paper-Scissors system (Bayliss et al., 2020) where, under influence of large grazers, dynamic intransitive interactions occur between different plant species (Laird & Schamp, 2006; Soliveres & Allan, 2018): the grazing-tolerant lawn species (Rock) are invaded by tall grazing-defended species (Paper), which are in turn outcompeted by spatially associated competitive grazing-intolerant plant species (Scissors), and then these are lost again through grazing and the patch turns into lawn (Rock). The concept of cyclic shifting mosaics has successfully been applied to explain spatial dynamics in various grazed wood pastures and savannah landscapes in Europe (Smit et al., 2005; Smit et al., 2008; Van Uytvanck & Hoffmann, 2009; Van Uytvanck et al., 2010; Smit & Verwijmeren, 2011). Recently, the importance of bioturbating macrodetritivores such as earthworms, termites and dung beetles for maintenance of heterogeneity in vegetation mosaics has been acknowledged: their bioturbation activities can counteract the impacts of (biocompacting) large grazers on soil physical and chemical properties and so generate spatial heterogeneity in soil conditions, locally promoting the growth of taller vegetation in grazed systems (Howison et al., 2017). The strength of these below-ground processes varies both spatially and temporally (Neutel et al., 2007; Schrama et al., 2013), and it is very likely that this variation thus contributes to vegetation patch dynamics in grazed rangelands, but this has yet to be explicitly tested.

Thus, despite these three main groups of ecological theory on vegetation patterning, we still poorly understand the dynamics and

underlying ecological processes of vegetation patches in rangelands (Veldhuis et al., 2018). Here, we propose a new conceptual framework to mechanistically explain patch dynamics within rangelands, combining theories of classical cyclical succession, self-organization and multitrophic feedbacks between brown- and green-food webs. We propose a detailed hypothesis of how large grazers, plant species, and bioturbators interact to determine vegetation patch dynamics in our model system, cattle-grazed salt marshes. We discuss how our framework could be applied to other types of rangelands with patch dynamics, and the relevance for restoration and conservation management.

### 3 | MODEL SYSTEM: CATTLE-GRAZED SALT MARSH OF SCHIERMONNIKOOG

To illustrate our conceptual framework for patch dynamics, we refer to the naturally occurring vegetation patches in the cattle-grazed salt marshes of the back-barrier Waddensea island Schiermonnikoog (53°29' N, 6°13' E), the Netherlands (Figure 1). The average temperature is 17.6°C in August and 3.6°C in February and the annual rainfall is c. 800 mm ([www.climate-data.org](http://www.climate-data.org)). The salt marsh is characterized by a salt-water flooding gradient with inundation decreasing with elevation, resulting in a vertical vegetation zonation based on plant species' salt and anoxia stress tolerance abilities (Olf et al., 1997; Bockelmann et al., 2002; Howison et al., 2015). Cattle grazing has strong impacts on vegetation structure in the eastern salt marsh which has a long history (>100 years) of rangeland use. The cessation of cattle grazing in the salt marsh in the 1950s allowed for the dominance of the highly competitive grass, *Elytrigia atherica*, and the development of monoculture with a decrease in plant diversity (Bakker, 1985). To increase plant diversity, low-density heifer cattle grazing (stocking rate of 1.3–1.7 animals ha<sup>-1</sup>) during the months of May to October



**FIGURE 1** Patchy vegetation patterns in the cattle-grazed salt marshes of Schiermonnikoog, with short grazed lawns dominated by the grazing-tolerant grass *Festuca rubra*, and tall patches formed by grazing-defended *Juncus maritimus* (dark green) dominating at the patch edges, and the grazing-intolerant competitive tall grass *Elytrigia atherica* (grey-green) dominating the interior of the patches (photograph courtesy: Matty Berg).

was implemented yearly since 1972 (Bakker, 1978) and maintained ever since. Small herbivores (body mass of 1–10 kg) include the brown hare (*Lepus europaeus*) that is present all year round (Schrama et al., 2015a) and spring-staging brent geese (*Branta bernicla bernicla*) and barnacle geese (*Branta leucopsis*; van der Wal et al., 2000).

Within the cattle-grazed salt marsh, distinct tall vegetation patches of ca. 10–300 m<sup>2</sup> occur that are dominated by the grazing-defended rush *Juncus maritimus* Lam. and grazing-intolerant grass *E. atherica* (Link) Kerguelen, scattered throughout the matrix of grazing lawns dominated by the grasses *Festuca rubra* L. and *Puccinellia maritima* (Huds.) Parl. (Howison et al., 2015; Figure 1). The rush *J. maritimus* is distributed in the salt marshes of Europe, West Africa and northern Asia (Menéndez, 2008) and is a long-lived, evergreen rush that spreads radially via rhizomes beneath the soil surface. Moreover, the rush deters grazing cattle because of its structurally tough, sharp-tipped stems that grow to c. 1 m in height (Fitter & Peat, 1994). In later successional stage salt marshes where cattle are excluded, the grass *E. atherica* is able to outcompete other plants and become the dominant species (Bockelmann et al., 2002; Bockelmann et al., 2003). The amphipod *Orchestia gammarellus* is the key bioturbating macrodetritivore in this salt marsh (Howison et al., 2015, 2016b; Schrama et al., 2015b; Smallegange & Berg, 2019) and occurs in highest densities in the low-elevation salt marsh where inundation is most frequent (Smallegange & Berg, 2019). Through digging and feeding activities, the amphipod promotes soil aeration, water infiltration and nutrient mineralization (Schrama et al., 2015b; Howison et al., 2016b).

## 4 | NEW FRAMEWORK FOR PATCH DYNAMICS IN RANGELANDS

We use this grazed salt-marsh system to illustrate a new vegetation patch dynamics framework (Figure 2). The patch dynamic consists of four key phases, that follow each other sequentially and in a cyclical way: (a) the initiation of patch formation by the establishment of the grazing-defended plant, (b) the establishment of the grazing-intolerant beneficiary plant within the patch, (c) expansion of the patch, and (d) degradation of the patch (after which the cycle starts again with patch initiation).

### 4.1 | Patch initiation

The patch initiation phase (Figure 2a) occurs when a grazing-defended plant species (here: the rush *J. maritimus*) establishes as a small patch amongst palatable grazing-lawn species (here: *F. rubra*). This invasion and establishment may happen via seed and/or via vegetative expansion. In salt marshes, seed dispersal of *J. maritimus* mainly occurs via water (Wolters et al., 2004) and wind, and sometimes even by endozoochory of cattle (Bakker et al., 2007), although the plant is not a preferred species. Vegetative expansion of

*J. maritimus* happens via rhizomes that radially spread beneath the soil surface. The rush is likely to promote self-generation through positive feedbacks via soil bioturbation (decompaction) and aeration via its roots, and trapping plant litter in the grazed salt marsh (Howison et al., 2015). This gives *J. maritimus* the advantage against the surrounding palatable plant species (e.g. *F. rubra*) under the disturbance of cattle and allows for lateral spread into the short-grazed lawns. Because the rush is structurally defended from large herbivores, it protects itself and the immediately adjacent plants from cattle grazing (Fitter & Peat, 1994; Howison et al., 2015), a process also known as associational avoidance (Milchunas & Noy-Meir, 2002) and a pattern termed defense guild (Atstatt & Odowd, 1976).

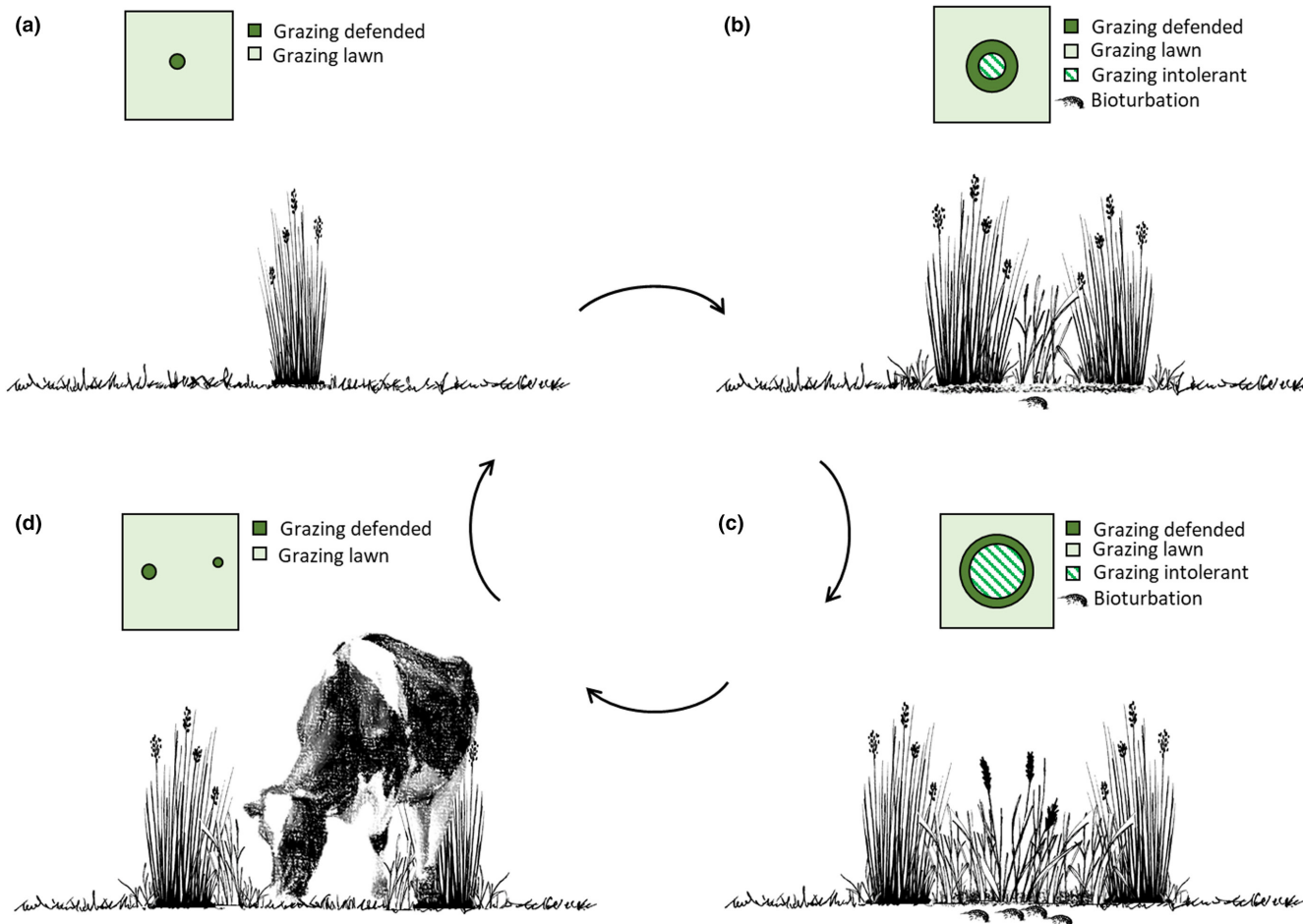
### 4.2 | Patch establishment

The establishment and growth of the grazing-defended *J. maritimus* (Figure 2b) creates niche space amongst its canopy by creating shade, aerating the soil and reducing compaction through root and stem growth, trapping plant litter and deterring cattle from grazing (Howison et al., 2015). This niche space is suitable for the highly competitive and grazing-intolerant grass *E. atherica* to invade and establish within the patch (Howison et al., 2015). *E. atherica* mainly reproduces clonally with rhizomes that can extend several metres, although sexual reproduction also occurs via seeds that are dispersed by tidal water and wind (Bockelmann et al., 2003; Atstatt & Odowd, 1976; Veeneklaas et al., 2011). Like other salt-marsh plants, *E. atherica* forms aerenchyma in roots and rhizomes to facilitate oxygen supply under inundated conditions (Rozema et al., 1985). However, the palatable *E. atherica* is sensitive to herbivory and soil compaction by trampling cattle (Kuijper et al., 2004; van Klink et al., 2015), which is why under grazed conditions, *E. atherica* spatially associates with the grazing-defended *J. maritimus* (Howison et al., 2015), indicating associational avoidance (Milchunas & Noy-Meir, 2002).

### 4.3 | Patch expansion

The tall patches consisting of *J. maritimus* and *E. atherica* produce litter, shade, and moist conditions, and so forms an attractive habitat for bioturbating, litter-feeding soil macrofauna, such as the amphipod *O. gammarellus* in salt marshes (Howison et al., 2016a, 2016b). Their increased bioturbation reduces anoxia and soil compaction and increases litter decomposition and nutrient mineralization, favouring plant growth in the patch (Schrama et al., 2015b). Given that *E. atherica* is a strong competitor for light and nutrients, it expands in the centre of the patch at the cost of *J. maritimus* that is pushed towards the edges of the patch where it invades the surrounding grazing-tolerant lawn species, likely a result of shading out the grazing-lawn species (Howison et al., 2015). As a consequence of these processes, that is, *E. atherica* pushing *J. maritimus* to the patch edges, and *J. maritimus* outcompeting the lawn species, the patches expand over time and their diameters increase (Figure 2c).





**FIGURE 2** Conceptual framework for cyclic patch dynamics in rangelands with tall grazing-defended vegetation patches in a matrix of short-grazed lawns, driven by positive and negative feedbacks between plants, soil macrofauna and large herbivores, and four distinguished phases: (a) patch initiation by invasion of grazing-defended plant species (depicted: *Juncus maritimus*) in short-grazed lawn, (b) patch establishment by grazing-intolerant competitive plant species (depicted: *Elytrigia atherica*) establishing inside a grazing-defended patch via plant–plant facilitation, (c) patch expansion into grazing lawn, where the grazing-intolerant competitive plants profit from increased bioturbating soil macrofauna (depicted: *Orchestia gammarellus*) that prefer prevailing (a)biotic conditions and litter for food, (d) patch degeneration where patches disintegrate and/or dissolve when large herbivores start grazing patch interior, shortening vegetation, removing litter and decreasing the abundance of bioturbating soil macrofauna, leading to the return of grazing-tolerant stoloniferous grazing-lawn species. The cycle may restart again when a remnant of the grazing-defended species in the degenerated patch (D) initiates a new patch (A patch initiation) in the grazing lawn. Green squares represent aerial views of each phase, with grazing-defended species (dark green), grazing-intolerant competitive species (dashed green), and grazing-resistant lawn species (light green).

#### 4.4 | Patch degeneration

The degeneration phase (Figure 2d) occurs when cattle increasingly start to enter the enlarged patch to consume the dominant *E. atherica* inside the patch centre. Besides the removal of the biomass of *E. atherica* and the subsequent decrease of vegetation cover and litter, cattle will increasingly trample and compact the soil, thus degrading the habitat for the bioturbating *O. gammarellus* (Andresen et al., 1990; Schrama et al., 2013) that will disappear from the patch centre. Also *J. maritimus* will locally reduce in density and disappear due to the increased trampling and grazing of the cattle that will graze away the less preferred species (*J. maritimus*) together with the target palatable species (*E. atherica*) at small spatial scale, a process called associational palatability (Olf et al., 1999). As a consequence

of these processes, the local environmental conditions become suitable again for the (re)invasion of the light-preferring and grazing-tolerant lawn species such as *F. rubra*. As a result, through these processes, the once sizeable patch gets opened up from the interior and will dissolve or partly disintegrate into one or a few remaining patch fragments of *J. maritimus*. The cycle may restart again when a remnant of *J. maritimus* in a degenerated patch (or newly dispersed seed) initiates a new patch in the grazing lawn (Figure 2a).

## 5 | DISCUSSION

In our vegetation patch dynamics concept for rangelands, we combined elements of existing theories on vegetation pattern formation

and explicitly added in multispecies and trophic interactions for an improved mechanistic understanding. Our concept is primarily based on data gathered during the numerous field and laboratory studies performed in this salt-marsh system over the last two decades, but also from similar studies in rangelands with patchy vegetation structure elsewhere (e.g. Howison et al., 2017). As a result, for many of the proposed four cyclical phases, we have gathered empirical evidence in our system, and studies from other rangelands suggest that similar processes occur there too. For example, the protective effects of unpalatable *Juncus* species on spatially associated palatable species have been well documented in rangelands (Van Uytvanck et al., 2008; Howison et al., 2015; Boughton et al., 2020), and also other unpalatable, herbivore-defended plants—either via physical or chemical defence traits—have been shown to lead to local patch expansion or succession in different types of rangelands (e.g. Bakker et al., 2004; Smit et al., 2005; Smit et al., 2008; Smit et al., 2010; Root-Bernstein et al., 2017). Concerning bioturbating soil fauna, the impacts of the amphipod *O. gammarellus* in our system have been well established via a series of field and laboratory experiments (Howison et al., 2015, 2016b; Schrama et al., 2015b; Smallegange & Berg, 2019), and similar effects have been found for other bioturbating soil organisms such as termites, earthworms or dung beetles in grasslands across the world (e.g. Howison et al., 2016a; Li et al., 2018; Taylor et al., 2019). At the same time, while we have empirical support for most of the proposed four phases in our system, we still lack appropriate spatial-ecological studies that analyse where, and at what rate, the proposed shifts between the different phases take place in our system, for example via analysis of high-resolution satellite images or remote-sensing data, to assess the level of patch dynamics in rangelands. For many other rangelands, it is the other way round: information on changes over time of vegetation patchiness in the landscape is available (Kefi et al., 2007; Kröpfl et al., 2013; Verwijmeren et al., 2019), but empirical data on the contribution of the different key species and their interactions is often absent or scarce, despite such data being essential for an improved mechanistic understanding. Hence, this is a call to collect specific empirical data on plant–plant, plant–herbivore, and plant–soil fauna interactions and test our model in other rangelands.

We believe that our model would fit many grazed terrestrial ecosystems with sufficient forage quality and quantity to support large herbivores, and with soil types that can be compacted, thus excluding permafrost, very sandy or pure organic soils, and very dry (<400mm rain) or wet (>1200mm rain) systems, in line with Howison et al., 2017. For example, our model applies to African savannahs where large herbivores species such white rhinoceros (*Ceratotherium simum*), via their frequent grazing and trampling, create grazing lawns consisting of e.g. *Digitaria longiflora*, *Cynodon dactylon*, and *Sporobolus nitens*, while avoiding tall patches of the less palatable bunch grasses (e.g. *Themeda triandra*, *Sporobolus pyramidalis*; Howison et al., 2016a, 2016b), in line with the patch initiation phase (Figure 2a). It is typically in these tall patches of bunch grasses that woody species may establish, indicative of associational resistance

(Figure 2b, patch establishment). In a field experiment, different species of soil macrofauna, such as earthworms, termites or dung beetles were found to increase the cover of the bunchgrasses at the cost of lawn grass species (Howison et al., 2016a, 2016b), which is largely in line with the patch expansion phase (Figure 2c). To what extent patch degeneration (Figure 2d) in these savannahs occurs via increased herbivory at the centre of the patches remains unclear; on the one hand, elephants (*Loxodonta africana*) may open up tall patches by removing established shrubs and trees (Augustine & McNaughton et al., 2004), but fire also plays a large role in savannah vegetation dynamics and frequently removes the build-up biomass of tall vegetation (Higgins et al., 2000).

Vegetation patchiness is a common phenomenon in rangelands and grazed ecosystems worldwide (Howison et al., 2017), and site productivity and grazing intensity are important interlinked determinants of grazing impacts on vegetation structure (Nolte et al., 2014). However, we know very little about how these factors determine the rate of shifts between the four proposed phases in rangelands. One could speculate that when grazing intensity is in balance with site productivity, all four phases are present in the system and phase shifts should regularly occur over time. However, when grazing intensity is too high (that is, a mismatch between productivity and grazing intensity), one would expect a reduction in spatial heterogeneity of the vegetation structure (e.g. see Kiehl et al., 1996; Bakker et al., 2020) and a decline of the number and size of patches, associated with a loss of species diversity (Kefi et al., 2007; Nolte et al., 2014; van Klink et al., 2016). Similarly, when grazing intensity is low relative to site productivity, this may lead to the disappearance of patchiness, with the dominance of one or a few competitive tall plant species and, as a result, a loss of species diversity (Koerner et al., 2018). In addition, as vegetation patchiness, in particular the patch size distribution, is already considered a health indicator of semi-arid ecosystems and rangelands (Kefi et al., 2007; Henderson & Davis, 2014), we propose here that also the dynamics—thus the occurrence of shifts between patch phases—should be considered as a health indicator of rangelands, in particular in light of the increased conservation values that come with increased dynamics.

In synthesis, we believe that our patch dynamics model is a useful framework, not only for mechanistically explaining phase shifts of patches in time and space in our study system and other rangelands elsewhere, but may also serve as a potential indicator of the conservation value of rangelands in general. We invite other researchers to apply and test our framework to their rangelands and recommend specifically that future studies should explore how grazing intensity relative to site productivity impacts our proposed model of patch dynamics in rangeland and the resulting consequences for biodiversity and conservation values.

#### AUTHOR CONTRIBUTIONS

Christian Smit and Isabelle P. R. Buyens conceived the research idea, with contributions from Peter C. le Roux; Christian Smit and Isabelle P. R. Buyens wrote the paper; all authors discussed and commented on the manuscript.

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## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

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