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SPATIO-TEMPORAL HETEROGENEITY OF SWARD STRUCTURE: VEGETATION DYNAMICS, PRIMARY AND SECONDARY RESPONSES

Porto Alegre (RS), Brasil
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CARLOS ALBERTO BISSANI
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À Malena,

minha filha, que nascerá praticamente junto com essa tese.

Luzeiro que está vindo irradiar a família com muito amor.

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Dedico.

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Ver a vida renovada
Na Malena, nossa filha
É algo que não cabe no peito
É o sentimento perfeito
De plenitude em família!

Nossa filha em teu ventre
É o amor a esperar...
É pura poesia sentida
Nas mulheres da minha vida
Que eu sempre hei de amar!

Ao mate, companheiro dos meus silêncios e pensamentos.

Seguimos, porque o porvir é incerto e é isso que nos move!

HETEROGENEIDADE ESPAÇO-TEMPORAL NA ESTRUTURA DO PASTO: DINÂMICA DA VEGETAÇÃO, RESPOSTAS PRIMÁRIAS E SECUNDÁRIAS[1]

Autor: Gentil Félix Da Silva Neto
Orientador: Paulo César de Faccio Carvalho
Orientador: Jérôme Bindelle

RESUMO

Os ecossistemas pastoris fornecem uma ampla gama de serviços ecossistêmicos e o manejo do pastejo impacta diretamente o funcionamento desses ecossistemas. A heterogeneidade é uma propriedade inerente às pastagens, uma vez que o processo de pastejo cria heterogeneidade mas também responde à heterogeneidade pré-existente na vegetação. No entanto, ainda há uma lacuna de conhecimento sobre como a heterogeneidade evolui e impacta a produção primária e secundária sob pastejo. Nesse contexto, um experimento foi realizado para estudar como a heterogeneidade evolui a partir de dois níveis iniciais de heterogeneidade na estrutura do pasto (homogêneo vs. heterogêneo), bem como os impactos nas produções primária e secundária. No Capítulo II são apresentados os resultados referentes à dinâmica da estrutura do pasto sob dois níveis iniciais de heterogeneidade. No Capítulo III são apresentados os resultados do desempenho de ovinos e produção de forragem sob dois níveis iniciais de heterogeneidade em pastos manejados em uma moderada intensidade de pastejo. O processo de pastejo rapidamente cria heterogeneidade na vegetação, sendo que o nível de heterogeneidade oscila ao longo do período de pastejo (Capítulo II). A homogeneização inicial da estrutura do pasto não traz benefícios para a produção animal nem vegetal sob moderada intensidade de pastejo. Sob moderadas intensidades de pastejo o aumento na heterogeneidade é inevitável e pesquisas futuras devem levar em consideração a heterogeneidade espaço-temporal da vegetação para entender como essa heterogeneidade interage com o processo de pastejo e como atua na prestação de diferentes serviços ecossistêmicos.

Palavras-chave: processo de pastejo, heterogeneidade espaço-temporal, dinâmica da vegetação, estrutura do pasto, desempenho de ovinos, produção de forragem.

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SPATIO-TEMPORAL HETEROGENEITY OF SWARD STRUCTURE: VEGETATION DYNAMICS, PRIMARY AND SECONDARY RESPONSES[2]

Author: Gentil Félix Da Silva Neto
Advisor: Paulo César de Faccio Carvalho
Advisor: Jérôme Bindelle

ABSTRACT

Pastoral ecosystems provide a wide range of ecosystem services and grazing management directly impacts the functioning of these ecosystems. Heterogeneity is an inherent property of grasslands, as the grazing process creates heterogeneity but also responds to pre-existing heterogeneity in the vegetation. However, there is still a lack of knowledge about how heterogeneity evolves and impacts primary and secondary production under grazing. In this context, an experiment was carried out to study how heterogeneity evolves from two initial levels of heterogeneity in sward structure (homogeneous vs. heterogeneous), as well as the impacts on primary and secondary production. In Chapter II, results are presented regarding the dynamics of pasture structure under two initial levels of heterogeneity. In Chapter III, the results of sheep growth performance and herbage production under two initial levels of heterogeneity in swards managed at moderate grazing intensity are presented. The grazing process rapidly creates heterogeneity in the vegetation, with the level of heterogeneity fluctuating over the grazing period (Chapter II). The initial homogenization of the sward structure does not bring benefits to animal or herbage production under moderate grazing intensity. Under moderate grazing intensities, an increase in heterogeneity is inevitable and future research should take into account the spatio-temporal vegetation heterogeneity to understand how this heterogeneity interacts with the grazing process and how it acts in providing different ecosystem services.

Key words: grazing process, spatio-temporal heterogeneity, vegetation dynamics, sward structure, sheep growth performance, herbage production

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CHAPTER I

1.1 GENERAL INTRODUCTION

Grasslands are important ecosystems distributed globally. In addition to the expressive area (52.5 million km²) covered by these pastoral ecosystems (White, Murray & Rohweder, 2000), they offer a wide range of services to humanity, called ecosystem services (MEA, 2005). A key service provided by the grasslands is food production, since pastures are low-cost sources of forage for grazing domestic animals. Grasslands also provide environmental and social services such as pollination, pest control, potential for mitigation of greenhouse gases, soil conservation, resistance to weed invasion, regulation of soil fertility, nutrient cycling, biodiversity maintenance and cultural values (Duru et al., 2018; Herrero et al., 2016; Sala et al., 2017). Herbivores play a fundamental role in the dynamics of these ecosystems, therefore, applying grazing management strategies that deal appropriately with these multiple functions is challenging.

Heterogeneity is an inherent property of these ecosystems. It is present in both natural or cultivated grasslands. On the other hand, vegetation communities are heterogeneous in space and time, due to numerous factors such as biotic interactions, variations in soil fertility and water availability, excreta depositions and dispersion mechanisms of plant species (Parsons & Dumont, 2003; Chapman et al., 2007). This spatio-temporal variation in food resources across ecological landscapes impacts many wild herbivores species (Fryxell et al., 2005) where it is mainly studied.

On the other hand, the grazing process is also heterogeneous in time and space, and foraging decisions of herbivores interact with multiple scales (Laca & Ortega, 1995; Zhao & Jurdak, 2016). Thus, herbivores, through the grazing process both respond and contribute to the spatial heterogeneity of the vegetation (Parsons & Dumont, 2003; Laca, 2008) constituting a complex of interactions that impact from individuals to ecosystem functioning.

Many management approaches try to reduce heterogeneity, such as sowing monocultures pastures, cuts or traditional management that aims to promote homogeneity through uniform distribution of livestock grazing across the landscape, being some specialized managements employ extreme measures to override livestock behavior (Fuhlendorf & Engle, 2001). According to Fuhlendorf et al. (2017) heterogeneity is the basis for rangeland management because only with the understanding of this inherent property of these ecosystems is it possible to enhance multiple ecosystem services.

As the grazing process plays a fundamental role in these ecosystems, a special focus should be given to grazing management strategies with an emphasis on the multifunctionality of the ecosystem. As sward structure plays a fundamental role in the ingestive behavior of animals (Carvalho, 2013), the purpose of this study is to investigate how grazing creates heterogeneity and what are the impacts of different levels of heterogeneity on the productive responses of plants and animals.

1.2 LITERATURE REVIEW

Grazed grasslands provide many ecosystem services and grazing management impact their ability to do so (Sollenberger et al. 2019). Grazing is a multiscale process, varying in space and time, involving a combination of one-time confined choices to perform bites on specific feeding stations to large movements of the animals across the whole pasture. What happens at the bite level influences the whole grazing pattern and subsequent animal performances (Carvalho, 2013).

1.2.1 Grazed grasslands are meant to be heterogeneous

Beyond the spatial heterogeneity in soil and topography, grazed grasslands are heterogeneous, firstly, because herbivores remove a diversity of plant material by selecting plant species and parts of plants variable in chemical composition and mass, which makes up the heterogeneity of bites. After one single bite that needs a second to be taken, the regrowth takes several days to weeks. Hence, herbivores can graze only a small proportion of the whole grazable area each day (Schwinning & Parsons, 1999). Secondly, when performing bites over one or several feeding stations, animals look for specific plant species, plant parts and plant structures that allows them to optimize their intake rate. The major limitation for grazing ruminants to fulfil their daily feed requirements is usually set by the limited amount of time they have to collect their daily forage allowance through tens of thousands of individual bites (Carvalho, 2013). Recent works led the the group I come from in Brazil showed that a sward structure does exist, mainly determined through its height, that allows herbivores to maximize their short-term intake rate (STIR) through an optimal combination of bite mass and time required to manipulate the vegetation. Plotting changes in STIR against sward height usually produces a bell-shaped curve that is specific for each forage species e.g. (Szymczak et al. 2020). Thirdly, the efficiency in the grazing process decreases with grazing down level, as the lower animals get in the vegetation, the lower the harvest per bite while still on average 50% of the residual sward height is taken per bite. Finally, in addition to plant removals, management influences the spatial distribution of both, selection, intensity and excreta depositions which in turn affect plant diversity and nutrient cycling (McKenzie et al., 2016; Sanderson et al. 2010). As a consequence, herbivores turn the grazed pasture into a vegetation with patches with different regrowth stages whatever the stocking method.

Vegetation heterogeneity refers to variability in the structure and composition of plant communities, i.e. diversity in kind or arrangement, over space and time. For decades, stocking management methods have sought to reach a homogeneous vegetation aiming to offer a specific plant structure to the animal during the whole grazing season and to maintain a tight sward where perennial species dominate and have no time to flower in order to maximize harvest efficiency and provide more predictable options for farmers. In temperate intensively managed pastures, this often results in preferring rotational over continuous stocking and high over low harvest efficiencies (ratio of forage consumed to herbage produced) (Savian et al., 2018; Fulkerson & Donaghy, 2001). Contrary to this vision, Fuhlendorf et al. (2017) argue that understanding grassland ecosystems from a resilience perspective cannot be achieved without a focus on heterogeneity at various scales. In addition, heterogeneity has a major impact on biodiversity and ecosystem functioning, therefore, scientists should seek an understanding of these relationships in order to leverage ecosystem services as an alternative to the short-sighted focus on maximizing agricultural output (Fuhlendorf et al., 2017).

1.2.2 Sward height - a key factor of sward structure for grazing dynamics

Beyond the more obvious effect of spatial arrangement of species that can impact heterogeneity in grasslands, sward height is the key structural component that drives animal foraging behaviour and subsequent plant regrowth. Indeed, the sward structure is the distribution and arrangement of above-ground plant parts that present themselves to the animal at the time of the bite execution (Laca & Lemaire, 2000) with key descriptors being sward height, or herbage bulk density. As explained above, recent work has shown that sward height is the most influencial to short-term harvest efficiency that allows herbivores to maximize their short-term intake rate (STIR) through an optimal combination of bite mass (bite depth x bite area) and time required to manipulate the vegetation. In addition, post-grazing sward height and subsequent remnant light interception by the canopy drive the response of the vegetation to grazing events (Fulkerson & Donaghy, 2001).

1.2.3 Heterogeneity in sward height, an underexplored lever for improved grazing management

Interestingly, using a stochastic dynamic mathematical model, Pontes-Prates et al. (2020) have shown that increasing levels of heterogeneity, can enhance the functional response of herbivores (i.e. the function instantaneous intake rate to sward height), minimizing grazing time.

This opportunity for animals to take advantage of heterogeneity in sward structure questions the homogeneity paradigm of modern-day stocking methods. But since it is widely accepted that plant productivity and intake rate are determined by local sward characteristics at the scales (resolutions) of 10^{-2} to 1 m and seconds to minutes, and most grazing studies and models use average sward characteristics over extents of 10 – 10^{2} m and hours to days (Gordon & Benvenutti, 2006; Bailey & Provenza, 2008), the scale of representation and study of the mechanisms of interaction between primary (vegetation) and secondary (animal) productivity and plant community dynamics do not match. The spatial distribution of both plant composition and sward structure at the right resolution seems a key element to investigate in order to propose stocking methods based on animal selectivity and patterns of defoliation, thus determining selection of plant species and parts, forage harvest efficiency, post-grazing growth rate, and animal performances. Furthermore, many studies on heterogeneity in grasslands are focused on describing the heterogeneity of vegetation associated with grazing intensities (Nunes et al. 2019; Cid & Brizuela, 1998), neither describing its evolution, nor how animals exploit this heterogeneity. This is due to the fact that heterogeneity has not yet been studied in isolation from grazing intensity, **pointing to a crucial knowledge gap that I wish to contribute to**.

The impact of sward structure and, especially, the average sward height, on the efficiency in the grazing process has been well characterized under the hypothesis of homogeneous swards, but the functional response of grazing herbivores towards increasing level of heterogeneity at the scales of the feeding station and the paddock remains unknown. This knowledge gap hinders a sound use of heterogeneity as a factor for increased stability in innovative socking methods despite the fact that technological advances nowadays allow a fine scale characterization of the grazing behavior (geolocated activity sensors) and vegetation traits (UAV-derived maps) (Bindelle et al. 2021). Studying different levels of vegetation heterogeneity at a similar (moderate) grazing intensity could provide valuable data on its possible role in the functioning of pastoral ecosystems.

1.2.4 Designing efficient and sustainable production strategies for pastoral ecosystems

Herbivores grazing is the primary use of grasslands worldwide so grasslands are important sources of meat, milk, wool, and leather products. Livestock sector is critical to building sustainability and sustainable intensification of agriculture is a global need, being that this concept aims contribute to all four pillars of food security – availability, access, utilization and stability – in a manner that is environmentally, economically and socially responsible over time.

In addition, sustainability requires the conservation of natural resources, such as natural grasslands, which are often converted into crops. An example of this phenomenon is the natural grasslands of Pampa Biome, affected by changes in land use that bring negative impacts to biodiversity and reduce the ecosystem services provided by these environments (Modernel et al., 2016). Thus, it is essential that these natural ecosystems are better exploited to meet productive demands and slow down the conversion into crop areas.

The specialized systems present in agroecosystems also deserve attention. Crop and livestock production systems with excessive specialization and homogeneity (Lemaire et al., 2017) are based on the excessive application of inputs (Tilman et al., 2002) and bring several negative impacts to the environment such as water-quality degradation, decrease in groundwater levels, rising atmospheric greenhouse gas (GHG) concentrations, soil erosion and degradation and loss of biodiversity (Lemaire et al., 2017; Franzluebbers et al., 2011; Peyraud et al., 2014, Kronberg & Ryschawy, 2017). An alternative to these specialized systems are the integrated crop-livestock systems (ICLS), which contemplate the approach of sustainable intensification through a space-time planning of multifunctional agricultural activities (e.g. soybean and animal production), exploring synergies arising from diversity and system complexity (Lemaire et al., 2014; Moraes et al., 2018).

In this sense, grazing process plays a fundamental role, because, through this process animals generate heterogeneity in pastoral ecosystems (natural and integrated), in addition to other sources of heterogeneity from animals such as excreta distribution and trampling, catalyzing processes such as nutrient cycling and driving changes in the agro- ecosystem (Carvalho et al., 2010; Carvalho et al., 2018).

Grazing management strategies when impacting the foraging process of herbivores also impact the dynamics and functioning of ecosystems (cascading effects). Thus, through a holistic view, new production strategies must be proposed considering the inherent heterogeneity of the processes and elements involved to design new production systems that include efficiency and sustainability.

1.3 HYPOTHESIS

The following chapters were developed based on the following hypotheses: (1) grazing process rapidly creates heterogeneity in initially homogenized swards managed at moderate grazing intensity that benefits animal performance (Chapter II); (2) initial sward heterogeneity does not impair animal performance and herbage production (Chapter III).

1.4 OBJECTIVES

The objectives of the studies presented below were: (1) to characterize the spatial heterogeneity of sward structure and describe how it evolves over the stocking season under two initial levels of heterogeneity at moderate grazing intensity. (Chapter II); (2) to assess individual and area animal production as well as forage production and sward height variations (vegetal and animal responses) throughout a growing season under two initial levels of heterogeneity at moderate grazing intensity (Chapter III).

CHAPTER II[3]

Spatio-temporal sward structure dynamics of two initial levels of heterogeneity at moderate grazing intensity

[3] Manuscrito.

Spatio-temporal sward structure dynamics of two initial levels of heterogeneity at moderate grazing intensity

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Abstract

Spatio-temporal heterogeneity is an inherenty property of grassland ecosystems related to several ecosystem services. We evaluated the evolution of heterogeneity in sward structure over the stocking season under two initial levels of heterogeneity (homogeneous x heterogeneous) at moderate grazing intensity. The grazing process quickly (4 days) creates heterogeneity in an initially homogeneous vegetation. Additionally, fluctuations in sward structure heterogeneity levels at moderate grazing intensity occur throughout the stocking season and are associated with the average target sward height, being impacted by stocking rate adjustments and morphological and phenological changes in plants. Similar grazing conditions can lead to different levels of heterogeneity, so studies must consider stocking rate and spatial grazing patterns to understand what drives intra-paddock variations. These outcomes provide a baseline for understanding the dynamics of heterogeneity decoupled from grazing intensity to advance in detailing the relationships between plants and herbivores in pastoral ecosystems.

Keywords: sward height, perennial ryegrass, grazing management, patch grazing, vegetation dynamics, herbivory, temporal pattern

Introduction

Heterogeneity is an inherent property of grassland ecosystems. Heterogeneity in grassland vegetation refers to the variability in species composition, structure, and functional traits of plant communities within a grassland ecosystem. This variability can be driven by various biotic and abiotic factors such as disturbance regimes, soil characteristics, topography and climate (Bloor & Pottier, 2014). Maintaining heterogeneity in grasslands can contribute to their resilience and stability, enhance ecosystems services and provide habitat for diverse array of wildlife species (Fuhlendorf et al. 2017; Hovick et al. 2015; Fuhlendorf et al. 2006).

Grazing is a fundamental process in these complex and dynamic ecosystems. The ecosystem functioning is directly affected by the grazing process, moreover, the grazing process creates heterogeneity in the vegetation and the ingestive behavior of herbivores is also a response of the pre-existing heterogeneity in the vegetation (Adler et al. 2001). Carvalho (2013) demonstrated that the sward structure is crucial for grazing management and the sward height is a key characteristic of the sward structure that directly impacts the ingestive behavior of herbivores and ultimately their growth performance. Therefore, it is necessary to understand how heterogeneity occurs in sward structure to better manage pastoral ecosystems.

According to Fuhlendorf et al. (2017), heterogeneity is the basis for rangeland management because only with the understanding property of these ecosystems is it possible to enhance multiple ecosystem services. Furthermore, many studies on heterogeneity in grasslands are focused on describing the heterogeneity of vegetation associated with grazing intensities (Cid & Brizuela, 1998; Nunes et al. 2019), neither describing its evolution, nor how animals exploit this heterogeneity. This is because heterogeneity has not yet been studied in isolation from grazing intensity, pointing to a crucial knowledge gap that needs to be explored.

Despite the evidence regarding the importance of heterogeneity, many management practices try to eliminate vegetation heterogeneity either through the use of mechanical interventions or through the use of high animal densities that aim to eliminate the selective behavior of animals and generate a more uniform distribution of livestock grazing (Fuhlendorf & Engle, 2001). In grazing situations, vegetation uniformity only occurs in overgrazing situations, which is well known to impair both the growth performance of animals, herbage production and related ecosystem services (Cid & Brizuela, 1998; Nunes et al. 2019). Thus, understanding the role of heterogeneity at moderate grazing intensity is essential to propose nature-based solutions for pastoral ecosystems that integrate knowledge about the processes related to this inherent property of vegetation and mimic the processes of natural ecosystems in production systems.

In this research we generated two levels of initial heterogeneity, through anthropic intervention, considering the sward height to advance mechanistic understanding how it is created and how fast sward structural heterogeneity evolves at moderate grazing intensity. We hypothesize that the grazing process rapidly creates heterogeneity in initially homogenized swards managed at moderate grazing intensity that benefits animal performance. Our objectives were: To characterize the spatial heterogeneity of sward structure and describe how it evolves over the stocking season under two initial levels of heterogeneity at moderate grazing intensity.

Material and methods

Site and treatments

The mechanistic grazing experiment was conducted at the AgricultureIsLife experimental farm, (University of Liège experimental farm, Belgium), using a sward composed predominantly of perennial ryegrass (*Lolium perenne*) with different heterogeneity gradients and as animal model sheep managed under continuous stocking method. The two treatments were applied on experimental paddocks as follows:

Treatment 1: a randomized heterogeneity treatment at the patch level (25 m^2);

Treatment 2: a homogeneous treatment, the entire paddock with a homogeneous initial sward height (see Figure 1 and Figure 2).

We generated two levels of heterogeneity, considering the sward height as metric for heterogeneity, through a single mechanical cut before the animals accessed the area. The aim of the cutting combinations was to yield at the beginning of the experiment an average sward height on the paddocks of 10 cm whatever the treatment. Hence, in the homogeneous treatment the whole area was mowed to reach a height of 10 cm at the beginning of the experiment. In the heterogenous treatment, each paddock was subdivided in 80 randomly distributed patches of 5 × 5 m (25 m^2) each. Forty of those patches were mowed a couple of days before the beginning of the experiment to reach a sward height of 15cm. The other 40 were mowed to reach 5 cm when the animal was set to graze, aiming an average of 10 cm at the paddock level. The value around 10 cm ± 5 sward height was used as target for a moderate grazing intensity, which in perennial ryegrass pastures indicates a non-limiting condition for the ingestive process of the animals (Bazely, 1988). A total of three replicates per treatment (totaling six experimental units) was initially planned, however, due to mechanical cutting not being effective in controlling the heterogeneity of a homogeneous treatment paddock, data from this paddock were not included in this paper. The experimental design was a randomized complete block with three replicates of the heterogeneous treatment and two replicates of the homogeneous treatment, totaling five experimental units.

The stocking season lasted 92 days, starting in 8 May 2021 and finishing at 8 August 2021.

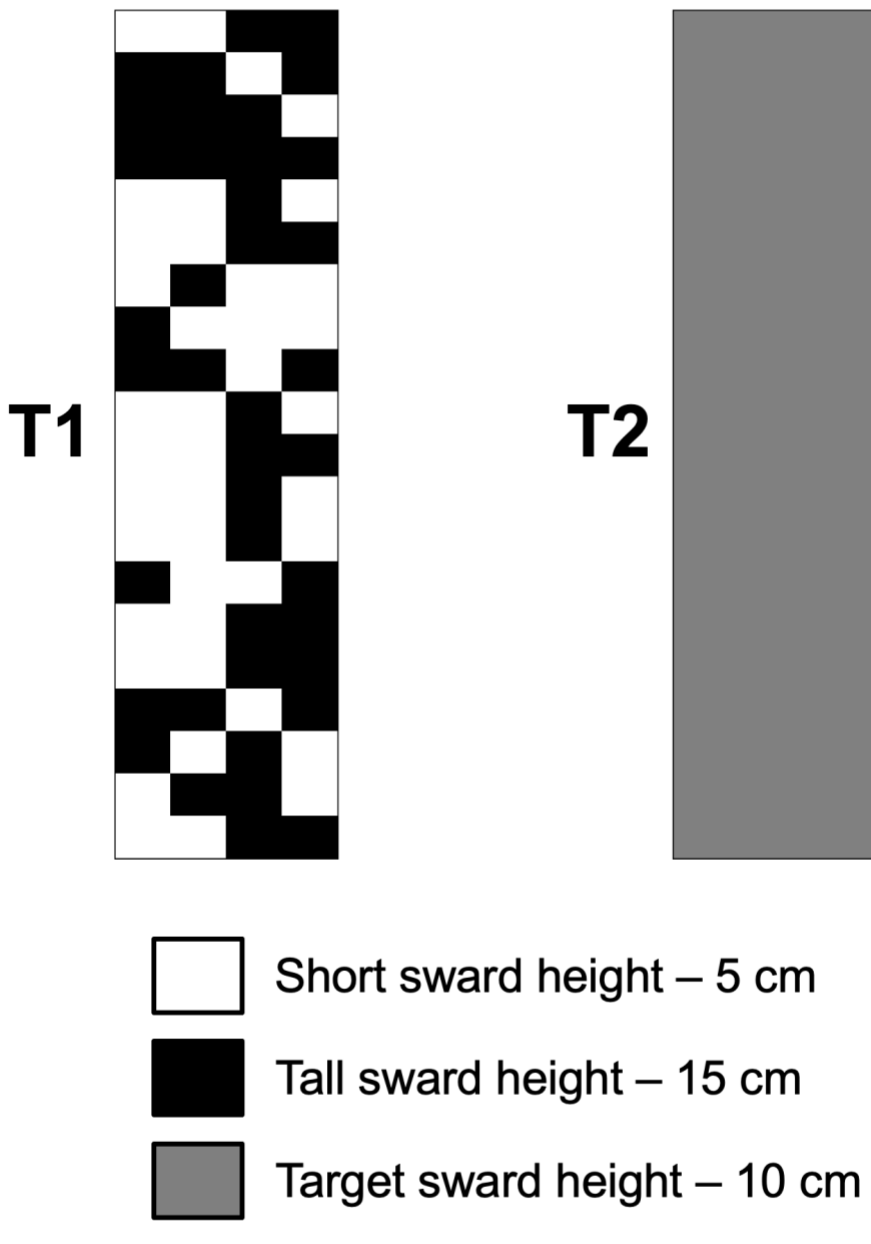


Figure 1. Representation of the two treatments.

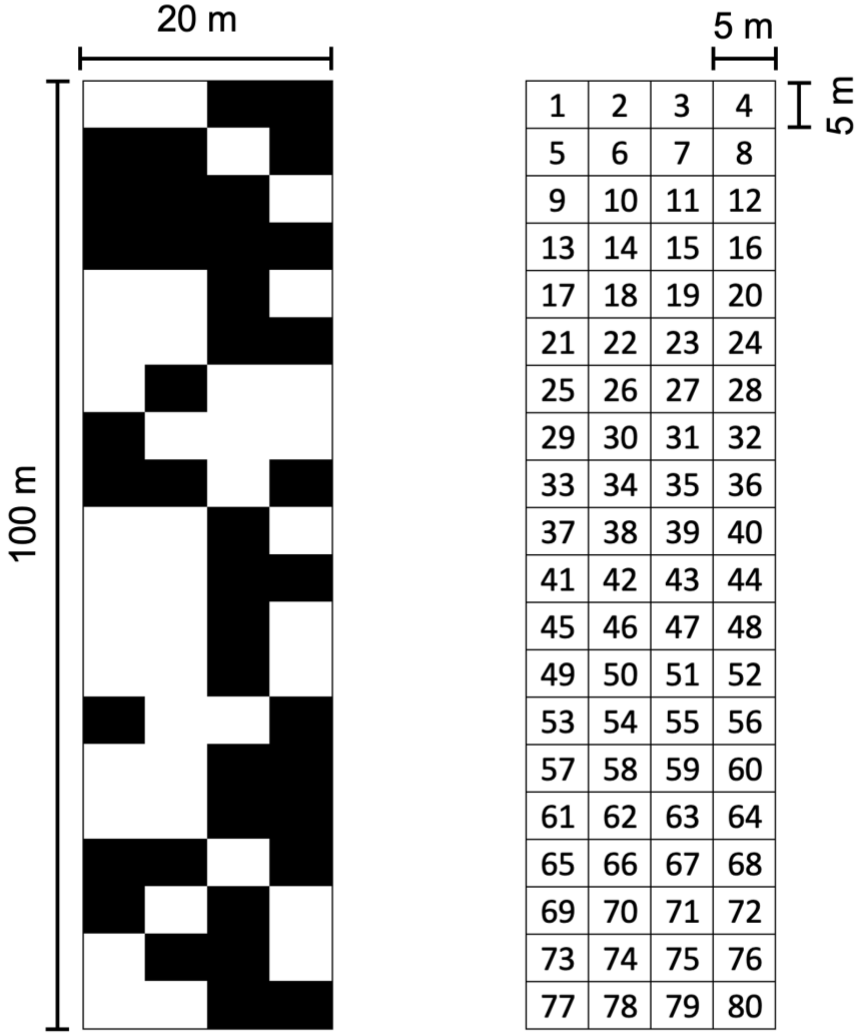


Figure 2. Representation of the organization of heterogeneous treatment. Each paddock of the heterogeneous treatment was divided into 80 quadrants (5 x 5 m). A draw was carried out so that the heights of each quadrant were randomly arranged.

Vegetation

In the experimental area of 3.0 ha, six paddocks were demarked. The area of each paddock was dimensioned to accommodate at least three test animals. The pasture (or vegetation) consists of perennial ryegrass (*Lolium perenne*) predominantly in addition to species such as white clover (*Trifolium repens*), Kentucky bluegrass (*Poa pratensis*), Yorkshire fog (*Holcus lanatus*), dandelion (*Taraxacum* sp.).

Vegetation Measurements

Monitoring

The sward structure was evaluated in each experimental unit (EU) in all treatments. The sward surface height was measured using a sward stick recording the plant species as well (Barthram, 1985) were measured 200 points (along a fixed grid spatialized in a GIS) once a week approximately, totaling 12 samplings. Data were collected on May 5 (pre-grazing), May 12, May 19, May 26, June 2, June 9, June 16, June 23, July 7, July 21, July 28 and August 4.

Animals

The experimental animals were growing lambs. The animals were an approximate age of 6 months and an average live weight of 25 kg. Each experimental unit (paddock) received three (03) test animals (permanent animals over the whole stocking season) and a variable number of put-and-take animals (adjustment animals) (Mott & Lucas, 1952). The stocking rate adjustment was performed whenever necessary (once a week) to maintain the target sward heights. In all, fifteen (15) lambs were used permanently plus a varying number of put-and-take animals.

Grazing Management

The stocking rates adjustments were made with the aim of maintaining the sward height around the targeted sward height of 10 cm (Figure 5 - Appendix). During the experiment the height fluctuated around the target height (10 cm) but the condition of moderate grazing intensity was met for both treatments which is confirmed by the similar herbage allowance between treatments (Silva Neto in prep.).

Statistical Analysis of Spatial Heterogeneity

Geostatistical analysis were conducted for investigated grassland spatial heterogeneity. Isotropic experimental semivariograms of each paddock were calculated using GS+ software version 10 (Robertson, 2008), considering the 2 m x 2 m grid separation distance between points and a maximum separation distance of 80 m to obtain a minimum of 30 pairs of points as recommended by Journel & Huijbregts (1978) and in this study we obtained a minimum of 95 pairs. Semivariogram specifically address how variance varies as a function of scale (spatial variability identification) (Palmer 2002) and is a useful and unbiased tool that allows to quantify heterogeneity and to identify the spatial scale at which different heterogeneity degree occurs (spatial dependence). The semivariograms were calculated using equation 1:

$$\gamma(h) = \frac{1}{2N\,(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z\,(x_i + h)]^2$$

Where: The geographic distance between two samples is termed the spatial lag. $\gamma(h)$ is the estimated semivariance at a spatial lag of h. $N(h)$ is the number of pairs of samples (observations) separated by a distance of (h) and z $Z\,(x_i + h)$ is the observed value of a location at distance h from (x_i).

Spherical, exponential or linear isotropic mathematic models were fitted in the experimental semivariograms (Robertson, 2008) to characterize vegetation spatial patterns and the patchiness measures depend on the type and shape of the model fitted to the semivariogram (Augustine & Frank, 2001). The model with the lowest residual sum of squares (RSS), the highest coefficient of determination (R^2), and by visual examination (Webster & Oliver, 2001) of the pattern of semivariance vs. distance were the criteria for choosing the best fit model.

For more details on the types of models and ecological interpretations see Augustine & Frank (2001). For each semivariogram model the following parameters were adjusted: The mean diameter of patches or range (A) was the maximum distance where the best-fit model reaches an asymptote (Robertson & Gross, 1994) (over which the measured sward height exhibited significant spatial dependence) (sill, C0 + C1), beyond which there is no more spatial relationship between points (maximum population variance). (C0) is the y-intercept or the nugget effect of the best-fit model which represents analytical error or variability occurring at scales smaller than the sampling interval (Clark, 1980; Robertson & Gross, 1994).

The degree of spatial dependence (DSD) is the proportion of the total variance explained by the spatially structured variance in relation to the nugget effect [C1/(C0 + C1)], where random, unfitted semivariograms are purely composed by nugget effect. Spatial dependence was categorized as strong (>0.75), moderate (0.75 – 0.25), or weak (<0.25) (Cambardella et al., 1994).

To test the effects of two initial sward conditions (heterogeneous vs. homogeneous) and grazing on the dynamics (evolution) sward structure heterogeneity over stocking season, semivariances of each paddock were calculated for separation (lag) distances of 2 up to 80 m, with increments of 2 m (lag interval), and were derived from a minimum of 95 up to 1,109 pairs of points, being considered robust. Semivariograms of each paddock in each sampling date are presented.

The data were interpolated using ordinary kriging and used to generate interpolated maps of spatiotemporal patterns of sward height using Smart-Map plugin (Pereira et al. 2022) in QGIS software version 3.22 Białowieża (QGIS Development Team). Kriging process uses measured values to estimate unmeasured neighboring values, according to trendless criteria and minimal variance.

Results

The dynamics (evolution) of sward height spatial heterogeneity over stocking season is shown in Figure 3. The initial condition, before animals accessed the area (grazing) the paddocks showed different semivariances with a pattern according to treatment (Figure 3 – May 6 2021), where the heterogeneous treatment paddocks presented higher semivariance and the homogeneous treatment paddocks presented lower semivariance meeting the initial conditions proposed for the two treatments (heterogeneity vs. homogeneity). For two paddocks of the heterogeneous treatment (1 and 6) the fitted model was the spherical, for all paddocks the fitted model was exponential and the range was close (Table 1). The heterogeneous treatment paddocks showed a high degree of spatial dependence (>0.75) while the homogeneous treatment paddocks showed a moderate degree of spatial dependence (0.75 – 0.25) (Table 1).

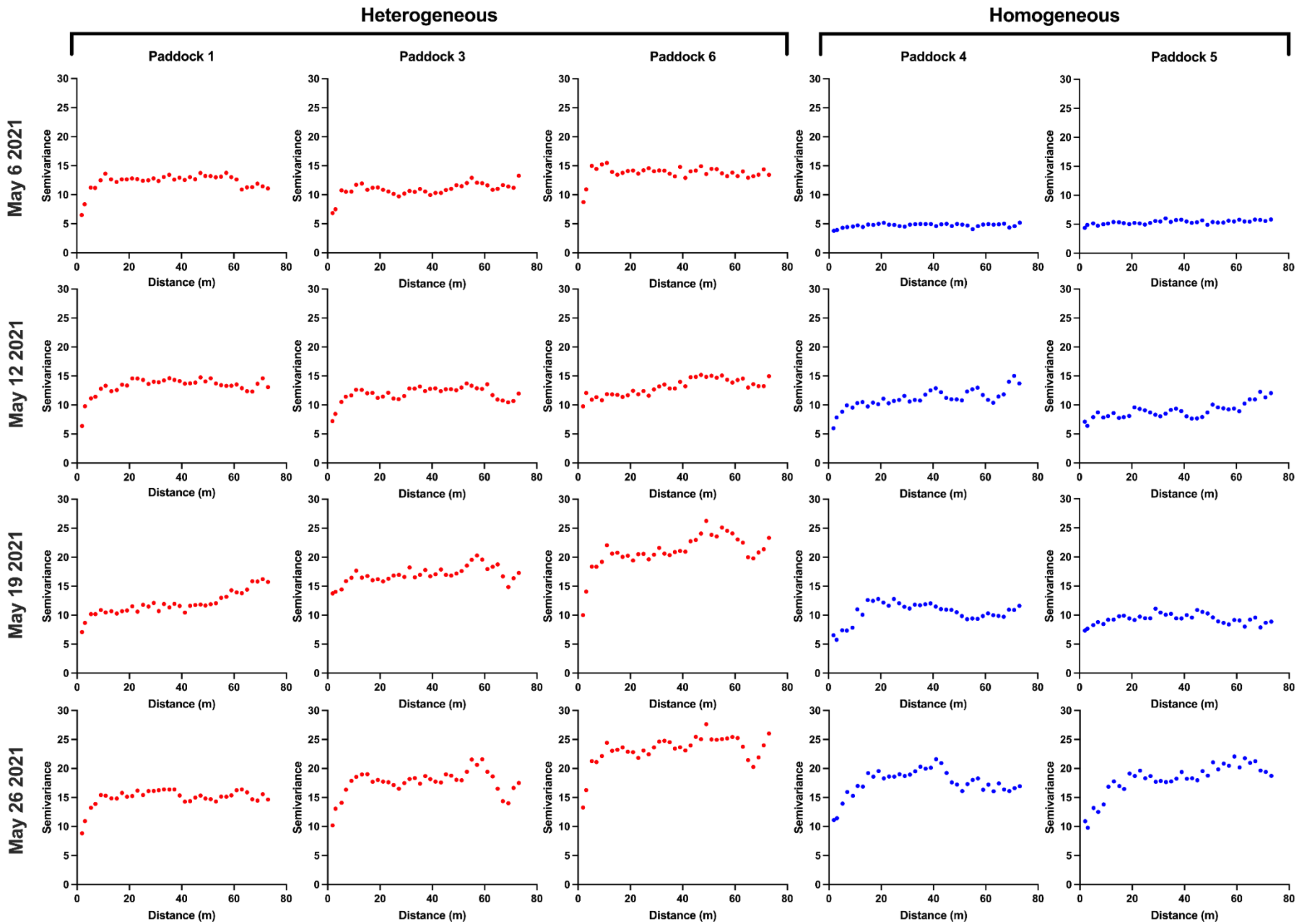
Grazing rapidly altered the vegetation structure of this grassland ecosystem. The spatial heterogeneity increased rapidly (4 days after start grazing) in the paddocks of the homogeneous treatment while remaining stable in the paddocks of the heterogeneous treatment (Table 1), which is indicated by the semivariograms (Figure 3 – May 12 2021) and maps (Figure 4 – May 12 2021).

As of June, there was a significant increase in semivariance for all paddocks and treatments (Figure 3), with some semivariograms showing more than one peak. Some degree of differences was found in paddocks of the same treatment (Figure 3 and 4) evidencing intra treatment spatial variability for the two treatments.

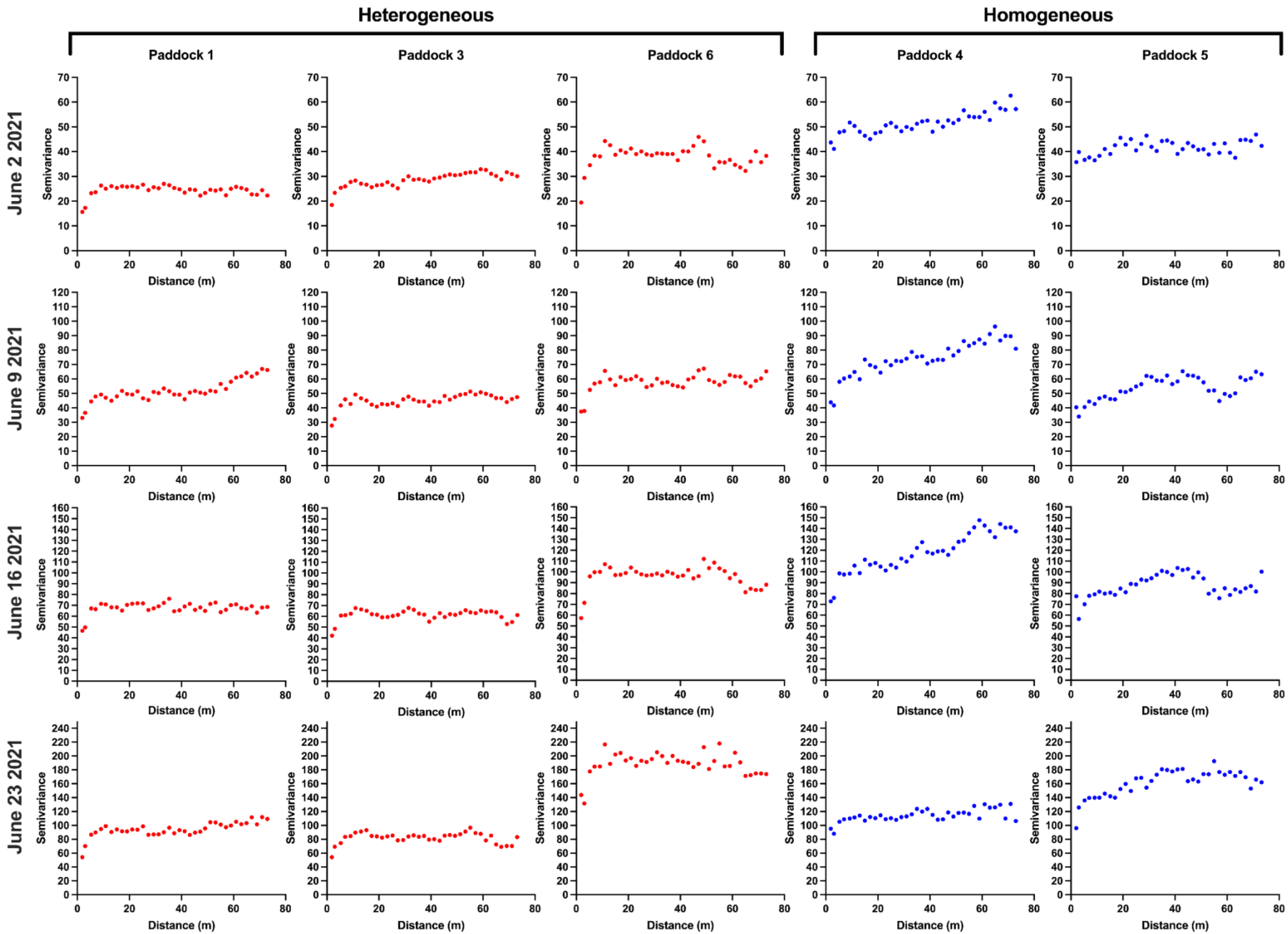
Between June 16 2021 and June 23 2021 the maximum sill for each paddock was reached (Table 1) indicating an increase in sward structure spatial heterogeneity. From June until the end of the experiment (August 4 2021), the sward structure spatial heterogeneity remained high, which is shown in the semivariograms (Figure 3) and its parameters (Table 1) as well as can be seen in the maps that show the occurrence of different degrees of heterogeneity in each paddock (Figure 4).

In June 9 2021 and June 23 2021 the model fitted was exponential for all paddocks (Table 1). In July 21 2021 paddock 4 and in August 4 2021 paddock 6 exhibited pure nugget effect (Table 1) that is a combination of random error associated with measurements and variance that is spatially dependent at scales smaller than the minimum lag interval sampled.

Grazing created different patches in each paddock and treatment. Furthermore, between paddocks of the same treatment, the spatial pattern of mosaic showed marked differences, e.g. July 28 2021 (Figure 4). The degree of spatial dependence (DSD) varied between samplings but were always between the categories moderate (0.75 – 0.25) and strong (>0.75) (Table 1).


Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
May 6 2021
May 12 2021
May 19 2021
May 26 2021
Semivariance
Distance (m)

164


Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
June 2 2021
June 9 2021
June 16 2021
June 23 2021
Semivariance
Distance (m)

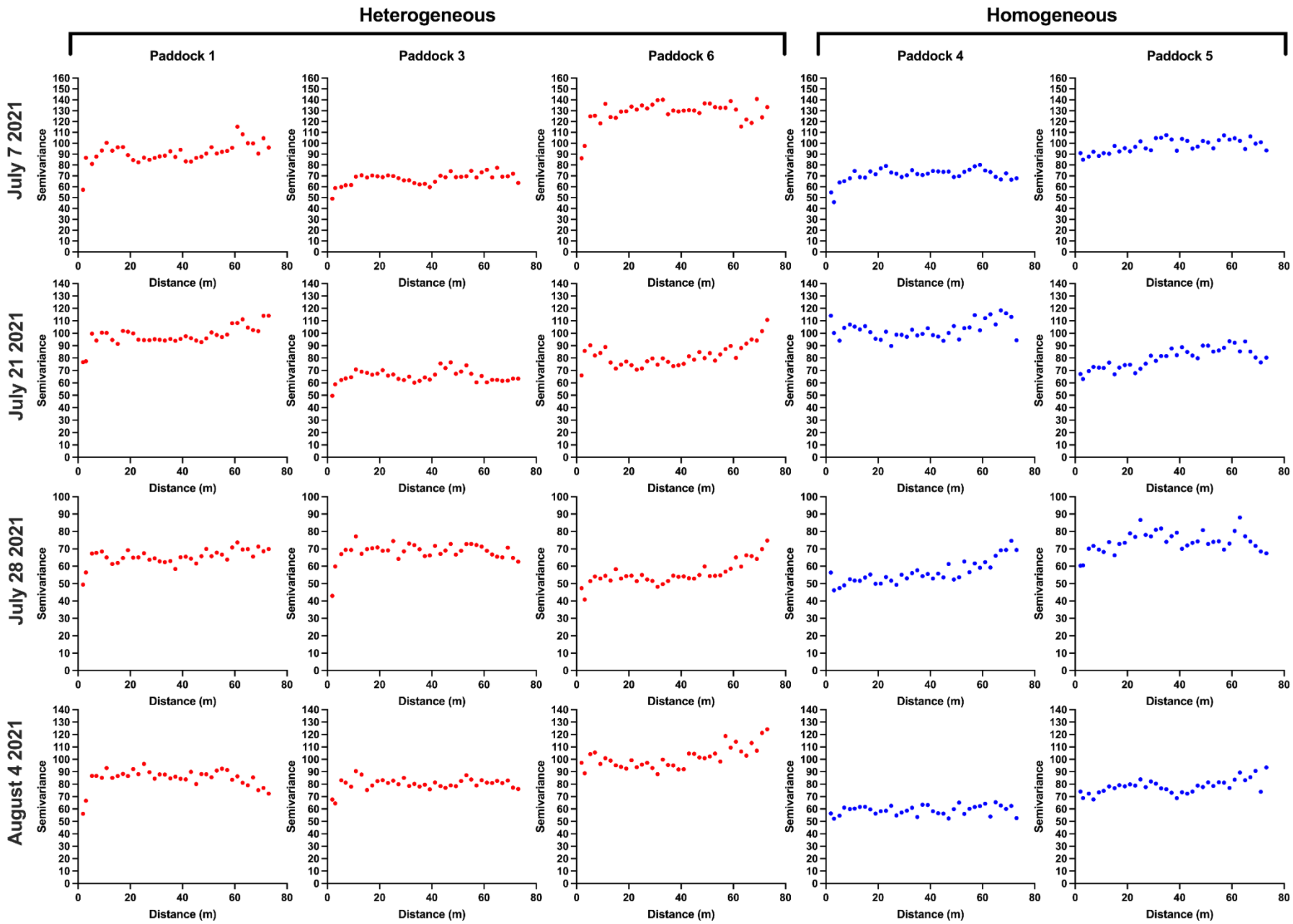

Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
July 7 2021
July 21 2021
July 28 2021
August 4 2021
Semivariance
Distance (m)

Figure 3. Experimental semivariograms of sward height spatial patterns over stocking season in paddocks with two initial levels of heterogeneity.

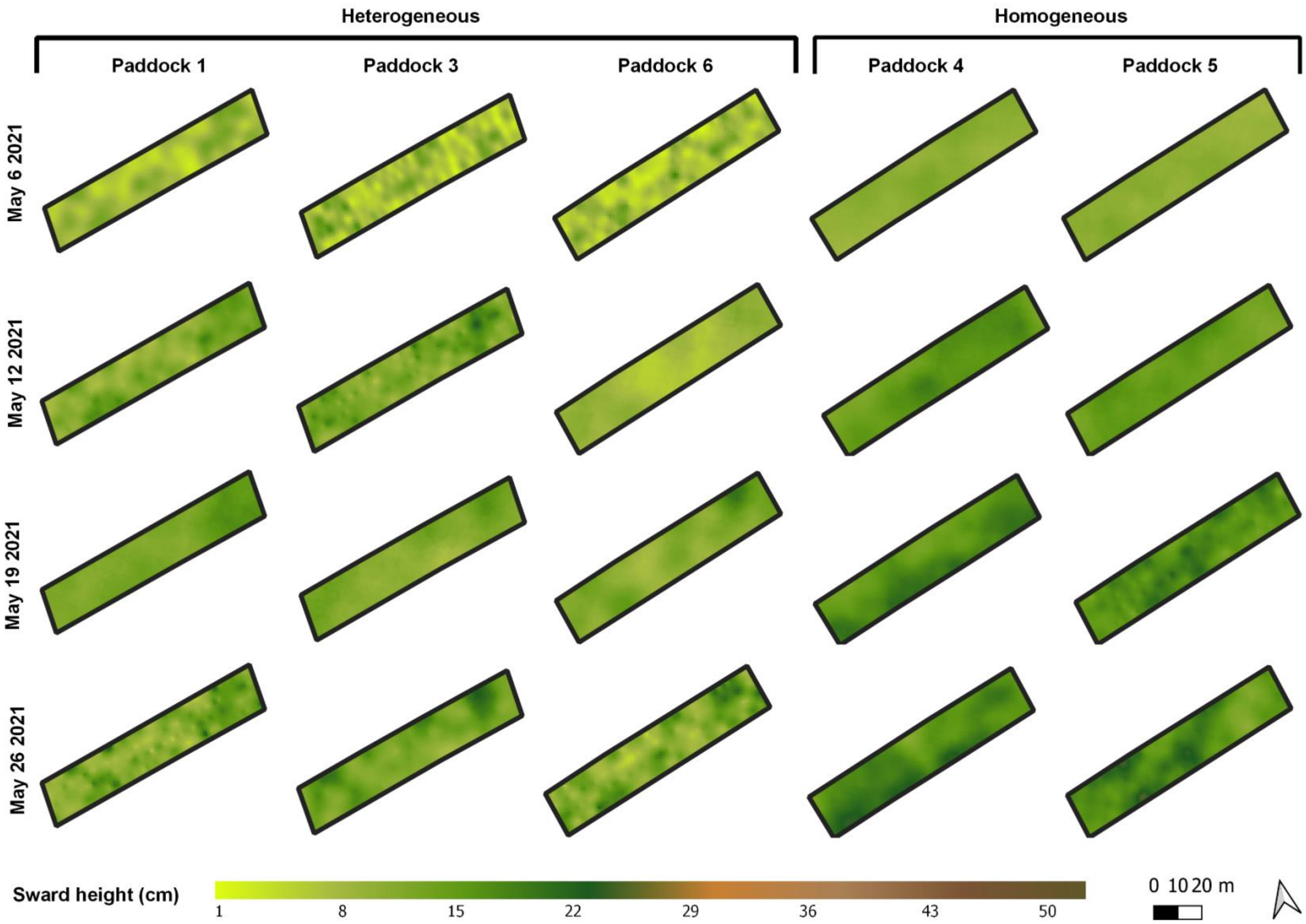
Table 1. Evolution of fitted geostatistical models and their parameters over stocking season for two initial levels of sward structure heterogeneity on perennial ryegrass-based pastures grazed by growing lambs (data of each paddock).

			Parameters						
Sampling date	Treatment	Paddock	Model	C_0	$C_0 + C_1$	A (m)	DSD	R^2	RSS
May 6 2021	Heterogeneous	1	Spherical	2.690	12.580	8.00	0.786	0.740	18.85
	Heterogeneous	3	Exponential	2.350	11.170	8.10	0.790	0.565	22.16
	Heterogeneous	6	Spherical	3.010	14.010	5.50	0.785	0.716	13.94
	Homogeneous	4	Exponential	1.360	4.798	6.00	0.717	0.458	2.033
	Homogeneous	5	Exponential	1.520	5.411	4.80	0.719	0.324	2.838
May 12 2021	Heterogeneous	1	Exponential	3.840	13.780	12.90	0.721	0.823	15.71
	Heterogeneous	3	Exponential	3.110	12.240	9.60	0.746	0.609	24.70
	Heterogeneous	6	Linear	11.040	15.028	73.12	0.265	0.647	26.23
	Homogeneous	4	Exponential	2.030	11.630	14.10	0.825	0.554	44.96
	Homogeneous	5	Linear	7.210	10.671	73.15	0.324	0.581	25.85
May 19 2021	Heterogeneous	1	Exponential	8.710	20.700	333.60	0.579	0.765	33.46
	Heterogeneous	3	Exponential	4.030	17.220	6.00	0.766	0.323	50.20
	Heterogeneous	6	Exponential	4.620	21.930	12.90	0.789	0.669	101.8
	Homogeneous	4	Spherical	3.820	11.070	16.70	0.655	0.641	39.34
	Homogeneous	5	Exponential	2.140	9.420	6.00	0.773	0.291	19.08
May 26 2021	Heterogeneous	1	Exponential	4.450	15.430	10.20	0.712	0.805	15.29
	Heterogeneous	3	Exponential	2.130	18.410	9.30	0.884	0.448	129.7
	Heterogeneous	6	Exponential	5.610	23.970	10.20	0.766	0.706	70.85
	Homogeneous	4	Exponential	3.870	18.260	12.00	0.788	0.604	73.22
	Homogeneous	5	Exponential	7.340	19.760	30.30	0.629	0.833	48.87

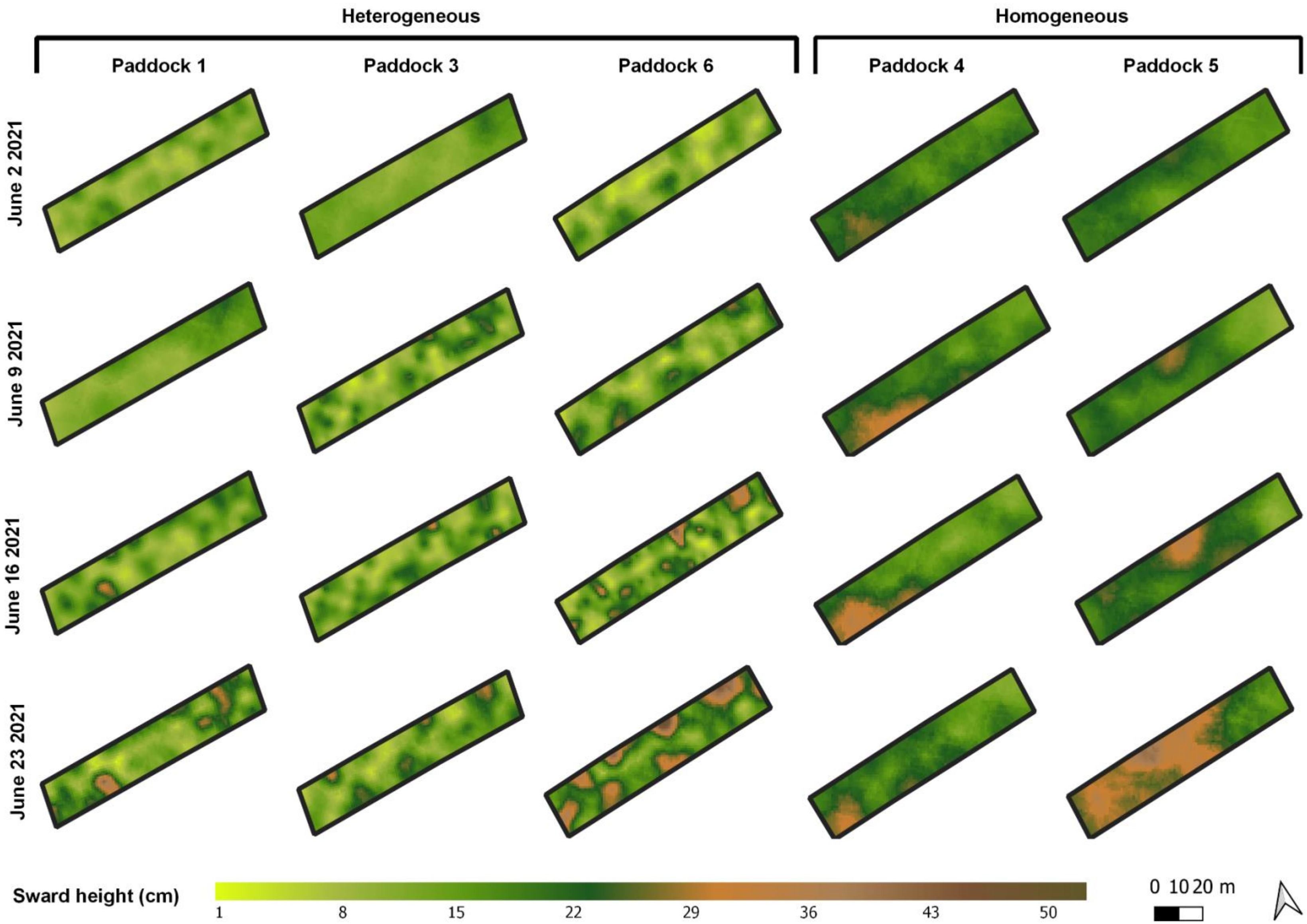
June 2 2021	Heterogeneous	1	Spherical	5.520	24.770	6.40	0.777	0.686	60.33
	Heterogeneous	3	Exponential	8.180	29.280	9.00	0.721	0.545	134.7
	Heterogeneous	6	Spherical	5.800	38.680	6.60	0.850	0.571	329.0
	Homogeneous	4	Linear	43.700	58.839	73.05	0.257	0.736	202.7
	Homogeneous	5	Exponential	11.070	41.840	3.90	0.735	0.142	261.6
June 9 2021	Heterogeneous	1	Exponential	11.800	53.580	11.10	0.780	0.393	1209.0
	Heterogeneous	3	Exponential	12.300	46.100	8.70	0.733	0.630	285.8
	Heterogeneous	6	Exponential	14.500	59.500	9.00	0.756	0.672	426.7
	Homogeneous	4	Exponential	45.900	91.810	95.40	0.500	0.843	832.4
	Homogeneous	5	Exponential	28.610	58.030	33.90	0.507	0.607	916.9
June 16 2021	Heterogeneous	1	Exponential	18.000	68.820	7.20	0.738	0.693	337.5
	Heterogeneous	3	Spherical	13.800	62.020	5.30	0.777	0.569	409.7
	Heterogeneous	6	Spherical	17.600	97.300	6.00	0.819	0.566	1644.0
	Homogeneous	4	Spherical	86.700	173.500	151.20	0.500	0.867	1602.0
	Homogeneous	5	Exponential	22.500	89.200	9.60	0.748	0.282	2928.0
June 23 2021	Heterogeneous	1	Exponential	23.200	96.600	9.00	0.760	0.587	1704.0
	Heterogeneous	3	Exponential	19.000	83.290	6.60	0.772	0.426	1366.0
	Heterogeneous	6	Exponential	47.300	192.100	7.20	0.754	0.488	5340.0
	Homogeneous	4	Exponential	31.000	115.900	6.30	0.733	0.348	2016.0
	Homogeneous	5	Exponential	86.400	172.900	31.50	0.500	0.774	3184.0
July 7 2021	Heterogeneous	1	Spherical	10.300	92.200	4.30	0.888	0.378	1951.0
	Heterogeneous	3	Exponential	17.400	68.510	6.60	0.746	0.468	584.8
	Heterogeneous	6	Exponential	37.400	130.900	8.10	0.714	0.690	1300.0
	Homogeneous	4	Spherical	36.300	72.610	10.90	0.500	0.657	515.1
	Homogeneous	5	Exponential	29.000	98.400	3.60	0.705	0.114	1174.0
July 21 2021	Heterogeneous	1	Exponential	24.000	99.300	5.70	0.758	0.403	1271.0
	Heterogeneous	3	Exponential	15.300	65.980	5.10	0.768	0.337	611.4
	Heterogeneous	6	Spherical	4.700	82.400	3.20	0.943	0.087	2721.0

	Homogeneous	4	Pure Nugget Effect	–	–	–	–	–	–
	Homogeneous	5	Linear	67.900	91.454	73.15	0.258	0.597	977.3
July 28 2021	Heterogeneous	1	Exponential	17.100	66.160	5.10	0.742	0.465	388.8
	Heterogeneous	3	Spherical	14.500	69.250	5.00	0.791	0.678	350.5
	Heterogeneous	6	Exponential	8.700	56.530	5.40	0.846	0.158	1286.0
	Homogeneous	4	Linear	46.900	65.717	73.05	0.286	0.674	522.0
	Homogeneous	5	Exponential	17.200	74.980	5.40	0.771	0.307	892.3
August 4 2021	Heterogeneous	1	Spherical	17.500	85.970	5.30	0.796	0.576	872.3
	Heterogeneous	3	Exponential	20.900	80.950	4.80	0.742	0.409	485.8
	Heterogeneous	6	Pure Nugget Effect	–	–	–	–	–	–
	Homogeneous	4	Exponential	16.000	59.300	3.00	0.730	0.048	471.9
	Homogeneous	5	Exponential	17.600	78.610	3.00	0.776	0.047	1157.0

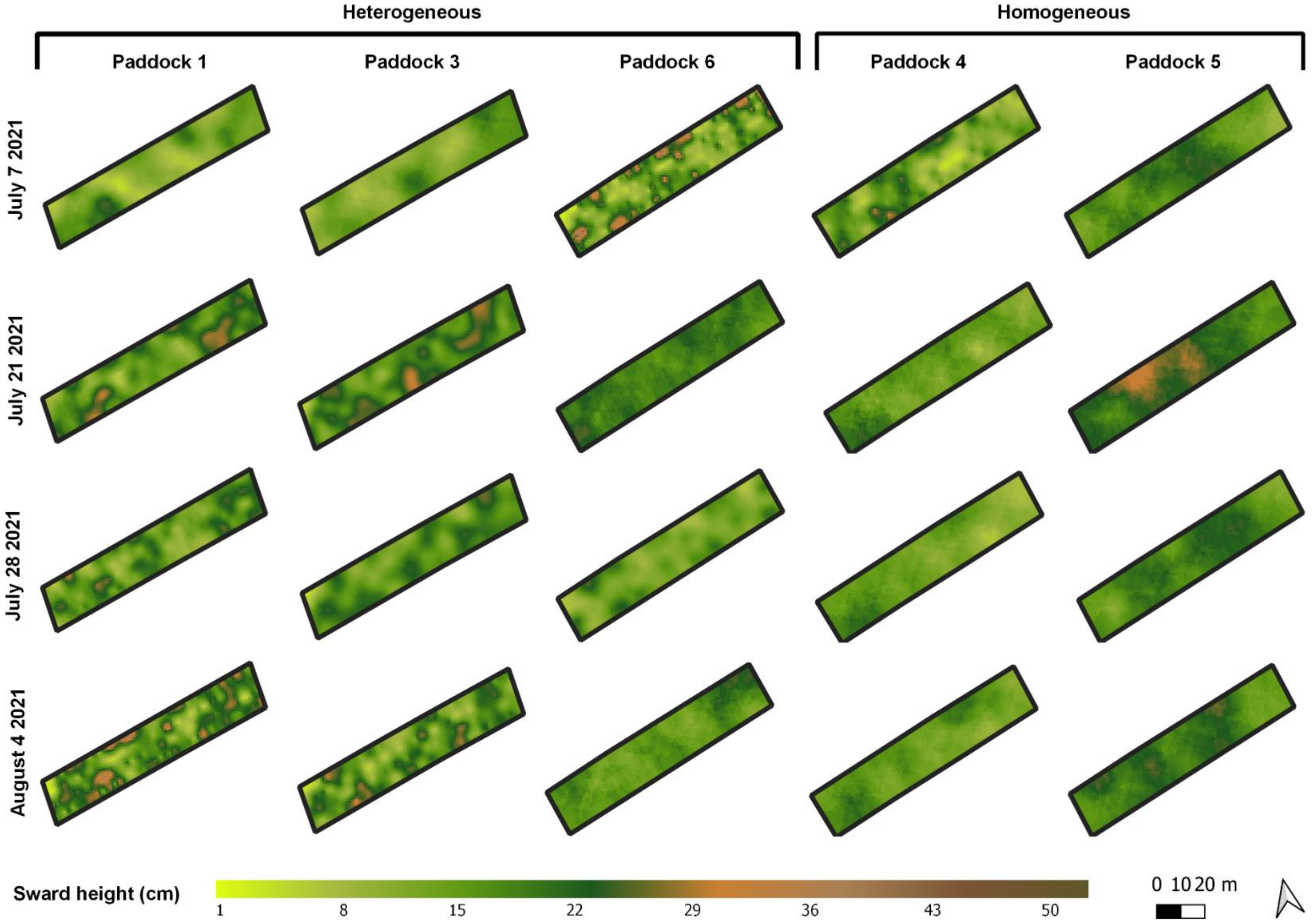
Abbreviations: C_o: nugget effect; C_o+C_1: sill; (–): no data available; A: range; DSD: degree of spatial dependence; R^2: coefficient of determination; RSS: residual sum of squares.


Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
May 6 2021
May 12 2021
May 19 2021
May 26 2021
Sward height (cm)
1
8
15
22
29
36
43
50
0 10 20 m

173



Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
June 2 2021
June 9 2021
June 16 2021
June 23 2021
Sward height (cm)
1
8
15
22
29
36
43
50
0 10 20 m


Heterogeneous
Homogeneous
Paddock 1
Paddock 3
Paddock 6
Paddock 4
Paddock 5
July 7 2021
July 21 2021
July 28 2021
August 4 2021
Sward height (cm)
1
8
15
22
29
36
43
50
0 10 20 m

175

Figure 4. Sward structure heterogeneity dynamics (evolution) over stocking season in maps derived from ordinary kriging of sward heights (cm) in paddocks with two initial levels of heterogeneity.

Discussion

Grazing is a fundamental driver shaping heterogeneity, the functioning and stability of grasslands. By quantifying sward structure heterogeneity across spatial scales in a grassland ecosystem, to the best of our knowledge, our study provides the first evidence of how fast the grazing process creates heterogeneity in initially homogeneous swards (Figure 3), being that four days after the animals accessed the area, the heterogeneity of paddocks of the homogeneous treatment reached levels close to paddocks of the heterogeneous treatment. This response can be explained by selective grazing, which pronouncedly alters the sward structure with regard to the spatial distribution of the sward height, even in situations of moderate grazing intensity.

After the vegetation rapidly assumes a heterogeneous behavior caused by the grazing process (Figure 3 - May 6 2021) the semivariance threshold gradually changed. Furthermore, in most samplings, significant semivariance fluctuations were observed beyond the first peak (Figure 3). These fluctuations beyond the first peak indicate that over stocking season the grazing process shaped the vegetation so that both small-scale patchiness and regular arrangement of those patches (patches arranged regularly across the paddock) occur, as demonstrated in previous studies (Palmer, 2002; Augustine & Frank, 2001; Pastor et al., 1998). This response is consistent with findings of Fuhlendorf & Smeins (1999) who demonstrated that grazing can alter scaling effects and heterogeneity at several levels.

The effects of the grazing process on the mean diameter of patches were variable throughout the stocking season, showing that a moderate grazing intensity causes variations due to the initial vegetation condition (homogeneous vs. heterogeneous), and also within the same initial condition (between paddocks of the same treatment) (Table 1), being that an indicator of the patch diameter is the range (Robertson & Gross, 1994; Augustine & Frank, 2001; Townsend & Fuhlendorf, 2010). In this sense, our study provides a clue that temporal stocking rate changes to maintain the same grazing intensity e.g average sward height (see Silva Neto et al. in prep.) when generating different instantaneous stocking rates between paddocks due to variability in plant growth rates can generate differences in patch sizes, altering the spatial distribution of vegetation (Figure 4). It is well known that grazing intensity is a determining factor of the proportion occupied by different types of patches in a grassland (Tonn et al. 2018), however, studies focusing on vegetation heterogeneity related to the grazing process must consider stocking rate adjustments that can generate independent situations between paddocks of the same treatment (similar average condition) or have more detailed information on the spatial grazing patterns of the animals, but these issues still need to be elucidated.

Fluctuations in heterogeneity levels can be related to oscillations in average sward height (Figure 5 – Appendix). These oscillations are due to the fact that the stocking rate adjustments with put-and-take animals, although performed weekly, were not fully effective in controlling the sward height, which showed higher growth rates than usually observed for the area due to an extreme wet year. In addition, heterogeneity reached higher levels in the middle of the stocking season (Figure 3 – June 16 2021; June 23 2021) when the vegetation presented drastic structural changes due to the change of phenological stage from vegetative to reproductive as well as morphological changes (e.g. leaf /stem ratio; bulk density) at several levels. These responses modify the use of patches (selective grazing) (Ginane et al. 2003; Griffiths et al. 2003) accentuating the contrast between short, medium and tall patches.

Under moderate grazing intensities, when the average height of the sward is high, heterogeneity is greater (Figure 3 – June 16 2021; June 23 2021, Figure 5 – Appendix) which enables the formation of a greater number of patch classes. As previously mentioned, it is necessary to elucidate the interactions between oscillations in stocking rate and average sward height at moderate grazing intensity to understand how different levels of heterogeneity can be generated in a similar management condition and the implications of these dynamics on ecosystem functioning. This will bring a new level of detail to the processes that occur in these ecosystems. It is well known that moderate grazing intensity increased large-scale heterogeneity by creating conditions that lead to patch grazing (Fuhlendorf & Smeins, 1999).

Adler et al. (2001) highlighted the importance of the geostatistics approach to understand the effects of grazing on vegetation heterogeneity, since spatial heterogeneity varies with scale, so only with the use of these methods is it possible to obtain more robust evidence on how these relationships occur in the pastoral ecosystem. The same authors mention that many studies explore how grazing increases heterogeneity, but few studies provide evidences on the causes of decreased heterogeneity by grazing, with the exception of situations where overgrazing occurs, which leads to a homogeneous distribution of vegetation. At moderate grazing intensity, our study provides a clue which may be the average handling height, which when decreasing the average sward height at paddock scale can lead to a decrease in heterogeneity, indicated by the semivariance (Figure 3), being a direct effect of the instantaneous stocking rate used to reach a certain target sward height which changes the number of patch classes as mentioned previously.

Furthermore, the grazing process generates cascading effects not only through the consumption of plant material but through the deposition of dung and urine, causing spatial asynchrony in above- and below-ground responses that could have significant implications for both plant-plant interactions and plant -soil feedbacks involved in the regulation and coupling of grassland carbon and nitrogen cycling (Bloor et al. 2020; Augustine & Frank 2001). Thus, the description of vegetation dynamics and grazing influences on grasslands requires a multiscale approach (Fuhlendorf & Smeins, 1999). Our results clearly showed that the grazing process quickly creates heterogeneity in the vegetation under moderate grazing intensity. It is important to highlight that heterogeneity is an inherent and unavoidable property in grassland ecosystems. However, further research should look to what extent (time) patterns imposed via anthropic intervention, such as those generated in this study, are stable.

Conclusions

This is the first time that a study shows the description of spatial patterns of sward structure in high temporal resolution (weekly), and that shows the dynamics (evolution) of vegetation spatial heterogeneity over stocking season under two initial levels of heterogeneity in sward structure (homogeneous and heterogeneous) managed at moderate grazing intensity. Thus, the study provides a baseline for understanding the role of heterogeneity decoupled from grazing intensity (which may be a confounding factor) across a wide range of spatial scales, in addition to providing a robust measure that can be connected with the ecological function of grasslands under grazing.

Our findings especially highlight that the grazing process (4 days) rapidly creates heterogeneity in grassland vegetation. Fluctuations in sward structure heterogeneity levels at moderate grazing intensity occur throughout the stocking season and are associated with the average target sward height, being impacted by stocking rate adjustments and morphological and phenological changes in plants. Similar grazing conditions can lead to different levels of heterogeneity, so studies must consider stocking rate and spatial grazing patterns to understand what drives intra-paddock variations. Finally, it is widely known that moderate grazing intensity promotes better animal production and, in this sense, we believe that to enhance the multiple role of grasslands it is necessary to understand how heterogeneity at moderate grazing intensity can benefit the fulfillment of diverse ecosystem services, exploring also its possible potentialities in climate change scenarios.

Declaration of interest

The authors declare no conflict of interest.

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Appendix

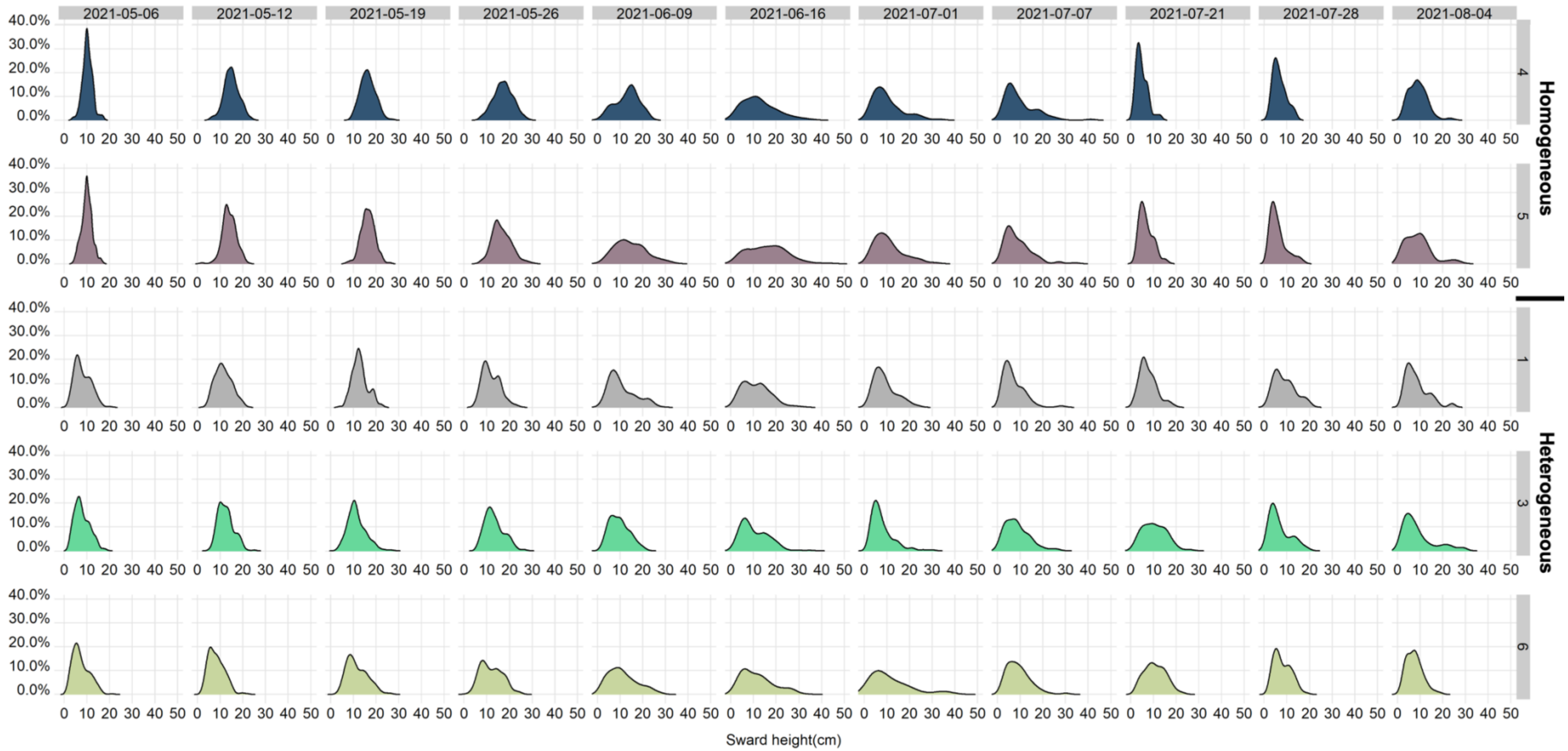

Figure 5. Distribution of sward height in each paddock over stocking season of sheep grazing perennial ryegrass-based pastures during eleven samplings. Paddocks 4 and 5 (top) refer to homogeneous treatment, while paddocks 1, 3 and 6 (bottom) refer to heterogeneous treatment.

CHAPTER III[4]

Initial spatial heterogeneity in sward structure at moderate grazing intensity does not affect animal and herbage productivity

[4] Manuscrito.

Initial spatial heterogeneity in sward structure at moderate grazing intensity does not affect animal and herbage productivity

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Abstract

Heterogeneity is an inherent property of grasslands that impact the performances of grazing operations. We evaluated the growth performance of sheep grazing perennial ryegrass-based pastures and herbage production under two initial levels of heterogeneity in sward structure (homogeneous and heterogeneous) at the patch level under moderate grazing intensity. No differences were found in average herbage mass (HM) and daily herbage accumulation rate (DHAR) between treatments ($p>0.05$). Average daily gain (ADG), live weight gain per hectare (LWGha) and stocking rate (SR) had no significant differences between treatments detected ($p>0.05$) over stocking season. We conclude that the initial homogenization of sward structure does not result neither in improvements in individual and per area animal production, nor in herbage production when managed at moderate grazing intensity. These outcomes are important to redesign and bring to the fore new models of livestock production that consider heterogeneity as an intrinsic property of these ecosystems, using this to enhance ecosystem services and adapt to climate change scenarios.

Keywords: sward height, perennial ryegrass, grazing management, patch grazing, herbage production, sheep performance

Introduction

Grazed grasslands provide many ecosystem services and grazing management impact their ability to do so. Heterogeneity is an inherent property of these ecosystems. This property of vegetation communities influences from smaller scales for both plants and animals, such as the grazing patterns of herbivores, through increases in the diversity and stability of plant species, bird and insect communities (Jerrentrup et al., 2014; Hovick et al., 2015; Fuhlendorf et al., 2006; Rook & Tallowin, 2003). The synergies between heterogeneity and biodiversity also span at larger scales such as landscape level, where they can enhance the provision of multiple ecosystem services (Lavorel et al. 2022). Thus, for a better understanding of the interactions between herbivores and vegetation, grasslands should be treated as complex systems (Anand et al., 2010) and heterogeneity should be seen as a key mechanism supporting the multifunctionality of these ecosystems (Lavorel et al. 2022).

On the one hand, vegetation communities are heterogeneous in space and time, due to numerous factors such as biotic interactions with soil, variations in soil fertility and water availability, excreta depositions and dispersion mechanisms of plant species (Parsons & Dumont, 2003; Chapman et al., 2007). Heterogeneity in grassland vegetation does not only occur in natural grasslands. Although monospecific and cultivated swards appear homogeneous, they also show some degree of heterogeneity (Barthram et al., 2005; Hirata, 2000).

On the other hand, grazing is a multiscale process, also heterogeneous, varying in space and time, involving a combination of one-time confined choices to perform bites on specific feeding stations to large movements of the animals across the whole grassland (or landscape) (Bailey & Provenza, 2008; Zhao & Jurdak, 2016). Thus, the grazing process creates heterogeneity through selective grazing where animals select plants and plant parts and through grazing distribution patterns, where some areas are more exploited than others (patch grazing) forming a dynamic mosaic (Adler et al. 2001; McNaughton, 1984; Coughenour, 1991; Bailey et al., 1998; Cid & Brizuela, 1998).

In this complex environment, bidirectional and cascading interactions occur. The grazing process creates heterogeneity and is itself influenced by the existing heterogeneity in the vegetation. Beyond the more obvious effect of spatial arrangement of species that can impact heterogeneity in grasslands, sward height is a key structural component that drives animal foraging behavior (Shipley, 2007) and consequently its functional response (Drescher, 2003) and subsequent plant regrowth. This sward height also shows some degree of heterogeneity with pastures composed of patches of grass at various regrowth stages.

Using a stochastic dynamic mathematical model, Pontes-Prates et al. (2020) have shown that increasing levels of heterogeneity, can enhance the functional response of herbivores, i.e. the function instantaneous intake rate to sward height, minimizing grazing time. This opportunity for animals to take advantage of heterogeneity in sward structure questions the homogeneity paradigm of modern-day grazing strategies. Many management approaches try to reduce heterogeneity, such as sowing monoculture pastures or applying equalization cuts. Even traditional grazing management aims to promote homogeneity through uniform distribution of livestock grazing across the landscape, being some specialized managements employ extreme measures to override livestock behavior (Fuhlendorf & Engle, 2001).

According to Fuhlendorf et al. (2017), heterogeneity is the basis for rangeland management because only with the understanding property of these ecosystems is it possible to enhance multiple ecosystem services. Furthermore, many studies on heterogeneity in grasslands are focused on describing the heterogeneity of vegetation associated with grazing intensities (Cid & Brizuela, 1998; Nunes et al. 2019), neither describing its evolution, nor how animals exploit this heterogeneity. This is because heterogeneity has not yet been studied in isolation from grazing intensity, pointing to a crucial knowledge gap that needs to be explored.

In this research we generated two levels of initial heterogeneity, through anthropic intervention, considering the sward height to advance mechanistic understanding of how sward structural heterogeneity at moderate grazing intensity impacts on animal performance. We hypothesized that initial sward heterogeneity does not impair animal performance and herbage production. Our objectives were: to assess individual and area animal production as well as forage production and sward height variations throughout a growing season under two initial levels of heterogeneity at moderate grazing intensity.

Material and methods

Site and treatments

The mechanistic grazing experiment was conducted at the AgricultureIsLife experimental farm, (University of Liège experimental farm, Belgium), using a sward composed predominantly of perennial ryegrass (*Lolium perenne*) with different heterogeneity levels and as sheep as model animal. Two treatments were applied on experimental paddocks as follows:

Treatment 1: a randomized heterogeneity treatment at the order level of 25 m^2 considered as patch level;

Treatment 2: a homogeneous treatment, the entire paddock with a homogeneous initial sward height (see Figure 1 and Figure 2).

We generated two levels of heterogeneity, considering the sward height as metric for heterogeneity, through a single mechanical cut before the animals accessed the area. The aim of the cutting combinations was to yield at the beginning of the experiment an average sward height on the paddocks of 10 cm whatever the treatment. Hence, in the homogeneous treatment the whole area was mowed to reach a height of 10 cm at the beginning of the experiment. In the heterogenous treatment, each paddock was subdivided in 80 randomly distributed patches of 5 × 5 m^2 each. Forty of those patches were mowed a couple of days before the beginning of the experiment to reach a sward height of 15cm. The other 40 were mowed to reach 5 cm when the animal was set to graze, aiming an average of 10 cm at the paddock level. The value around 10 ± 5 cm sward height was used as target for a moderate grazing intensity, which in perennial ryegrass pastures indicates a non-limiting condition for the ingestive process of the animals (Bazely, 1988). A total of three replicates per treatment (totaling six experimental units) was initially planned, however, due to mechanical cutting not being effective in setting the required heterogeneity level of one homogeneous treatment paddock at the beginning of the experiment, data from this paddock were not included in this paper. The experimental design was a randomized complete block with three replicates of the heterogeneous treatment and two replicates of the homogeneous treatment, totaling five experimental units.

The stocking season lasted 92 days, starting in 8 May 2021 and finishing at 8 August 2021. Three evaluation periods representing the months of May, June and July were hence considered as vegetation growth patterns changed over the course of the stocking period with changes in photoperiod and temperature.

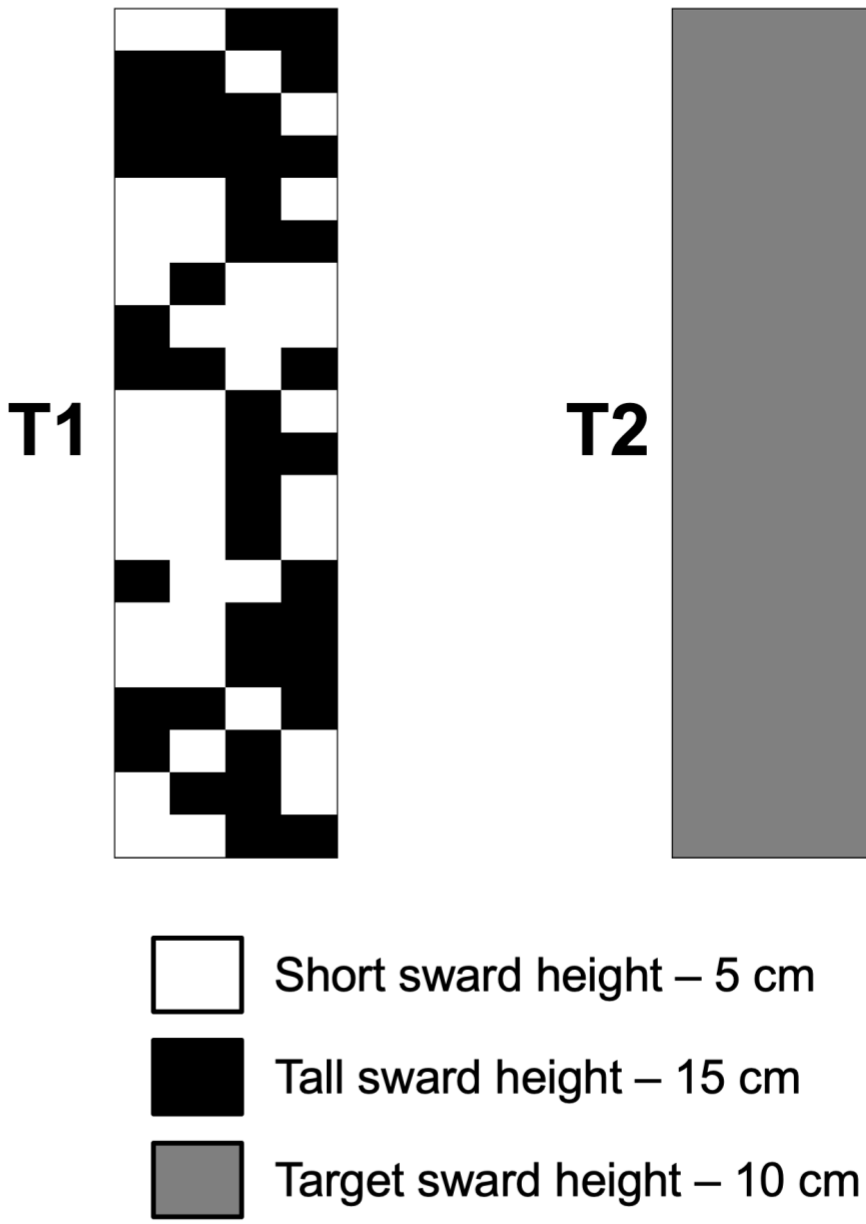

Figure 1. Representation of the two treatments

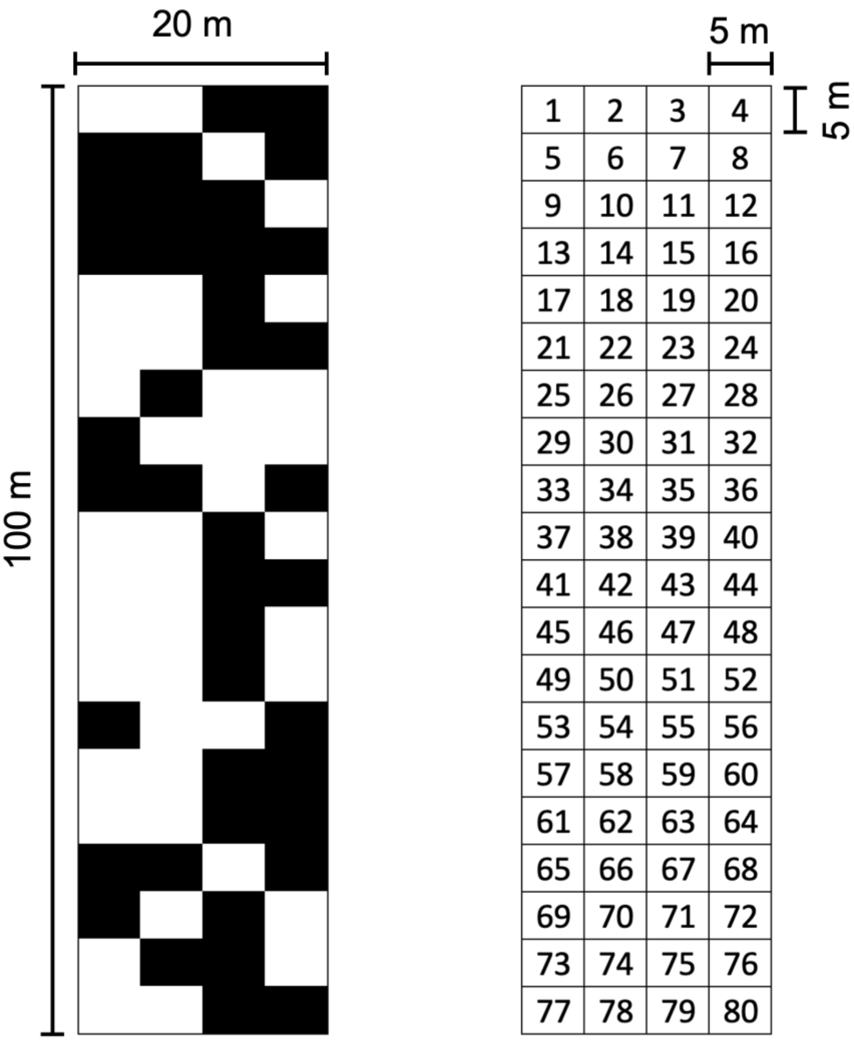

Figure 2. Representation of the organization of heterogeneous treatment. Each paddock of the heterogeneous treatment was divided into 80 quadrants (5 x 5 m). A draw was carried out so that the heights of each quadrant were randomly arranged.

Vegetation

In the experimental area of 3.0 ha, five paddocks were demarked. The area of each paddock was dimensioned to accommodate at least three test animals. The pasture (or vegetation) consists of perennial ryegrass (*Lolium perenne*) predominantly in addition to species such as white clover (*Trifolium repens*), Kentucky bluegrass (*Poa pratensis*), Yorkshire fog (*Holcus lanatus*), dandelion (*Taraxacum* sp.).

Vegetation Measurements

Initial assessment

The botanical composition of the paddocks was determined at species level and converted into function diversity. This initial assessment was performed along a fixed grid at a density of 200 points per paddock (every 2.0 m) and spatialized in a GIS to identify remarkable areas for the subsequent monitoring.

The initial herbage mass was determined by means of six random samplings, carried out at the beginning of the stocking period.

Monitoring

The sward structure was evaluated in each experimental unit (EU) in all treatments. The sward surface height was measured using a sward stick recording the plant species as well (Barthram, 1985) were measured 200 points (along a fixed grid) twice a week.

The herbage mass (HM, kg DM ha^{-1}) was measured by cutting at ground level using a quadrat of 0.25 m^2 (0.50 × 0.50 m) and replicated on six samples, was determined approximately every 30 days, in each EU (paddock). Herbage samples were oven dried at 55°C for 72 h.

The daily herbage accumulation rates (DHAR kg ha^{-1}), was determined using six grazing exclosure cages, i.e., (three per initial sward height in heterogeneous treatment) (Klingman et al., 1943).

The initial herbage mass added to the daily herbage accumulation rate and multiplied by the number of days in each stocking cycle, resulted in the total herbage production: total aboveground net primary productivity (ANPP) (kg DM ha^{-1}).

Instantaneous herbage allowance (kg DM 100 kg LW^{-1} day^{-1}) was calculated according to Sollenberger et al. (2005).

Animals

The experimental animals were growing lambs. The animals had an approximate age of 6 months and an average live weight of 25 kg. Each experimental unit (paddock) received three (03) test animals (permanent animals over the whole stocking season) and a variable number of put-and-take animals (adjustment animals) (Mott & Lucas, 1952). The stocking rate adjustment was performed whenever necessary, usually once a week, to maintain the target sward heights. In all, fifteen (15) lambs were used permanently plus a varying number of put-and-take animals.

Animal Measurements

Animal performance

The animals were weighed monthly throughout the stocking season after fasting from solids and liquids for approximately 12 h. The average daily gain (ADG, kg animal^{-1} day^{-1}) was calculated as the difference between the final and initial weights of the test animals divided by the number of days in each stocking period.

The stocking rate (SR, kg LW ha^{-1}) was calculated by average live weight (LW) of test animals and the LW of the put-and-take animals, multiplied by number of days that they remained on the EU (paddock). The live weight gain per hectare (LWGha, kg ha^{-1}) was obtained by multiplying the animals ha^{-1} by the ADG of the test animals and the number of total grazing days.

Statistical Analysis

Statistical analyses were performed in R (version 3.5.1, R Core Team, 2018). Data were analyzed using the lme4 package for mixed linear models (Bates et al., 2015). The treatments, evaluate periods and interactions were considered a fixed effect for all variables. The random effect was included the repeated measurement in time, that is, each paddock was evaluated over time (period). The Normality was verified by the Shapiro-Wilk test and homogeneity of variances by the Bartlett test ($p>0.05$). Independence of the residuals were test for visual plot. The ANOVA assumption for average daily gain variables was achieved after logarithmic transformation.

Results

Sward height

The vegetative sward height was 12.4 and 10.1 cm ($p<0.001$) and the global average of sward height was 16.9 and 13.6 cm ($p<0.001$) for the heterogeneous and homogeneous treatments, respectively. Despite a difference between the averages, the two treatments met the proposed condition of moderate grazing intensity which is confirmed by the similar herbage allowance between treatments (Table 1).

Table 1. Sward height and herbage allowance of perennial ryegrass-based pastures grazed by growing lambs managed under two initial levels of sward structure heterogeneity

Variables	Treatment		
	Homogeneous	Heterogeneous	P_{TREAT}
SHV	12.4	10.1	<0.001
SHT	16.9	13.6	<0.001
HA	2.85	2.86	0.9747

Note: P_{TREAT}, significance level for treatment. SHV, vegetative sward height (only leaves) (cm); SHT, total sward height (leaves, stems, inflorescences); HA, herbage allowance (kg DM kg LW^{-1} day^{-1}).

Herbage production

The characteristics of perennial ryegrass pastures grazed by growing lambs over the stocking season (May, June and July) (Table 2) showed no significant differences in average of daily herbage accumulation rate and herbage mass between treatments. The daily herbage accumulation rate was greater in June with an average of 131.8 kg DM ha^{-1}. Herbage mass was greater in July with an average of 4153 kg DM ha^{-1}.

Table 2. Characteristics of perennial ryegrass-based pastures grazed by growing lambs managed under two initial levels of sward structure heterogeneity

Variables	Treatment		Period			P_{TREAT}	P_{PER}	P_{T*P}
	Homogeneous	Heterogenous	1	2	3			
DHAR	99.5 (8.04) *	83.4 (6.81)	71.4 (7.9) b	131.8 (8.9) a	71.2 (10.3) b	0.213	0.009	0.680
HM	3360 (294)	3338 (240)	3039 (224) b	2859 (195) b	4153 (366) a	0.956	0.032	0.183
ANPP	12784 (1234)	10788 (1008)	–	–	–	0.2443	–	–

Note: P_{TREAT}, significance level for treatment; P_{PER}, significance level for evaluation period; P_{T*P}, significance level for interaction between treatment and period. When the interaction was not significant, the significance of the difference between the two levels of each factor is in the P_{TREAT} and P_{PER} columns. Means without common letters differ by Tukey test ($p < .05$) for those variables that exhibited significant interaction. Abbreviations: DHAR, daily herbage accumulation rate (kg DM ha^{-1}); HM, herbage mass (kg DM ha^{-1}); ANPP, total aboveground net primary productivity *= standard error of the mean; (–): no data available.

Animal performance and stocking rate

No differences were found in the average daily gain between treatments with an average of 0.148 kg animal^{-1} day^{-1} (Figure 3). The average daily gain was greater in May with an average of 0.242 kg animal^{-1} day^{-1} (Figure 3). The average daily gain decreased from May to June and July, respectively ($p<0.001$), with the lowest average in July, 0.061 kg animal^{-1} day^{-1} (Figure 3).

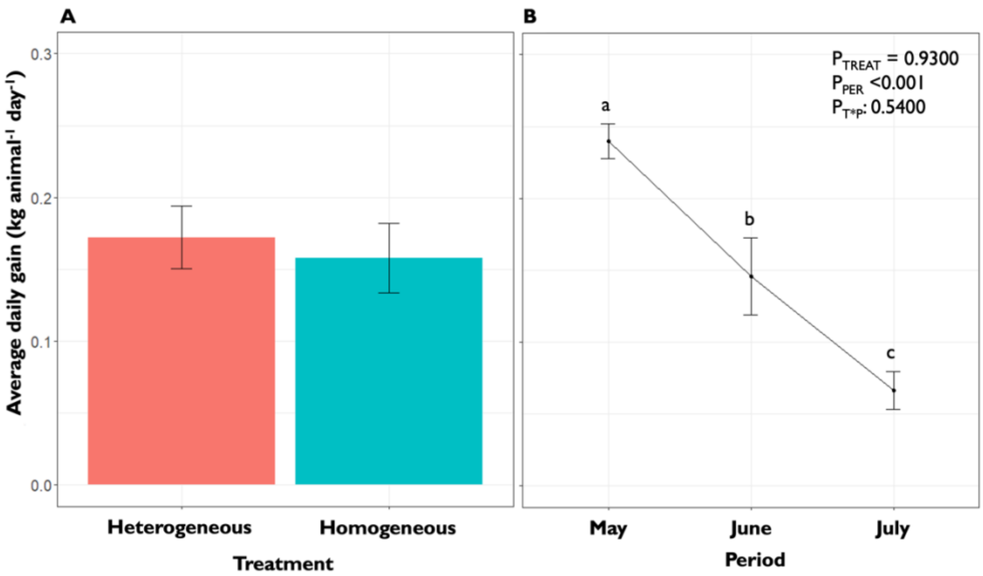

Figure 3. Average daily gain (kg animal^{-1} day^{-1}) of growing lambs grazing perennial ryegrass-based pastures in (a) different treatments and (b) per evaluation periods (May, June and July).

Live weight gain per hectare presented an average of 159.5 kg ha^{-1}, no significant differences were found between treatments(Figure 4). Over evaluation periods, the treatments showed a similar response of linear decrease in live weight gain per hectare (Figure 4).

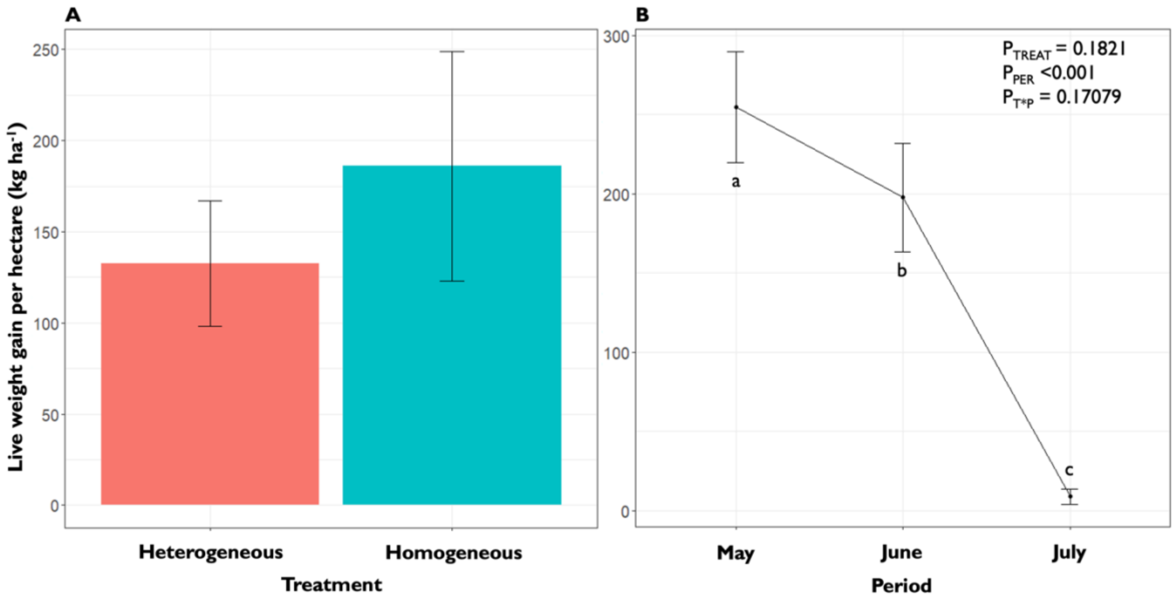

Figure 4. Live weight gain per hectare (kg ha-1) of growing lambs grazing perennial ryegrass based pastures in different treatments through evaluation periods (May, June and July).

No differences were found for the stocking rate between treatments with an average of 1445.5 kg LW ha^{-1} (Figure 5). Over the course of the stocking season, the stocking rate had to be increased to keep the sward height close to the proposed target (Figure 5). The stocking rate only differed in the first evaluation period (May) (p<0.001) with an average of 937 kg LW ha^{-1}, compared to 1658 and 1741 from the second and third period respectively (Figure 5).

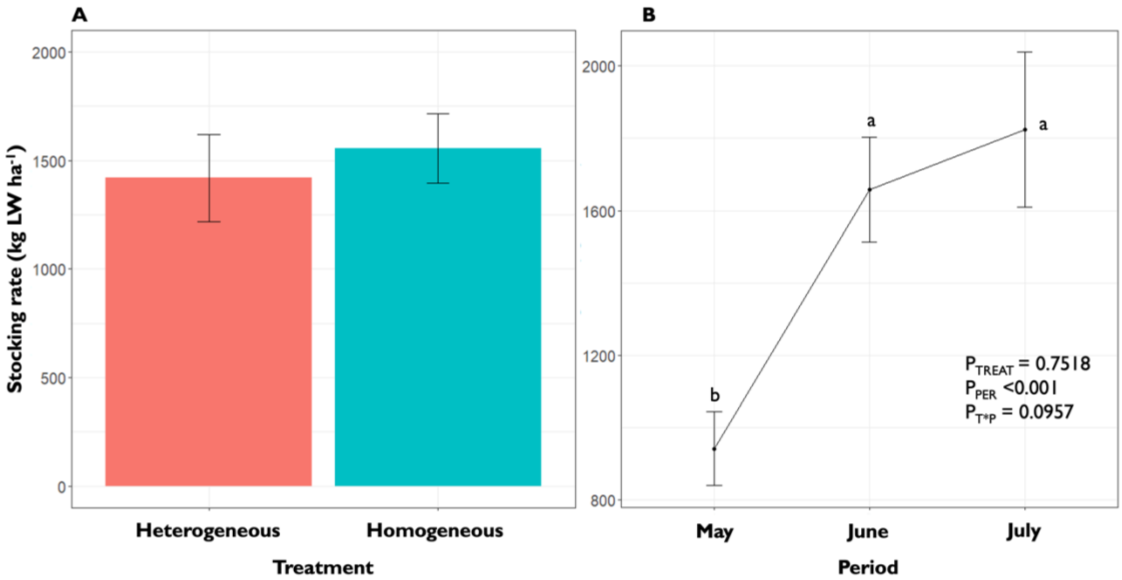

Figure 5. Stocking rate (kg LW ha^{-1}) of growing lambs grazing perennial ryegrass based pasture in different treatments and evaluation periods (May, June and July).

Discussion

In this paper, we have shown that initial sward structure heterogeneity at the patch level does not lead to decreases in animal performance nor herbage production under moderate grazing intensity. In addition to that, an attempt to homogenize the sward structure at the beginning of the stocking season does not generate benefits in terms of average animal and vegetal production, demonstrating that the sward structure heterogeneity at the patch level is not a problem, contrary to the current paradigm of grazing management.

Over the stocking season, sward height fluctuated around the average target height (10 cm) (Table 1) (Figure 7 – Appendix). These oscillations above the sward target height are due to the fact that the stocking rate adjustments with put-and-take animals, although performed weekly, were not fully effective in controlling the sward height, which showed higher growth rates than usually observed for the area due to an extreme wet year (Table 2). However, despite having presented values above 10 cm, this oscillation did not represent a limitation for the ingestion since for ryegrass-based pastures the bite mass increases linearly up to 20 cm of sward height (Gibb, 2006) while the daily herbage intake is practically constant between 10 and 20 cm of sward height (Gibb et al. 1996). Thus, as sward height is hierarchically the main component of the sward structure that determines the ingestive behavior mechanics of animals, although variations in sward height may represent some limitations in this study, the condition of moderate grazing intensity was met for both treatments which is confirmed by the similar herbage allowance between treatments (Table 1).

The effect of variables such as standing herbage mass and sward height on subsequent herbage accumulation rate is widely known and these variables can be used to predict herbage accumulation (Brougham, 1956; Barker et al. 2010). We found no difference in the average herbage masses nor in the daily herbage accumulation rate (Table 2) between initial levels of heterogeneity in sward ($p>0.05$). This can be explained by the grazing intensity used in the experiment, where despite the occurrence of short and tall patches, in general the plants conserved a high photosynthetically active leaf area, which contributed to growth. Furthermore, this agrees with Cid et al. (2008) who demonstrated that as long as no overgrazing occurs, short patches have lower productivity per unit area but higher relative growth rate than the taller patches, indicating that despite having lower biomass, they may have a higher photosynthetic capacity. This may explain the similar daily herbage accumulation rate between the two initial conditions. However, these mechanisms still need to be better elucidated.

Vegetation variables show that animals were kept in similar grazing conditions, despite the initial difference in sward structure heterogeneity at the patch level. No differences in animal performance between the two treatments was observed ($p>0.05$) (Figures 3, 4 and 5). Similar average daily gains between the treatments ($p>0.05$) was observed (Figure 3), which shows that the grazing intensity is a key management variable influencing by the sward structure, the ingestive behavior of the animals and the herbage intake, which finally determines the animal performance. This condition agrees with Briske et al. (2008) who argue that the selectivity of animals is not impaired at moderate grazing intensities. Furthermore, Pontes Prates et al. (2020) demonstrated that sward height heterogeneity can increase the functional response of animals, by providing a wider range of optimal grazing opportunities in terms of potential bite structure, which would also impact individual animal growth performance.

Although no treatment effect was detected for live weight gain per hectare ($p>0.05$), the lower average of live weight gain per hectare of the heterogeneous treatment can be attributed to the lower initial stocking rate that caused due by half of the paddock area of the heterogeneous treatment having been mechanically cut at 5 cm to generate the different initial levels of heterogeneity. In a real situation of moderate grazing intensity, heterogeneity is increased and patches with short sward do not occupy such a representative area of each paddock (Cid & Brizuela, 1998; Nunes et al. 2018). Thus, the lower live weight gain per hectare in the first period cannot be attributed to a negative impact of heterogeneity but to the intensity of intervention to generate the initial levels of heterogeneous treatment. There was an effect for the period in live weight gain per hectare, and in the third period (July) live weight gain per hectare was lower than the average of the first and second periods ($p< 0.01$) (Figure 4), which can be explained by factors such as structural changes in the sward with the more presence of reproductive stems at the end of the grazing season combined with the lower weight gain efficiency of animals close to finishing.

Stocking rate had no significant differences between treatments detected ($p>0.05$), however there was an effect of periods with an opposite response to live weight gain per hectare, where the stocking rate was higher in the second and third periods compared to the first period (Figure 5). This is because that the sward height showed growth and stocking rate adjustments were made in order to maintain the sward height around the target, which culminated in an increase in the stocking rate in the phases subsequent to the beginning of the experiment.

Despite the current perception of grazing management that homogenization is necessary to improve animal and plant productivity in pastures, our results showed an absence of beneficial effects from an initial homogenization in the sward structure when is managed at moderate grazing intensities. In addition, further studies should be carried out on the evolution of heterogeneity in time from the two initial levels of heterogeneity in sward structure, which was not our objective in the present study. It is important to highlight that the heterogeneity in sward structure does not harm animal and plant production and is related to several ecosystem services.

Conclusions

Our findings highlight that the initial homogenization of sward structure since management at moderate grazing intensity does not result in improvements in individual and per area animal production, nor in herbage production. Under moderate grazing intensity, increasing spatial heterogeneity is inevitable. Finally, we believe that to enhance animal performance in grasslands it is essential to use a grazing intensity that allows animals to express their selective behavior in a heterogeneous sward structure in time and space, which is in line with a better understanding of interactions existing in these complex and heterogeneous environments in order to redesign and bring to the fore new models of livestock production that enhance ecosystem services and adapt to climate change scenarios.

Declaration of interest

The authors declare no conflict of interest.

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Appendix

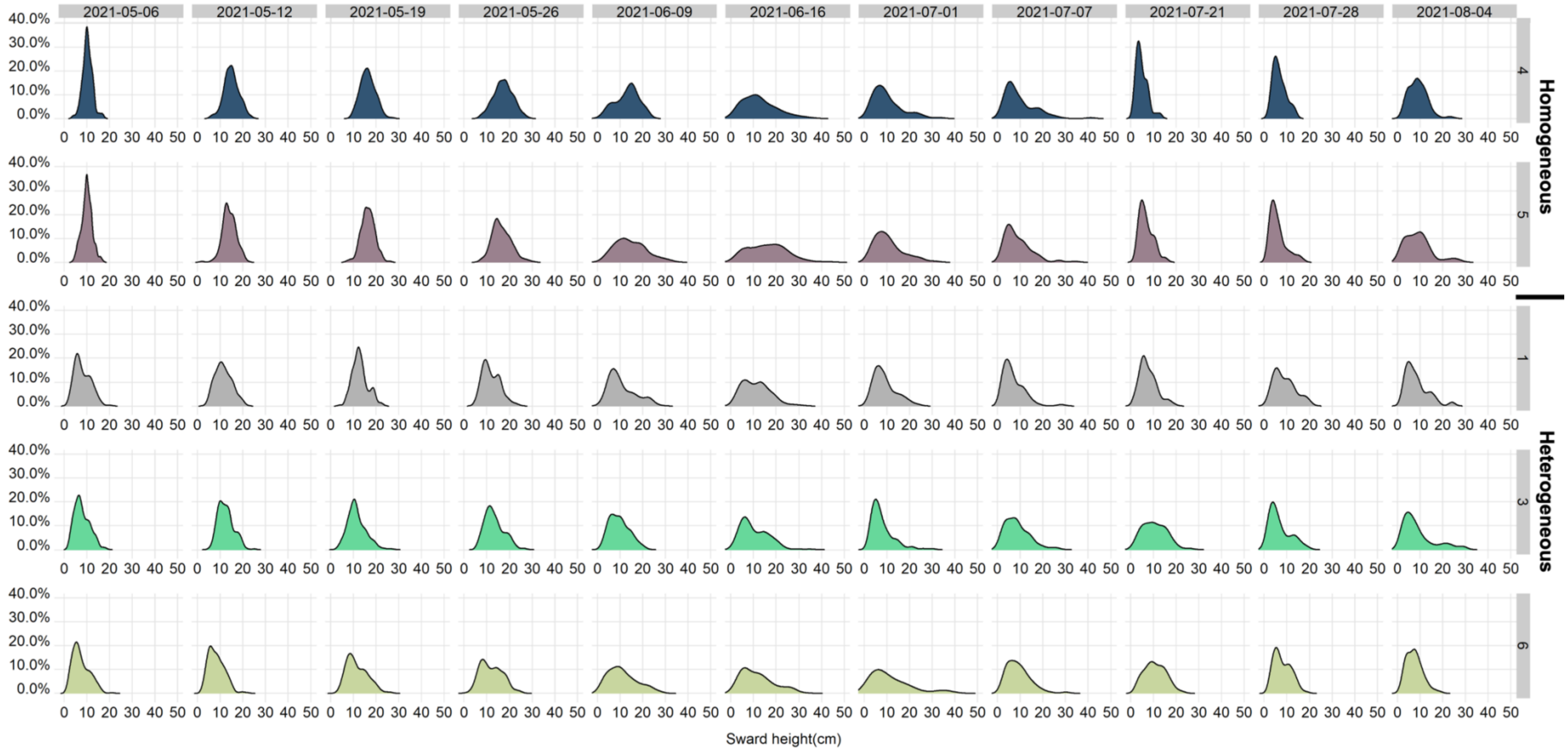

Figure 6 – Distribution of sward height in each paddock over stocking season of sheep grazing perennial ryegrass-based pastures during eleven samplings. Paddocks 4 and 5 (top) refer to homogeneous treatment, while paddocks 1, 3 and 6 (bottom) refer to heterogeneous treatment.

CHAPTER IV

4.1 FINAL CONSIDERATIONS AND PERSONAL REMARKS

The spatio-temporal heterogeneity of grassland vegetation increases rapidly with the grazing process, even in initially homogenized swards. Several studies have already shown that vegetation homogenization only occurs in overgrazing situations, where animal and herbage production are harmed, as well as the various ecosystem services provided by pastoral ecosystems are negatively affected, leading to system degradation. In our approach we explore how heterogeneity evolves from two initial conditions (homogeneous vs. heterogeneous) at moderate grazing intensity. For this we had to create heterogeneity through mechanical cuts in the vegetation.

How heterogeneity occurs at different grazing intensities is well documented in the scientific literature, however, the specific impacts of heterogeneity dissociated from grazing intensity are not yet known, given the complexity involved in isolating the grazing intensity factor. We often see studies in the literature that show: *"at moderate grazing intensities, animal and herbage production are higher as well as vegetation heterogeneity is greater"*, so the question remains: what is the effect of grazing intensity and what is the effect of vegetation heterogeneity? In this context, our focus was on trying to isolate grazing intensity to understand how heterogeneity occurs and how it impacts the pastoral ecosystem.

Our work is far from over, we need to better understand the role of heterogeneity at moderate grazing intensities (considered the optimal management range). We know that heterogeneity is an inherent property of pastoral ecosystems and is related to several ecosystem services and interactions with biodiversity. In this way, I briefly list some improvements and next steps for this work that could be developed and that are part of a larger project that I wrote together with Professor Bindelle and that we hope to materialize. This research project will contribute to disentangle the effect of grazing intensity and heterogeneity in sward structure with the scientific questions involved such as:

From the animal's perspective:

- What is the functional response of grazing herbivores towards heterogeneity in sward height?
- What is the right spatial scale (feeding station vs. paddock) to describe heterogeneity in sward height in this functional response?

- Do increasing levels of heterogeneity in sward height impact animal response similarly whatever the average height?

From the perspective of the grazed vegetation:

- Do pastures with similar average sward height but contrasting heterogeneity evolve towards similar levels of heterogeneity?
- Is primary productivity affected by heterogeneity in grazed swards?
- Do heterogeneous vegetation have greater stability towards weather variability?

To answer these questions, our scientific approach includes conducting new experiments and using a long-term historical data base, in perennial ryegrass-based pastures in Gembloux – Belgium and native grasslands of the Pampa Biome, in Rio Grande do Sul, South - Brazil.

In Belgium we will explore the impact of heterogeneity in sward height, in an experimental protocol similar to the one used in this thesis but advancing in the level of detail of the interactions between plants and herbivores. In native grasslands of the Pampa Biome the idea is: (1) to explore the interaction between heterogeneity in sward height and plant morphology; (2) to analyze the stability of pastoral systems with contrasting levels of heterogeneity.

These questions are open and can only be answered with fine-scale monitoring of both the vegetation and the foraging dynamics of the animals. In addition, using the historical data base, we will be able to assess the relationship between heterogeneity and system stability, as well as analyze the role of heterogeneity in the face of extreme weather events such as droughts, projecting the resilience of these environments in the face of climate change scenarios. Finally, I believe that only with an approach that considers the different interactions within the pastoral ecosystem is it possible to enhance the multifunctionality of grassland ecosystems by reconciling the provision of diverse ecosystem services.

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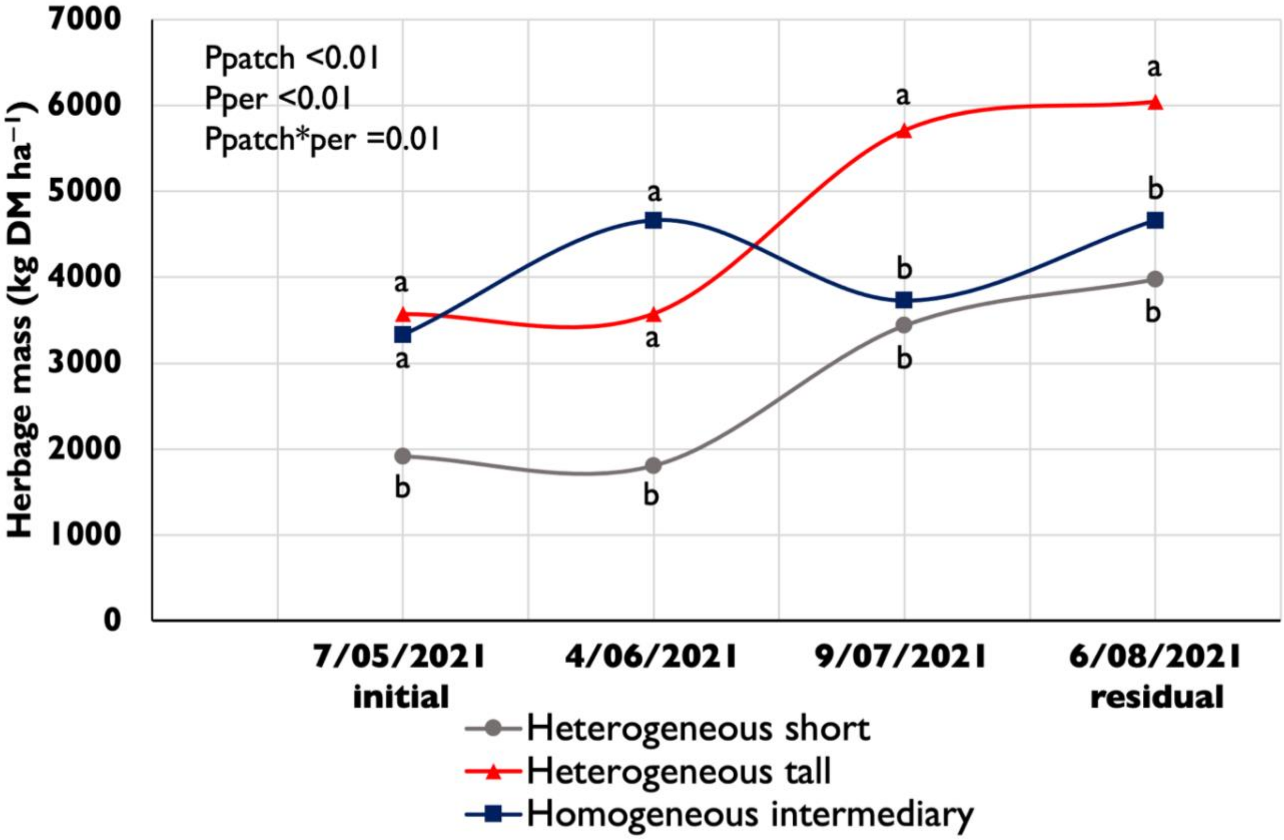
APPENDIX

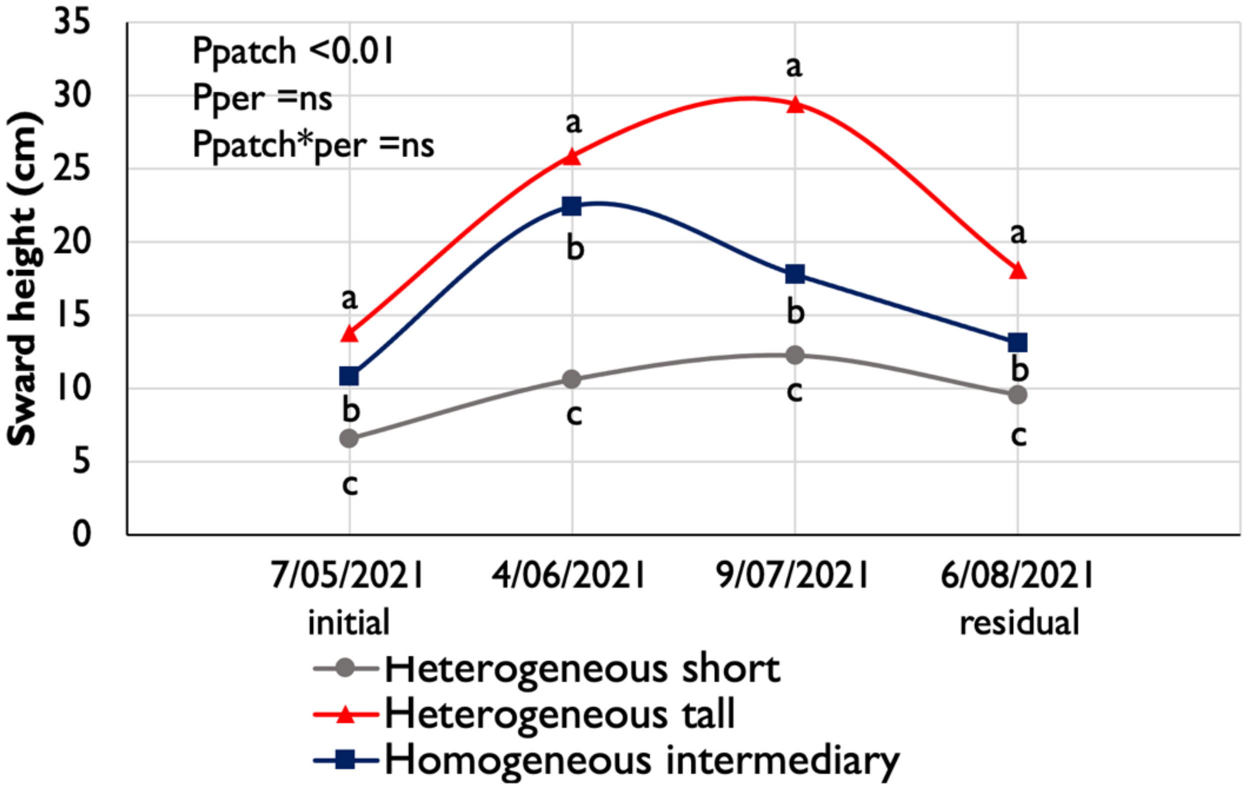
Appendix 1 – Aerial view of the experiment, Gembloux, Belgium (2021).

Appendix 2 – Aerial view of treatments applied to paddocks. The upper and lower paddocks correspond to the heterogeneous treatment, while the central paddock corresponds to the homogeneous treatment.

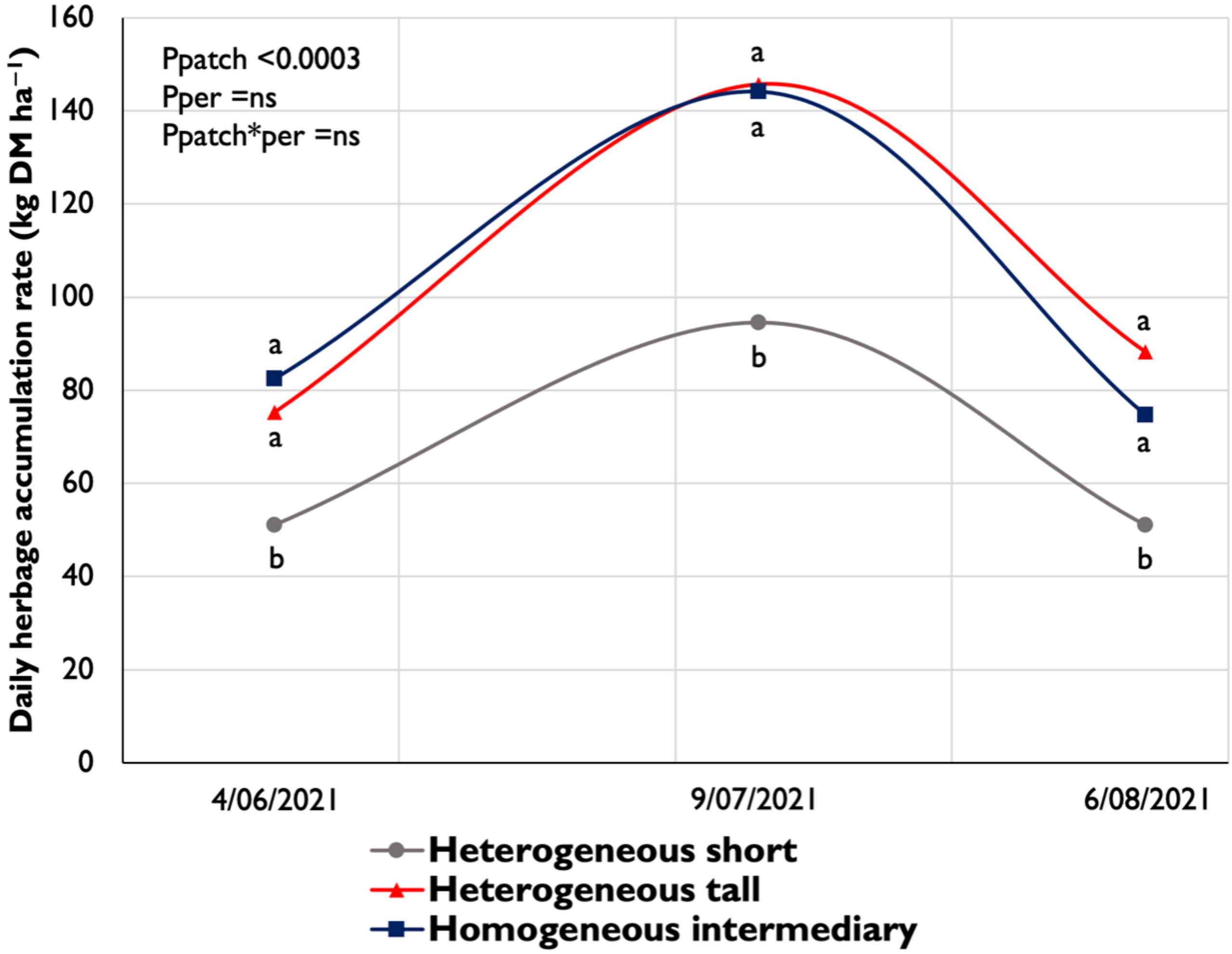
Appendix 3 – Average herbage mass (kg DM ha^{-1}) of each initial patch type throughout the stocking season.



Appendix 4 – Average of sward height (cm) of each initial patch type throughout the stocking season.

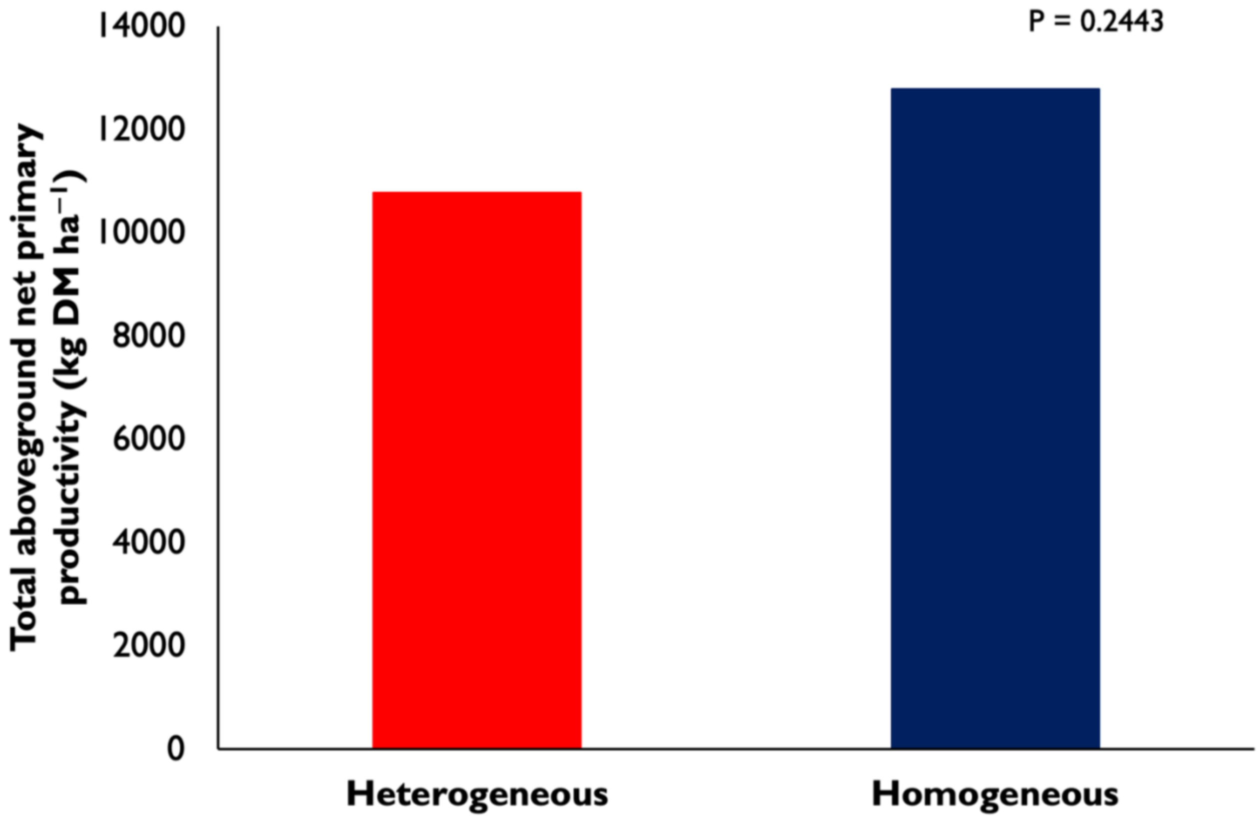


Appendix 5 – Daily herbage accumulation rate (kg DM ha^{-1}) of each initial patch type throughout the stocking season.

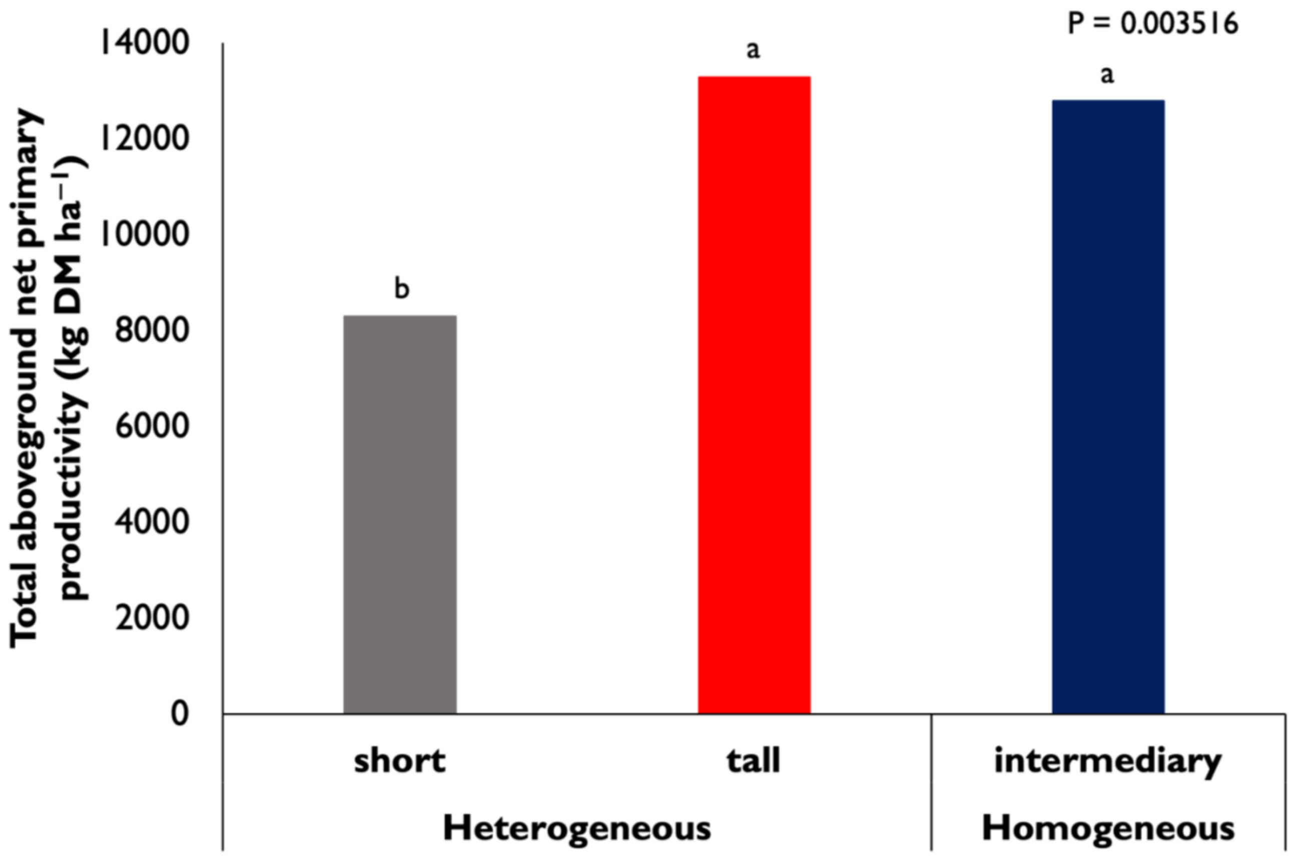


Appendix 6 – Global average of daily herbage accumulation rate (kg DM ha^{-1}) of each initial patch type.

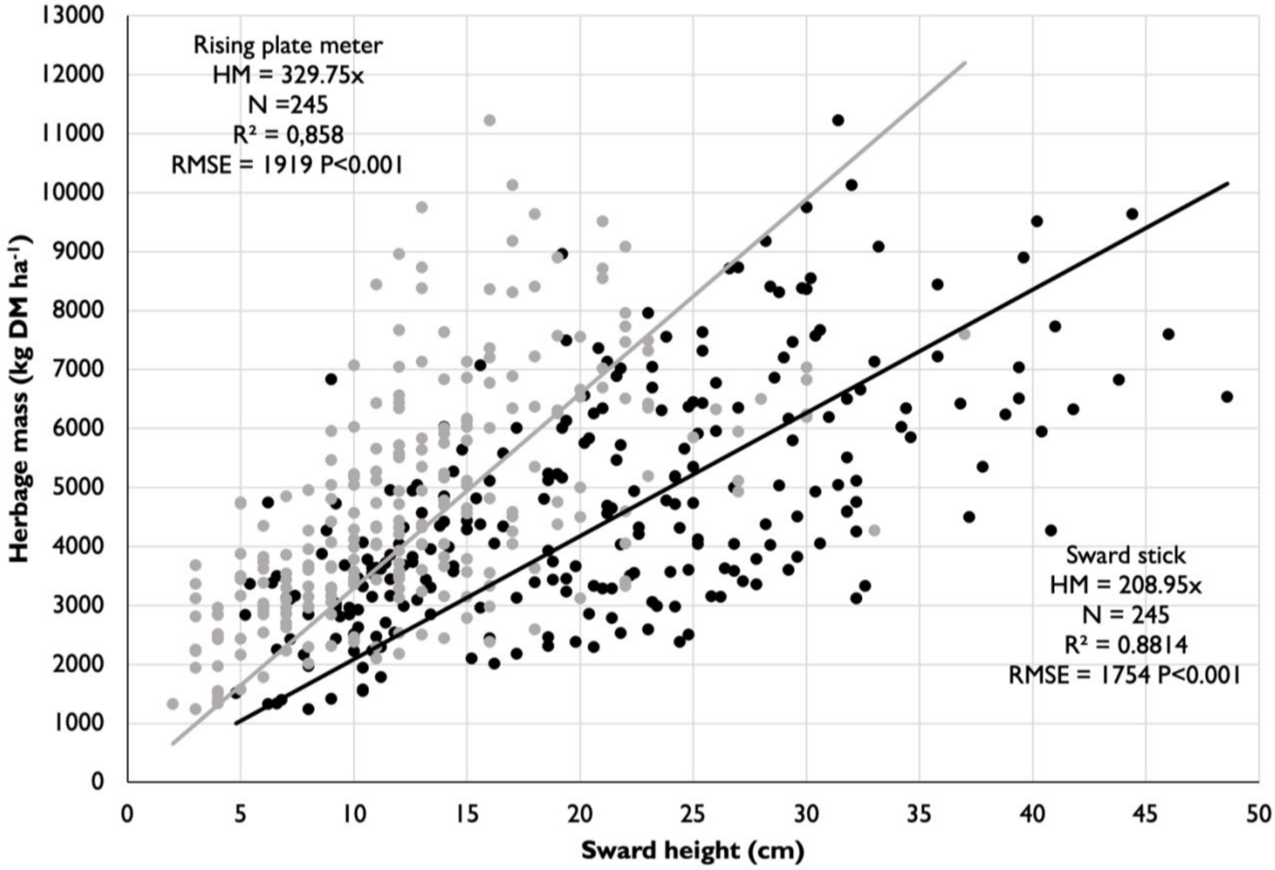
Appendix 7 – Total aboveground net primary productivity (kg DM ha^{-1}) of perennial ryegrass-based pastures under two initial levels of heterogeneity.



Appendix 8 – Total aboveground net primary productivity (kg DM ha^{-1}) of each initial patch type.



Appendix 9 – Relationships between compressed sward height obtained with the rising plate meter (RPM) x herbage mass, and between sward height (cm) x herbage mass for perennial ryegrass-based swards.



AUTHOR BIOGRAPHY

Gentil Félix Da Silva Neto was born on July 30, 1991 in Itaqui, West Border of Rio Grande do Sul, Brazil. Son of José João Sampaio da Silva and Sandra Maria Lopes de Lopes, e grew up between the city of Itaqui and Estância Querência, his grandfather's estância located in Três Bocas - Third District of Itaqui, currently managed by his father and where they breed horses, sheep, cattle and buffaloes. Since he was a child, he's been passionate for this environment, and it was precisely in those campos of the Pampa Biome, between whinnies of horses and mooing of cattle, that he learned from the campeiros about the management of the campos and the culture of the gaúcho people, which carries a rich country wisdom and values such as respect for nature and manliness. During the daily activities at Estância Querência, besides admiring the campos of the Pampa, he always remained curious and sought to understand what was happening between plants and animals in that heterogeneous environment. Even though he still didn't have the dimension of this, plant-animal relationships had already aroused his curiosity and admiration. Still during his childhood he had contact with the different kinds of literature from his grandfather's library, which has been maintained and enlarged by his father.

He finished high school in 2008. In 2010, he was approved to study Agronomy at the Federal University of Pampa (UNIPAMPA) - Campus Itaqui but due to compulsory military service he could not start the course that year. In 2011 he co-authored the book Querência: porque meu canto apampou-se authored by his father, the poet João Sampaio, where he recorded some poems related to the gaúcho's way of living and culture. That same year he began his degree in Agronomy after the end of compulsory military service.

In the second semester of the course he began working as a volunteer in research projects of the Group of Studies in Water and Soil (GEAS) under the guidance of Dr. Cleber Maus Alberto where later he became a fellow of the Academic Development Scholarship Program (PBDA) working with research related to agrometeorology, ecophysiology of crops and forage plants, and soil and water management.

In 2013, he started working as a fellow of the Tutorial Education Program (PET Agronomy of UNIPAMPA) in the areas of teaching, research and extension. In that same year, besides acting in GEAS and PET, he began to volunteer in research projects of the Group of Studies in Production and Nutrition of Ruminants (GENUR) under the guidance of Dr. Eduardo Bohrer de Azevedo.

In 2014, he obtained the 1st place in the area of Agrarian Sciences, oral modality, research category in VI SIEPE - International Salon of Teaching, Research and Extension, Federal University of Pampa - UNIPAMPA. In that year, he performed an extracurricular internship at the Grazing Ecology Research Group (GPEP) and was instigated by the research topics developed by this group, with which he shared the same philosophy. Through the internship, he was able to see with more clarity the dimension of the issues related to the 64 grazing process that had been present in his life since his childhood and decided that this was the line of research he wanted to follow.

In 2015, he completed his degree in Agronomy. At the end of that year, he was approved in the selection to the Master's degree in Agronomy at the Federal University of Santa Maria (UFSM) but decided not to attend because it wasn't related to his study interests - the interactions between plants and herbivores. At the end of 2016, he was approved in the selection process of three institutions for the Master’s degree in Animal Science: Federal University of Rio Grande do Sul (UFRGS), Federal University of Pampa (UNIPAMPA) and Federal University of Santa Maria (UFSM). He chose to study at the Federal University of Rio Grande do Sul (UFRGS) under the mentorship of Dr. Paulo César de Faccio Carvalho due to his interest in the scientific questions explored by the Grazing Ecology Research Group (GPEP).

In GPEP, he works on the plant-animal interface research line and developed his Master's dissertation studying the relationships between sward structure and the ingestive behavior of cattle, generating management goals based on the ingestive behavior of the animals and seeking to understand the dynamics of the grazing process by monitoring both vegetation and animals with a high degree of detailing using precision livestock tools. During this period, he was co-advised by Dr. Jérôme Bindelle from the Université de Liège, Belgium.

In 2018 he obtained an Erasmus + scholarship and spent the last five months of the Master's degree at the Université de Liège - Gembloux Agro-Bio Tech. From an agreement between UFRGS and ULiège he defended his Master's dissertation in Belgium at the University of Liège - Gembloux Agro-Bio Tech. In 2019 he was approved for the PhD in Animal Science at UFRGS under the mentorship of Dr. Paulo César de Faccio Carvalho, interested in further researching questions of plant-animal interface and understanding the dynamics of the grazing process. During this period he obtained an Erasmus+ scholarship to work again with Dr. Jérôme Bindelle at the University of Liège - Gembloux Agro-Bio Tech (Precision Livestock and Nutrition Unit). Due to the coronavirus pandemic, this only came to fruition in 2021, during which time he remained for a year conducting grazing experiments and working with Dr. Jérôme Bindelle. He was submitted to the PhD thesis committee on March 31, 2023.