Vegetation-ungulate interactions in heterogeneous Mediterranean environments

Juan Miguel Giralt Rueda

PhD Thesis 2022

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Vegetation-ungulate interactions in heterogeneous Mediterranean environments

Memoria presentada por el graduado en Ingeniería Forestal

Juan Miguel Giralt Rueda

para optar al título de Doctor por la

Universidad Pablo de Olavide de Sevilla.

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CERTIFICA

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral: Vegetation-ungulate interactions in heterogeneous Mediterranean environments, son aptos para ser presentados por el graduado en Ingeniería Forestal por la Universidad de Huelva, Juan Miguel Giralt Rueda ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad Pablo de Olavide. Y para que así conste, y en cumplimiento de las disposiciones legales vigentes, extendemos el presente certificado a 30 de mayo de 2022.

Director/Tutor

Luis Enrique Santamaría Galdón

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Index

Structure of the doctoral thesis

The present doctoral thesis consists of the following sections: a summary of the thesis, presented in both languages, English and Spanish; a general introduction to the main question of this study and to its theoretical framework; the general objectives of the thesis; three chapters, one published and the other two pending to be published in international journals; a final discussion of all studied topics throughout this thesis; and the general conclusions of this study.

Summary

Mediterranean and semiarid rangelands are subjected to important levels of climatic variability which result in strong fluctuations in primary production. Wild and domestic ungulates have to deal with such fluctuations and their grazing impact on foraging resources may amplify them, increasing the uncertainty over the availability of such key resources. During dry seasons, the combination of a limited primary production and a sustained grazing pressure may reduce plant biomass and deplete seed banks, with cascading effects to other trophic levels and long-term impacts on wildlife and ecosystems. These challenging dynamics will be exacerbated by climate change, which is already increasing the frequency and severity of droughts - multiplying the unpredictability of primary and secondary production. It is therefore essential to deepen our knowledge on the ungulate-vegetation interactions in Mediterranean and semiarid environments, in order to adapt traditional management practices to such rapidly changing scenarios. Traditional management usually promote the homogenization of rangelands, aiming at increasing control over vegetation and livestock. However, advances in rangeland science during the last decades highlight the pivotal role of functional heterogeneity in maintaining the stability of such systems.

The main objective of this thesis is to increase our understanding of the ungulate-vegetation interactions in environments with high variability in rainfall and primary production, and to quantify the role of functional heterogeneity as key driver of such relationships. To this end, we combined a 15-year series of remote sensing data on plant production (NDVI), vegetation distribution and water availability with meteorological data, ungulate abundance and livestock movement data in an iconic protected area (the Doñana National Park, SW Spain); and complemented them with a one-year series of newly-acquired data on ungulate movement, plant production (NDVI), vegetation distribution and water availability. We selected this study area because it holds high levels of habitat heterogeneity, hosts a diverse ungulate community, and the effects of seasonal climatic variability are strong.

We first investigated the impact of intra- and inter-annual variation in rainfall and herbivore pressure on the primary production of the main vegetation types of the study area. The results of these analysis were used to evaluate the potential impact of different policy strategies under expected climate change scenarios (Chapter 1). Plant production responded strongly to spatial and temporal variation in the rainfall regime (accumulated rainfall and its temporal distribution) and grazing pressure, and these responses varied greatly among vegetation types. Variation among vegetation types increased the resilience of the ecosystem to the negative impact of high livestock densities on primary production. However, buffering effects derived from habitat heterogeneity might be insufficient under the conditions predicted by climate change models – since, in the presence of moderate to high stocking rates, the expected reduction in rainfall levels will lead to severe reductions in primary production, possibly hindering plant regeneration and resulting in long-term ecosystem degradation.

We then explored how spatiotemporal variability in plant primary production and livestock density influence the population dynamics of the two wild ungulate species (Chapter 2). The phenological and functional complementarities among different vegetation types increased intra- and inter-annual forage availability for ungulates. In addition, differences in the responses of the two wild ungulate species to fluctuations in primary production of different vegetation types increased further the such complementarity effects. Moreover, while low to moderate livestock densities had positive effects on wild ungulates, high densities had negative impacts on wild them, limiting further the resilience of the plan-ungulate system to climatic variability and/or climate change.

Finally, we characterized the resource selection of two different livestock species (cattle and horse) and quantified its spatiotemporal variation. For this purpose, we explored the effect of plan production, vegetation type and water availability (distance to water sources) on livestock space use (Chapter 3). Livestock tracked the complex spatiotemporal gradients in primary production resulting from habitat heterogeneity in order to meet their dietary needs. Water availability modulated these responses in three different ways: by controlling the phenological responses of vegetation, constraining the land surface available for foraging during high flood, and constraining forage availability through piosphere effects during the dry season. Cattle and horse showed contrasting patterns of seasonal selection on the different vegetation types, with certain vegetation types representing ‘key areas’ of intensively selected, shared resources – thus prone to competition and overgrazing; and other types resulting in opposite selection patterns that fostered spatial space segregation and thus promoted coexistence. These patterns provide valuable information about potential improvements in management practices, based on an increased incorporation of the functional heterogeneity of both herbivores and vegetation.

This thesis sheds light on the complex ungulate-vegetation interactions in environments with high climatic variability, providing insights that may help to develop effective management practices that help to maintain the sustainability of rangelands in

Mediterranean and semiarid areas of high biodiversity value, in the face of climate change.

Resumen

Los sistemas ganaderos extensivos en ambientes mediterráneos y semiáridos están sujetos a importantes niveles de variabilidad climática que se traducen en fuertes fluctuaciones en la producción primaria. Los ungulados salvajes y domésticos tienen que lidiar con tales fluctuaciones y su impacto de pastoreo en los recursos de alimentación puede amplificarlas, aumentando la incertidumbre sobre la disponibilidad de tales recursos clave. Durante las estaciones secas, la combinación de una producción primaria limitada y una presión de pastoreo sostenida puede reducir la biomasa vegetal y agotar los bancos de semillas, con efectos en cascada a otros niveles tróficos e impactos a largo plazo en la vida silvestre y los ecosistemas. Estas dinámicas se verán exacerbadas por el cambio climático, que ya está aumentando la frecuencia y la gravedad de las sequías, multiplicando la imprevisibilidad de la producción primaria y secundaria. Por lo tanto, es esencial profundizar nuestro conocimiento sobre las interacciones ungulados-vegetación en ambientes mediterráneos y semiáridos, para adaptar las prácticas tradicionales de manejo a escenarios que cambian rápidamente. La gestión tradicional suele promover la homogeneización de los pastizales, con el objetivo de aumentar el control sobre la vegetación y el ganado. Sin embargo, los avances científicos en las últimas décadas destacan el papel fundamental de la heterogeneidad funcional en el mantenimiento de la estabilidad de tales sistemas.

El principal objetivo de esta tesis es aumentar nuestra comprensión de las interacciones ungulados-vegetación en ambientes con alta variabilidad en precipitaciones y producción primaria, y cuantificar el papel de la heterogeneidad funcional como factor clave de tales relaciones. Con este fin, combinamos una serie de 15 años de datos de teledetección sobre producción vegetal (NDVI), distribución de vegetación y disponibilidad de agua, con datos meteorológicos y abundancia de ungulados silvestres (ciervo y gamo) y domésticos (vaca y caballo) en un área protegida icónica (el Parque Nacional de Doñana, suroeste de España); y los complementamos con una serie de un año de datos recién adquiridos sobre movimiento de ganado, producción (NDVI) y distribución de vegetación y disponibilidad de agua. Seleccionamos esta área de estudio porque tiene altos niveles de heterogeneidad de hábitat, alberga una comunidad diversa de ungulados y los efectos de la variabilidad climática estacional son fuertes.

Primero investigamos el impacto de la variación intra e interanual en las precipitaciones y la presión de los herbívoros en la producción primaria de los principales tipos de vegetación del área de estudio. Los resultados de estos análisis se utilizaron para evaluar el impacto potencial de diferentes estrategias de gestión bajo escenarios de cambio climático (Capítulo 1). La producción de la vegetación respondió fuertemente a la variación espacial y temporal en el régimen de lluvias (lluvia acumulada y su distribución temporal) y la presión del pastoreo, siendo las respuestas de los distintos tipos de vegetación claramente diferenciadas. Esta variación entre los tipos de vegetación aumentó la resiliencia del ecosistema al impacto negativo de las altas densidades de ganado en la producción primaria. Sin embargo, los efectos amortiguadores derivados de la heterogeneidad del hábitat podrían ser insuficientes en las condiciones previstas por los modelos de cambio climático, ya que, en presencia de moderadas a altas cargas ganaderas en combinación con el descenso esperado en los niveles de precipitación conducirá a reducciones severas en la producción primaria, lo que posiblemente limite la regeneración de la vegetación y resulte en la degradación del ecosistema a largo plazo.

Luego exploramos cómo la variabilidad espaciotemporal en la producción primaria de la vegetación y la densidad del ganado influyen en la dinámica de población de las dos especies de ungulados silvestres (Capítulo 2). Las complementariedades fenológicas y funcionales entre los diferentes tipos de vegetación aumentaron la disponibilidad intra e interanual de recursos para los ungulados. Además, las diferencias en las respuestas de las dos especies de ungulados silvestres a las fluctuaciones en la producción primaria de los diferentes tipos de vegetación amplificaron aún más estos efectos de complementariedad. Sin embargo, mientras que las densidades de ganado bajas o moderadas tuvieron efectos positivos en los ungulados silvestres, las densidades altas produjeron impactos negativos en ellos, lo que limitó resiliencia del sistema de vegetación-ungulados a la variabilidad climática y/o el cambio climático.

Finalmente, caracterizamos la selección de recursos de las dos especies ganaderas diferentes (vaca y caballo) y cuantificamos su variación espaciotemporal. Para este propósito, exploramos el efecto de la producción primaria, el tipo de vegetación y la disponibilidad de agua (distancia a las fuentes de agua) sobre el uso del espacio del ganado (Capítulo 3). El ganado rastreó los complejos gradientes espaciotemporales en la producción primaria resultantes de la heterogeneidad del hábitat para satisfacer sus necesidades tróficas. La disponibilidad de agua moduló estas respuestas de tres maneras diferentes: controlando las respuestas fenológicas de la vegetación, restringiendo la superficie terrestre disponible para la alimentación durante las inundaciones y restringiendo la disponibilidad de forraje a través de los efectos de piosfera durante la estación seca. El ganado vacuno y equino mostraron patrones

diferenciados de selección estacional de la vegetación, donde ciertos tipos de vegetación representan recursos compartidos intensamente seleccionados por ambas especies, por lo tanto, propensos a la competencia y al pastoreo excesivo; y otros tipos que resultaron en patrones de selección opuestos (complementarios) que fomentaron la segregación espacial y, por lo tanto, promovieron la coexistencia. Estos patrones brindan información valiosa sobre posibles mejoras en las prácticas de manejo basadas en la heterogeneidad funcional tanto de los herbívoros como de la vegetación.

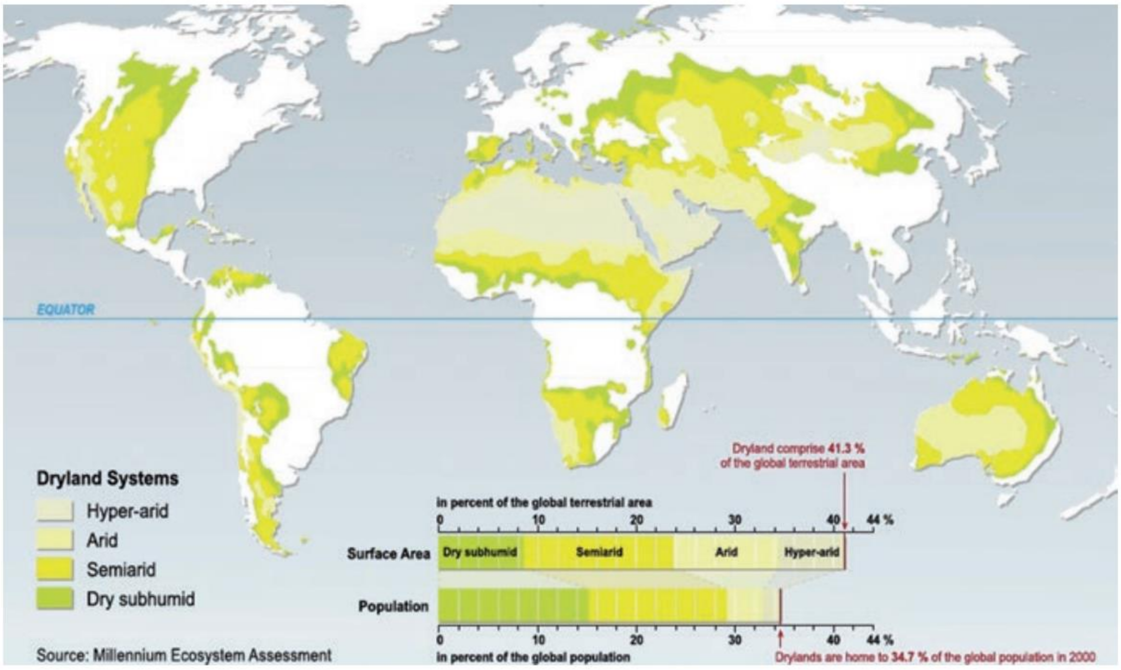
Esta tesis arroja luz sobre las complejas interacciones ungulados-vegetación en ambientes con alta variabilidad climática, proporcionando un conocimiento que puede ayudar a desarrollar prácticas de manejo efectivas que ayuden a mantener la sostenibilidad de los sistemas ganaderos extensivos en áreas mediterráneas y semiáridas con gran valor para la conservación de la biodiversidad, frente a cambio climático.

Introduction

Rangelands in Mediterranean and semiarid environments

Rangelands represent the most extensive land cover type on Earth (Lund 2007) and most of them occur in drylands. Rangeland were considered within the drylands category of the Millennium Ecosystem Assessment, which includes cultivated land, scrublands, shrublands, grasslands, savannas, semideserts and true deserts (MA 2005). Due to their reduced rainfall levels and high evaporation, drylands are characterized by low soil water content that pose considerable limits to their productivity. Along the global gradient of increasing primary productivity, drylands can be classified as hyper-arid, arid, semi-arid and dry sub-humid (Dietz & Veldhuizen, 2004).

Drylands cover 41% of the Earth’s land (6 billion of hectares). Of these, 69% of them support 2 billion humans and 50% of global livestock (MA 2005). Due to their high levels of heterogeneity, rangelands provide numerous ecosystem services. However, their limited and highly variable productivity make them extremely vulnerable to ecological disturbances and human perturbations (Briske 2017). Around 70% of drylands are suffering accelerated soil degradation and 10-20% of them are already degraded (MA 2005). Most human population inhabiting drylands are characterized by limited levels of well-being and tend to score low in several development indicators, and 90% of them reside in developing countries (MA 2005). Among the various human-induced stressors affecting rangelands, inadequate management of livestock and wild ungulate populations is acknowledged to be one of the most threatening factors (Lazaro et al., 2001; Velamazan et al., 2020). This factor is further compounded by the increasing impact of climate change, and it is therefore expected to cause major socio-ecological impacts in rangelands worldwide in the coming years (Lohmann et al., 2012).



Source: Millennium Ecosystem Assessment

Figure 1. Distribution of global drylands as classified by the UNCCD (Millennium Ecosystem Assessment (2005))

Ungulates are keystone pieces of ecosystems

Large ungulates are keystone species in many ecosystems. They are also highly valued natural resources that provide a variety of social, cultural, and economic services (Gordon et al. 2004). However, in recent decades, the unfettered increase in their populations has raised important conservation and management concerns in many areas around the world (Côté et al. 2004, Putman et al. 2011). The reasons behind this situation are complex and entail a number of factors, including land abandonment (Garbarino et al. 2011), the increased number of ranches focused on trophy hunting (Côté et al. 2004; Bueno et al. 2009; Forrester and Wittmer 2013), the lack of predators (Porter 1992) and the unforeseen impact of conservation and management policies (Warren 2011). The increase in wild ungulate populations coincides with an increase in livestock stocking rates in extensive rangelands, aimed at maximizing profits and maintaining their competitiveness in the global market (Plieninger & Wilbrand, 2001), with significant impacts worldwide (Voeten, 1999; Rawat, 2007; Bhattacharya et al., 2012). The overpopulation of wild ungulates and the intensification of livestock both generate multiple impacts on vegetation, which include changes in plant composition and diversity (Mathisen et al., 2010), reductions in tree and shrub recruitment and survival (White 2012; Perea, Giraldello & San Miguel., 2014), reductions in plant productivity (Pastor et al., 1993), changes in nutrient cycles (e.g., by nitrification processes; Kuijper et al. 2009; Carpio et al., 2015), seed bank depletion (Côté et al. 2004), and soil degradation (e.g. by erosion and/or trampling; Cumming & Cumming, 2003). These effects often cascade to other trophic levels (Rooney & Waller, 2003; Mathisen, 2014), resulting in widespread impacts that threaten the stability of ecosystems and may push them into undesirable degradation states (Rietkerk & van de Koppel 1997; Augustine et al., 1998).

In areas where wild and domestic ungulates coexist, which is a common scenario in many Mediterranean and semi-arid environments, the combined grazing pressure might be compounded by the synergic effects of climatic variability and its subsequent changes in plant production and phenology, leading to increased impacts on vegetation (Beschta et al., 2013) that often feed-back on the wild ungulate populations (Suryawanshi et al., 2010). Indeed, the centuries-old interplay between natural and cultural processes typical of Mediterranean and semi-arid environments has led to high levels of habitat heterogeneity (Perevolotsky and Seligman, 1998; Naveh and Carmel, 2004) that add more complexity to plant-herbivore interactions, limiting our ability to predict the rapid changes triggered by global and climate change. Understanding how ungulate populations interact with such environmental and anthropogenic stressors in heterogeneous landscapes is a challenging task, yet it may hold the key to successfully adapt to such changes (Jeltsch, Weber & Grimm, 2000; Vetter, 2005; Gillson & Hoffman, 2007; Lovari et al., 2007; Alves et al., 2014).

Resource ecology

Resource ecology addresses central questions in ecology related to trophic interactions between consumers and resources, such as plant-herbivore interactions (herbivory). It also provides the basis for understanding the structure and dynamics of multispecies assemblages (Langevelde & Prins, 2008; Schweiger et al., 2015). Foraging is the key process in resource ecology and it is considered to determine the survival, growth and reproduction of the animal. Foraging resources are often distributed heterogeneously in space and time, and herbivores must adapt (both evolutionary and behaviorally) to such spatiotemporal dynamics to maximize their fitness (Owen-Smith, 2008). Ungulates, for example, are known to forage selectively influenced by vegetation structure (Hanley 1997) while being, at the same time, major drivers of landscape heterogeneity (McNaughton 1979; De Knegt et al., 2008; De Jager & Pastor, 2009). Since ungulate activity generally affect all trophic levels of ecosystems, understanding their spatial distribution and foraging ecology is a major element of modern environmental management and conservation.

According to Langevelde & Prins (2008), to properly address this topic ungulates are especially suited for several reasons:

- They have major impacts on the availability and quality of resources. Hence, they affect the spatial and temporal heterogeneity of resources.
- They use a quite accurate spatial memory in their search for resources, which allows them to anticipate to the spatiotemporal heterogeneity of such resources.
- They spend the majority of the day searching and foraging.
- They are highly mobile, and they forage selectively on areas of high-quality food while actively avoiding the depletion or food and other (e.g., water) resources.
- They are considered as keystone pieces of ecosystems and play important roles from the point of view of conservation.

Therefore, is fundamental to deepen our knowledge on the spatial ecology of large herbivores, their foraging behavior and population dynamics. For this purpose, a key area of advance must focus in ascertaining the effect of the spatiotemporal changes in resource availability across heterogeneous environments.

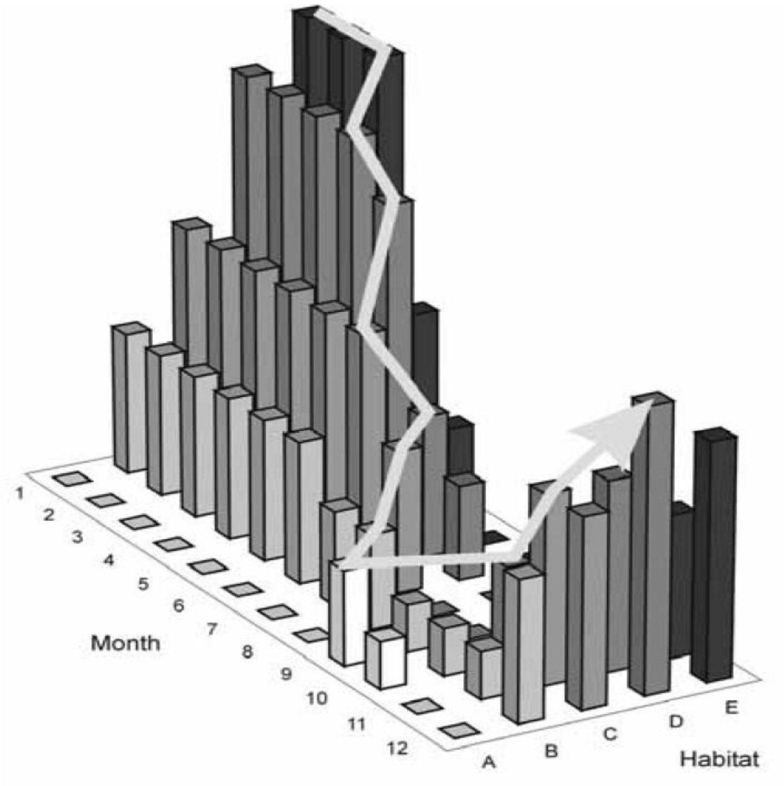


Figure 2. The broken fitness landscape, with regular troughs and irregular pitfalls that organisms must traverse over time in order to survive and reproduce (from Owen-Smith, 2008)

The development of rangeland management

The societal development of the relationship between humans and the natural world, from humans as ‘natural resource users’ to humans as ‘natural resource stewards’ (Chapin et al. 2009) has led to a sequential progress of natural resource management models (Briske 2017). The long preindustrial period of low-impact anthropic use was followed an exploitation period of rangelands based on the idea of unlimited open-access resources during the late nineteenth and early twentieth centuries (Briske, 2017). The degradation of natural resources caused by this period of intensified exploitation raised the concern about the need of an improved rangeland management discipline, rooted on a steady-state management framework that focused on maximizing the sustainable yield of the resulting goods. This model implied the control of ecosystem variation by suppressing natural disturbances such as fire; the introduction of homogenizing measures such as predator control and rangeland fencing; and the management of forage resources to maximize the production of target resources (Hobbs et al., 2008). This model is still the basis of rangeland management in many areas worldwide, despite the shortcomings identified as rangeland science progressed (Koontz & Bodine, 2008; Bestelmeyer & Briske, 2012).

The acknowledge that effective management must incorporate a more integral consideration of the ecosystems that a sustain the rangeland exploitations, accepting at face value their inherent variability and taking into account the increased societal demand for ecosystem services resulted in the development of a new management paradigm, often referred to as “ecosystem management”. This model, originated in the 1970s, considered new concepts such as adaptive management and ecosystem services (Nie 2013) and was increasingly used during the following decades, initially in the USA and Canada (Briske 2017) and later across the world (Holmes, 2002; Fernandez-Gimenez & Batbuyan 2004). The recognition of the inevitability of change and uncertainty in both ecosystem processes and social demands resulted in the formulation of the resilience theory. Resilience-based management focuses on guiding such continuous, ongoing change in order to provide diverse and sustainable ecosystem services for society (Chapin et al., 2009, 2010). Advances in rangeland science during the last decades, such as the recognition of non-linear vegetation dynamics, the introduction of the resilience theory, the use of state and transition models, and the development of non-equilibrium theory highlighted the need for an update of the traditional management of rangelands, and lay the ground for a thorough adaptation of rangeland science and management to the new socio-political context and the increasingly present challenge of climate change (Briske 2017).

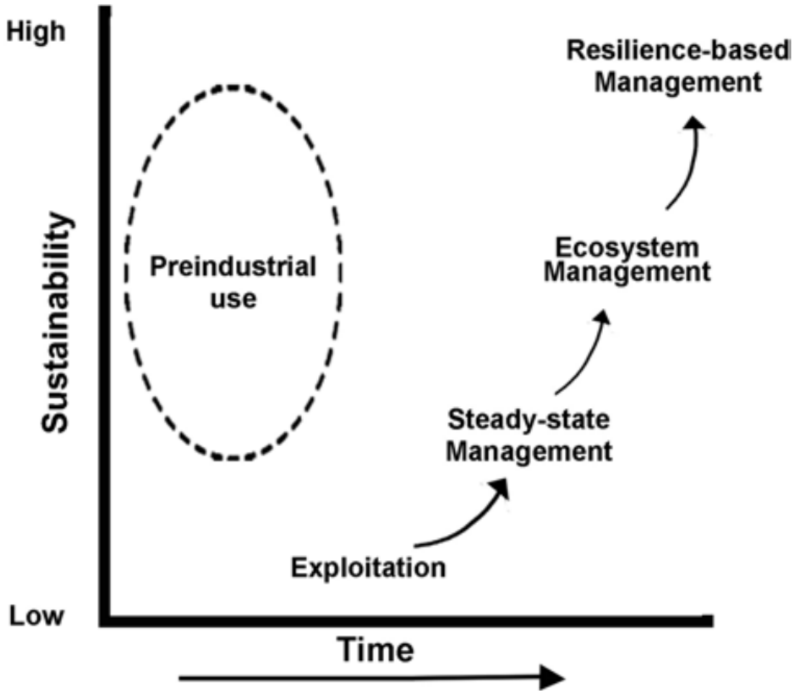


Figure 3. Progression of natural resource management models following human settlement (from Briske 2017)

The role of functional heterogeneity

The last three decades have witnessed the development of an important debate between two different paradigms in rangeland science, focused on the management of ungulate populations in arid and semiarid environments. On the one hand, the equilibrium model advocated for the relevance of density-dependence in controlling both ungulate populations and their feedback on vegetation. Hence, it postulated the concentration of management efforts on stocking rates, carrying capacity and range vegetation characteristics. On the other hand, the non-equilibrium paradigm argued that arid and semiarid rangeland systems are governed fundamentally by stochastic abiotic factors (mainly, the variability in rainfall), which leads to insignificant ungulate impacts on vegetation. This model suggests that the extreme and unpredictable variation in rainfall levels and, therefore, primary production prevents the establishment of equilibrium conditions between ungulate populations and foraging resources. New insights from rangeland ecology, however, suggest that both models are simultaneously correct and wrong – i.e., that they represent the archetypical extremes of a range of equilibrium and non-equilibrium situations and processes occurring at different spatiotemporal scales. Hence, current efforts focus on achieving a synthesis that recognize the importance of both resource heterogeneity and the variability in abiotic factors as drivers of plant-ungulate dynamics in arid and semi-arid rangelands.

An important element of such synthesis concerns the role of landscape and ecosystem heterogeneity, which may enhance the stability of ecosystem processes at multiple spatial and temporal scales (Fuhlendorf et al., 2017). It is ironic, however, that the homogenization of ecosystems using various management practices (such as fencing, rotations, pasture management, or the distribution of watering points), aimed at reducing promoting the predictability in natural systems, had the counterintuitive effect of reducing it in the long term (Hobbs et al., 2008). Indeed, natural systems are inherently subjected to complex biotic and abiotic processes that confer a high level of spatiotemporal variability linked to differences in soils, weather, climate, topography and disturbances, which lead to additional layers of variability as they influence the distribution and composition of plant and animal communities (Fuhlendorf et al., 2017). As consequence, management strategies focused on increasing homogeneity in natural systems often results in considerable investments and costs, in both energy and money. While heterogeneity is increasingly considered as a relevant concept in landscape and rangeland management (Illius & O’Connor, 2000; Cromsigt, Prins & Olff, 2009), it is still far from being adequately incorporated to management plans (Briske 2017). Reasons behind this situation might be related to the difficulty of understanding and measuring heterogeneity, as well as the socio-technical persistence of the old paradigm that considers homogeneity as a synonym of efficiency (Fuhlendorf et al., 2017).

Heterogeneity comes for two different sources, the inherent heterogeneity in vegetation composition, productivity, nutrient content and diversity, which is a direct consequence of the heterogeneity in soil types, topography, weather, etc- (McNaughton and Banyikwa 1995; Fynn et al. 2014); and the heterogeneity resulting from disturbances such as fire, pest outbreaks or extreme climatic events. Both types interact and vary in time and space, composing a non-stable, far-from-equilibrium mosaic of various ecosystem states. If some disturbances are maintained in intensity and during long periods of time on the same areas (e.g., as consequence of excessive grazing pressures due to fencing or herbivore aggregations around scarce water points), structural and compositional changes in plant communities may drastically reduce heterogeneity, causing regime shifts that may result in ecosystem collapse and may take decades to recover (Knapp et al. 1999; Archibald et al. 2005).

Heterogeneous environments provide multiple resources for herbivores. The spatial and temporal variation in the distribution and the availability of foraging resources is often the factor that enables herbivores to meet different their dietary needs along the year. In less productive sites, short pastures commonly offer higher nutrient concentrations and better digestibility (O'Reagain and Owen-Smith 1996; Coetsee et al. 2011); however, taller grasses dominating wetter and more productive areas, albeit less palatable, may also provide large amounts of biomass when other resources are lacking. Such functional heterogeneity derived from the variability in environmental conditions (e.g. geology, topography, water availability) therefore represents a spatial continuum of productivity and quality gradients that help herbivores to cover the high quality demands during critical reproductive and growth periods, while also offering foraging resources during less favorable seasons (such as summer), reducing body mass losses and the ensuing mortality (Maddock 1979; Hopcraft et al. 2010; Fynn et al. 2014). Those benefits are not merely related to dietary needs, but also to access to water and refuge (Allred et al. 2011). Therefore, enhanced functional heterogeneity reduce density dependence effects (Hobbs et al. 2008), limiting mortality (Walker et al. 1987; Scoones 1993) and increasing body size in wild and domestic herbivores (Albon and Langvatn 1992; Mysterud et al. 2001).

Since heterogeneity is always associated with spatiotemporal variation in patterns and processes (and its own interactions), the scale used to measure it represents a consideration of major importance. According to the functional heterogeneity concept (Li and Reynolds 1995), the spatiotemporal scale of observation must been set carefully according to the available knowledge on the processes or species in question (Kolasa and Rollo 1991, Twidwell et al. 2009). In this study, we considered both the intra-annual variation in plant productivity, as we introduced phenological peaks of the different vegetation types present in the study area (the Doñana National Park); and its inter-annual variation, by analyzing the differences in productivity and phenology among different years. Attention was also paid to the different spatial scales, by evaluating role of habitat heterogeneity and the spatial variability corresponding to the different management units.

In the past, environmental studies were constrained by the difficulty of measuring and monitoring such spatiotemporal patterns and processes at the required scales – which might range from meters to tens or hundreds of kilometers. These difficulties have been eased considerably by the recent advances in remote sensing. Currently, the use of satellite-derived vegetation indices as a proxy of vegetation productivity allows researchers to approach long-term and high-resolution studies on vegetation dynamics and thus, forage availability (Kerr and Ostrovski 2003; Pettorelli et al. 2005; Duffy and Pettorelii 2012; Naidoo et al. 2012; Borowik et al., 2013). Indeed, a number of recent studies have demonstrated eloquently the potential of its application to the study of animal ecology, animal population dynamics and distribution (Borowik et al., 2013). These advances, in combination with Global Positioning Systems (GPS) and Geographical Information Systems (GIS) have increased our capacity of studying animal behavior and habitat selection processes (Rodgers et al., 1996; Mourão & Medri, 2002).

Objectives of the thesis

This thesis investigates the interactions between vegetation and ungulates in Mediterranean ecosystems with high levels of climatic variability. To achieve this goal, it combines meteorological data, remotely sensed information on vegetation production, distribution and phenology, population counts of wild and domestic ungulates, and movement data of large domestic ungulates at the Doñana National Park (SW Spain) to explore three central themes:

(i) The impact of climatic variability and grazing pressure on the functional and phenological responses of vegetation, and its modulation by landscape heterogeneity

(ii) The effects of functional and phenological complementarities resulting from habitat heterogeneity on the population dynamic of wild ungulates, and its interplay with competition and/or facilitation by large domestic ungulates

(iii) The responses of vegetation and wild ungulate populations to the conditions predicted by climate change models under different management scenarios

(iv) The spatiotemporal changes in the resource selection by domestic ungulate species, and the impact of primary production and water availability on such patterns

The thesis includes a general introduction, three experimental chapters, and a general discussion and conclusions. The specific objectives of each chapter are:

Chapter1:

(i) Quantify the separated and combined impact of intra- and inter-annual variation in rainfall and grazing pressure exerted by wild and domestic ungulates on the production and phenology of the different vegetation types. (ii) Evaluate the resilience of vegetation to such stressors under the conditions predicted by climate change models and under different management scenarios. (iii) Derive adaptive management strategies for a sustainable combination of ranching and wildlife conservation.

Chapter 2:

(i) Investigate whether intra- and inter-annual differences in production and phenology among different vegetation types result in complementarity effects that increase resource availability for two wild ungulates (red and fallow deer). (ii) Quantify the responses of wild ungulate populations to these functional and phenological complementarities. (iii) Explore the effects of different livestock stocking rates on the population dynamics of both species of wild ungulates. (iv) Predict the responses of wild ungulate populations to different scenarios of primary production and livestock stocking.

Chapter 3:

(i) Characterize the resource selection by two different, free-ranging livestock species (cattle and horse). (ii) Explore the drivers of the observed patterns of livestock space use, with particular attention to plant production and water availability, and the impact of habitat heterogeneity thereupon. (iii) Estimate the effect of the current division in management units on livestock resource selection at the different seasons, and evaluate whether access to key resources (forage and water) could be improved.

Chapter 1

Complementary differences in primary production and phenology among vegetation types increase ecosystem resilience to climate change and grazing pressure in an iconic Mediterranean ecosystem

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Abstract

Plant primary production is a key factor in ecosystem dynamics. In environments with high climatic variability such as the Mediterranean region, plant primary production shows strong seasonal and inter-annual fluctuations, which both drive and interplay with herbivore grazing. Knowledge on the responses of different vegetation types to the variability in both rainfall and grazing pressure by wild and domestic ungulates, is a necessary starting point for the sustainable management of these ecosystems. In this work we combine a 15-years series of remote sensing data on plant production (NDVI) with meteorological (daily precipitation data) and ungulate abundance (annual counts of four species of wild and domestic ungulates: red deer, fallow deer, cattle and horse) in an iconic protected area (the Doñana National Park, SW Spain) to (i) estimate the impact of intra- and inter-annual variation in rainfall and herbivore pressure on primary production, for each of four main vegetation types, (ii) evaluate the potential impact of different policy (i.e., herbivore management) strategies under expected climate change scenarios. Our results show that the production of different vegetation types differed strongly in their responses to phenology (a surrogate of the effect of climatology on vegetation development), water availability (rainfall accumulated until the phenological peak), and grazing pressure. While the density of domestic ungulates shows a linear, negative effect on the primary production of three out of the four vegetation types, differences in primary production and phenology among vegetation types increase ecosystem resilience to both climatological variability and grazing pressure. Such resilience may, however, be reduced under the conditions predicted by climate change models, if the moderate reduction in rainfall levels predicted combines with moderate to high densities of domestic ungulates, resulting in important reductions in primary production that may compromise plant regeneration leading to irreversible degradation.

New management strategies taking advantage of habitat heterogeneity and phenological alternation, more flexible stocking rates and the redistribution of management units should be considered in order to mitigate these effects. The use of available remote sensing data and techniques in combination with statistical models represents a valuable tool for developing, monitoring and refining such strategies.

Keywords

Plant primary production; phenology; habitat heterogeneity; grazing; ungulates; livestock; climate change; remote sensing

1. Introduction

Plant primary production is a key factor in ecosystem dynamics. Knowledge on the spatiotemporal changes in response to environmental variables, such as precipitation regime or herbivore pressure, is essential for a better management of agropastoral systems and conservation areas (Cho et al., 2007; von Keyserlingk et al., 2021). In bioclimatic regions with high climatic variability, such as the Mediterranean and semiarid regions, forecasting plant primary production is, however, particularly challenging. In such regions, seasonal drought periods represent a fundamental limitation for plant primary production owing to the phenological shutdown of vegetation (Carmona et al., 2013) and vegetation recovery after such droughts is further limited by environmental and/or anthropogenic stressors (Mayor et al., 2013; Zhou et al., 2010).

In most of these regions, local flora has coexisted historically with large herbivores - both wild and, more recently, domestic. This prolonged interaction resulted in adaptive responses to grazing – which range from antagonistic traits, such as physical/chemical defenses or a high regrowth potential (Robles et al., 2009; Agrawal & Fishbein, 2006), to mutualistic ones, such as seed dispersal by large herbivores (Manzano, Malo & Peco, 2005). While moderate levels of grazing may enhance plant productivity, facilitate smaller herbivores and help maintaining more diverse communities (Albert et al., 2015), over-grazing may also lead to reduced productivity, degraded vegetation cover and impoverished ecosystems (Hobbs 1996; Mysterud 2006) - particularly in combination with drought (Ruppert et al., 2015). The combination of trophic and non-trophic effects (e.g., mechanical damage by trampling) in overgrazed areas may reduce strongly plant productivity (Kawamura et al., 2005) and usually generates other impacts, such as changes in plant species composition (favoring less palatable species), limited tree regeneration, erosion and soil degradation (Zhou et al., 2010; Zamora et al., 2001). Overgrazing impact on ecosystem resilience is particularly concerning since increased drought frequency and intensity caused by climate warming might be coinciding with increased stocking rates in extensive exploitations, incentivized by public regulations such as the per head payments of the European Common Agricultural Policy (Plieninger & Wilbrand, 2001).

Free-ranging livestock breeding (ranching hereafter) is a widely used farming system in many areas around the world, often within natural areas of high conservation value – including protected areas. In ranching exploitations, livestock coexist with wild ungulate populations, which often show high population densities due to concomitant factors, such as hunting limitations and predator removal (Côté et al., 2004; Carpio et al., 2021). In these cases, understanding the combined effect of plant-herbivore interactions with both groups of grazers (wild and domestic) is essential if we are to understand their impacts on ecosystem structure, functioning and resilience (Hegland et al., 2005; Manier & Hobbs, 2007). Even considering that low densities of livestock could in-crease plant production and benefit wild populations, the combined effect of wild and domestic ungulates may derive in major impacts on vegetation composition and structure (Beschta et al., 2013) and, if such pressures are maintained for long periods, shifts in plant communities could be irreversible or may require decades to recover (Archibald et al., 2005).

In Mediterranean and semiarid regions, the combined effects of the pronounced seasonality and the large inter-annual fluctuations in rainfall levels on plant productivity exacerbate the frequency and impact of overgrazing problems, and represent a key constraint for optimal ranch management (Lazaro et al., 2001; López-Sánchez et al., 2016; Velamazan et al., 2020). These impacts are compounded by the strong legacy effects of overgrazing on plant productivity (e.g., Naveh 1982). Overgrazing during dry years depletes asexual organs and the seed bank, decreasing plant reproduction and productivity in the following growth season(s) even under conditions of abundant optimal rainfall and reduced grazing (Odadi et al., 2011). Similarly, large recruitment rates and survival during wet years increase the grazing pressure during the dry years that may follow, decreasing the resilience of the plant populations (and thus the ecosystem) (Fuhlendorf et al., 2017). In both cases, the resulting decreases in plant productivity faces ranchers with a wicked alternative: they may reduce the stocking rates and/or provide supplementary food to livestock, reducing profits and risking 'overspill' overgrazing effects around areas of supplementary feeding (Milner et al., 2014; Vetter 2005); or they may maintain the stocking rates, assuming increasing levels of ecosystem and land degradation (Archibald et al., 2005; von Keyserlingk et al., 2020).

Avoiding the aforementioned risk of land and ecosystem degradation is often complex, as significant reductions in livestock, enough to prevent overgrazing in dry years, would result in a reduction in the economic incomes of the local farmers – with the associated risk of abandonment, which may be as detrimental as excessive intensification (Caballero et al., 2011). Hence, increasing effort is being devoted to the development of flexible management strategies that can be adapted to expected intra- and inter-annual fluctuations in plant primary production in response to rainfall (Graham et al., 2010; Weisberg et al., 2002). Ranches in the Mediterranean and semiarid regions, particularly those in protected areas, often host a variety of vegetation types that respond differently to seasonal and inter-annual changes in rainfall. The distribution of the different vegetation types is often associated with spatial heterogeneity in soil fertility and water content, and may reduce the risk of drought-induced overgrazing if adequately tailored to spatiotemporal grazing patterns (Vetter 2005) – e.g., in the presence of wetland vegetation, which may maintain high levels of productivity in dry years and ‘escape’ grazing in rainy years due to prolonged flooding (Gómez-Baggethun et al., 2013). The development and optimization of these management tools will become even more valuable when we consider the expected scenarios of climate change, which predict an amplification of the hydrological cycle, characterized by more extreme precipitation events and more extensive periods between events (e.g., Knapp et al., 2008; IPCC 2014). The broad spatial extension and dynamism of the processes that must be taken into account require, however, innovative approaches – which can be currently undertaken owing to the increasing availability of remote sensing data and tools. New advances in remote sensing and the increasing amount of freely accessible images and in-formation have improved our ability to study environmental patterns and processes at a broad array of spatial and temporal scales (Turner 2014), allowing us to use long-term, spatially-continuous data series essential for understanding ecosystem dynamics (e.g., Zhang et al., 2003) and integrating biodiversity monitoring data (Turner et al., 2003; Vihevaraara et al., 2017). The combination of remote sensing data, field observations and statistical modelling is already enabling scientists to address re-search questions that were unapproachable in the recent past, such as the detection of disruptions in ecosystem processes, the characterization of changes in plant phenology or the impact of climate change on vegetation (Lausch et al., 2018).

In this study we use a combination of remote sensing and in-situ information to characterize the main factors driving the spatiotemporal variation in plant primary production, using the four main vegetation types of an iconic, Mediterranean protected area (Doñana National Park) hosting traditional ranching as suitable case example. For this purpose, we analyzed its response to the two most important drivers: climatology (accumulated rain-fall and vegetation phenology) and the grazing pressure exerted by wild (red and fallow deer) and domestic (cattle and horse) ungulates. In doing so, we seek to: (1) Quantify the separate and combined impact that the population densities of wild ungulates and the stocking rates of domestic herbivores have on the production of the different vegetation types. (2) Evaluate the resilience of the vegetation to the combination of environmental stress (strong inter-annual fluctuations in rainfall and phenology) and grazing pressure, and the expected impact of climate change thereupon. (3) Derive adaptive strategies al-lowing for a sustainable combination of ranching and wildlife conservation in this type of areas.

2. Materials and Methods

2.1. Study area

The research is carried out in the Doñana National Park (DNP onwards), a protected area located on the Atlantic coast of the southwest of the Iberian Peninsula. The region is characterized by a Mediterranean climate classified as dry sub-humid with marked seasonality. Doñana is characterized by high landscape heterogeneity. The inland areas have coastal formations and sand dunes almost free of vegetation, forests dominated by conifers (Pinus pinea and Juniperus phoenicea) and cork oaks (Querqus suber), large shrub formations and grasslands and wet shrub formations in the vicinity of lagoon systems, in the topographical depressions and mainly at its border with the marsh, where it forms an ecotone in which soil moisture remains for practically all year round. In the marshland two main types of habitats can be differentiated, the saltmarsh, where the floods are not very prolonged, which is characterized by the presence of halophytes normally associated with certain levels of salinity in the soil (usually forming mosaics with grasslands) and the bulrush marsh, which can remain flooded for long periods every year and is characterized by extensive formations of plants of the family Cyperaceae.

In the study area coexist populations of wild ungulates, red deer (Cervus elaphus) and fallow deer (Dama dama) and domestic (cattle and horse) that are traditionally bred in the different management areas of the national park: Matasgordas (MAT), Los Sotos-Algaida (SOA), Biological Reserve of Doñana (RBD), El Puntal (PUN) and Las Marismillas (MAR). The density of the different species in the DNP (average density of the study period) is 6.26 red deer/km2, 6.01 cattle/km2 (excluding Matasgordas, where there is no presence of cattle), 3.89 fallow deer/km2 and 2.49 horses/km2 (excluding Matasgordas, where there is no presence of horses). Accounting for all herbivorous ungulates, the total density on study area is 18.73 individuals/km2 (10.15 and 8.58

individuals/km2 for cervids and domestic livestock respectively). The management areas are delimited by livestock-proof fences, limiting the movement of domestic ungulates within their own ranging area. Based on the average weight of the different ungulate species at the NPD (information provided by the National Park Office) the total biomass at the study area corresponding to such densities (average densities of the study period) are: 0.85 t/km2 for red deer, 0.20 t/km2 for fallow deer, 2.91 t/km2 for cattle and 1.15 t/km2 for horse.

2.2. Delimitation of vegetation types

Our analysis focused on the four vegetation types accessible to wild and domestic ungulates (i.e., excluding forested stands such as stone pines, cork oaks and coastal junipers) within the five National Park estates mentioned above. These include: saltmarsh, bulrush marsh, shrubland and grassland. The main vegetation types and their main characteristics are shown in Table 1.

Table 1. Vegetation types and description of the characteristics and main species.

Vegetation type	**Description**
Saltmarsh	Halophilous scrub (‘almajar’) on floodplain/marine brackish mudflats, dominated by glaucous glasswort (*Arthrocnemun macrostachium*) and shrubby sea-blite (*Suaeda vera*), interspersed with halophilous grass meadows.
Bulrush marsh	Seasonal meadows of tall sedges (Fam. *Cyperaceae*) on floodplain/brackish marshes. Dominant species are saltmarsh bulrush (*Bolboschoenus maritimus*), Blysmus bulrush (*Schoenoplectus litoralis*) and somerset rush (*Juncus subulatus*), which may be dominant or co-dominant.
Shrubland	Shrub formations on stabilized dunes, sometimes interspersed with sandy grasslands. These formations include a mosaic of two main types, respectively occupating more xeric and mesic sites: dry scrubland (‘monte blanco),

	dominated by *Halimium halimifolium, Cistus salvifolius, C. libanotis*, *Rosmarinus officinalis,* and *Lavandula stoechas*; and wet shrubland (‘monte negro’), dominated by heather (*Erica scoparia*, *E. umbellata*, *E. ciliaris*, *Calluna vulgaris*)*, Rubus ulmifolius, Ulex minor* and *Ulex australis*.
Grassland	Grassland formations with great variability in their extent as well as in their specific composition. Wet pasture formations usually spatially associated with lagoons and in the ecotone that form the marsh and inland areas, usually called "la vera". Dominated by the association of *Galium palustre* with *Juncus maritimus.*

To define the different vegetation types, we selected the corresponding classes of vegetation maps (Figure 1) elaborated in 2014 by the long-term monitoring program (PSPN; Andreu et al., 2014, pp. 37-59) of Doñana’s Singular Scientific-Technical Facility (ICTS-RBD), and grouped into the four types described above (Figure 1). Subsequently, the polygons occupied by each of these types within each ungulate management unit (see be-low) were used to calculate their respective area and the variables derived from satellite-obtained NDVI Values (see below). These tasks were performed with the ArcGIS 10.1 software (ESRI 2011).

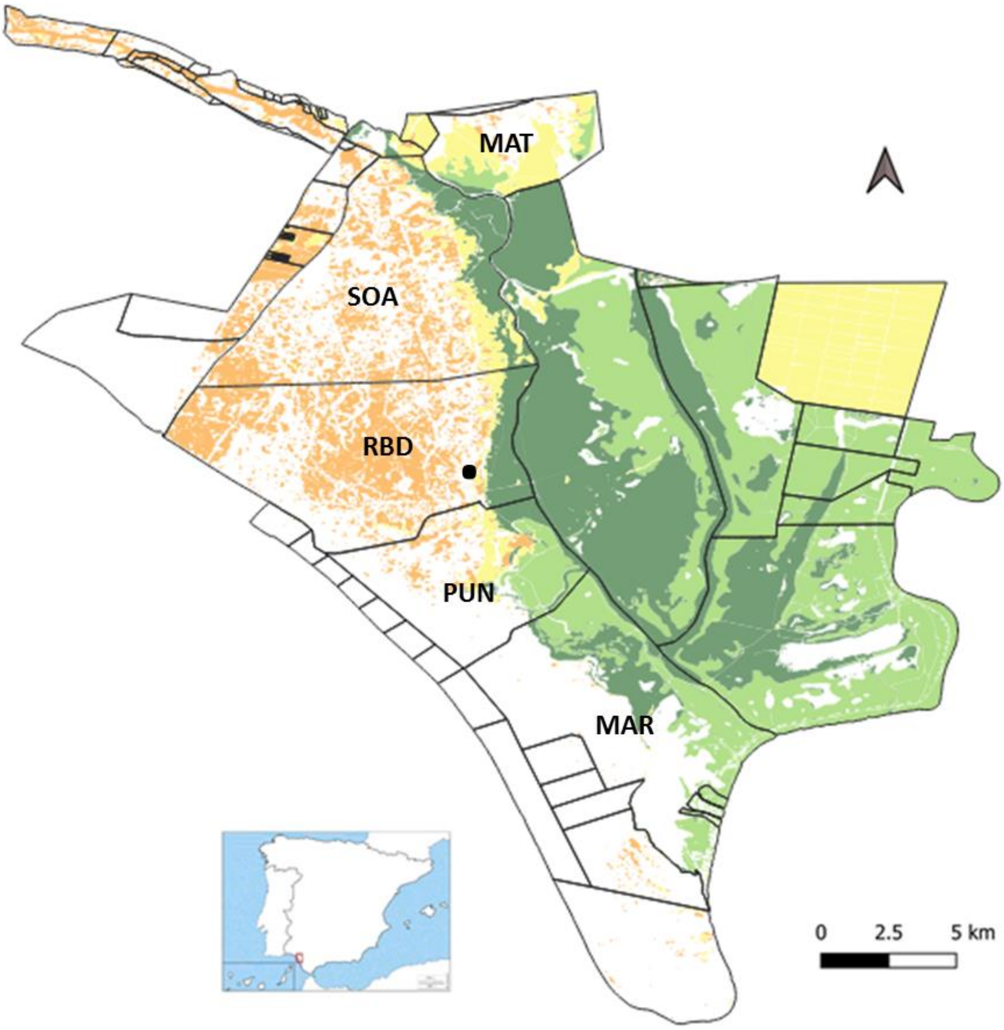

Figure 1. Distribution of the four vegetation types used in this study within the Doñana National Park. Black lines represent different management units (largely coinciding with property boundaries). Scrubland is showed in orange, grassland in yellow, saltmarsh in light green and bulrush marshland in dark green. The acronyms refer to the names of the management units included in the study. The black dot indicates the location of the meteorological station. White areas indicate areas of bare soil, forest stands or mixed vegetation (i.e., pixels where the dominant vegetation occupied less than 70% of the area) that were not used for the calculations of NDVI per vegetation type and management unit (as explained above).

2.3. Estimation of primary production

Satellite information obtained from the Institute of Surveying, Remote Sensing and Land Information (IVFL) of the University of Natural Resources and Applied Life Sciences (BOKU), Vienna, was used to estimate the production of different vegetation types during the study period. This institution offers remote sensing products – smooth and continuous Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) – from MODIS satellite images with different temporal resolution (From 16 to 7 days) from year 2000 to present. These products are the result of processing standard products from Terra and Aqua satellites, namely MODIS Level-3 16-day composite Vegetation Indices (VI) available at 250-m of spatial resolution. The combination of 16-day composites from these two satellites –Terra (MOD13 series) and Aqua (MYD13 series) – allows to obtain imagery at a temporal resolution of 7 days. Detailed information on the processes for creating such time series can be consulted in (Vuolo et al., 2012) and at BOKU's website (https://boku.ac.at/rali/geomatics).

For our study we use the Normalized Difference Vegetation Index (NDVI), a commonly used vegetation index that serves as a proxy of vegetation density and plant health (Gaitán et al., 2013). NDVI was demonstrated to reflect appropriately the vegetation response to rainfall variability (Helman et al., 2014) and extreme events (e.g., droughts) across different biomass around the world (Vicente-Serrano et al., 2013). We selected NDVI as a proxy of primary production because (1) we felt that it achieved the best balance between spatial resolution (pixel size) and robustness; and (2) we have already tested (i.e., calibrated and validated) a statistical model relating biomass production to NDVI for one of the main vegetation types (Lumbierres et al., 2013). Alternative products, such as MODIS NPP and GPP, had a lower spatial resolution (1 to 0.5 Km) than MODIS NDVI (0.25 km); and Landsat images, which provide a better spatial resolution (15-30 m) than MODIS, could not be processed by the TIMESAT software (which requires regular time intervals) to fit the phenological curves, and showed large gaps due to different reasons such as missing data (lines and columns), line shifts, radiometric incoherence, and the presence of clouds over the study area.

We took a number of precautions to address the limitations of using NDVI, as compared to NPP or GPP (which may work better in areas dominated by bare ground or with high tree cover) or Landsat (which provide better spatial resolution). First, the four vegetation types selected are structurally homogeneous and moderately productive; and explicitly excluded forest stands with dense canopies and areas of bare soil. Second, we excluded from out dataset all pixels with mixed vegetation cover (i.e., those where the dominant vegetation occupied less than 70% of the pixel's area).

We use the long-term series of NDVI values with the highest temporal resolution available (every 7 days) for the study period (January 2000 – august 2014, corresponding to the period for which ungulate population data were available). For each vegetation type and within each management unit, we extracted the average NDVI value at each observation date (i.e., every 7 days) of the study period, using the Zonal Statistics function available in ArcGIS 10.1 (ESRI 2011). The Zonal Statistics tool calculates a defined statistic (e.g., the mean) for each zone defined by a dataset (e.g., land cover classes contained in a land cover map) based on the values of another dataset (a NDVI value raster dataset) resulting in a single output value for every zone in the input dataset (land cover classes). The resulting data series provided the phenological curves at each observation unit (N=75 per vegetation type, arising from a combination of 15 years x 5 management units). We then used the TIMESAT software (Jonsson & Eklundh, 2004) to estimate the date and value of each annual NDVI peak, which we interpret as surrogates of the vegetation's phenology and production on each given growth period (referring, hereafter, to hydro-meteorological years, running from 1 September to 31 august). To filter the noise in the data we used the Savitzky-Golay filter fitting method and the default values for the rest of settings in TIMESAT, namely: no spike method, one season per year, no adaptation to the upper envelope of the curve, and nor-mal adaptation strength.

2.4. Rainfall

Rainfall data were also obtained from the database provided by Doñana's Singular Scientific-Technical Facility (ICTS-RBD). They provide long-term series of meteorological data collected at a meteorological station located inside the NPD (Figure 1). We used daily rainfall data to calculate, on a daily basis, the cumulative rainfall along each hydrological year. From this series, we obtained the cumulative rainfall value at the day of the phenological peak of each vegetation type, separately for each management unit and each year. This value thus represents the cumulative rainfall at the moment at which given vegetation type reached its maximum annual production, at each management unit.

2.5. Ungulate abundance

Data on the abundance of wild ungulates (red deer and fallow deer) at each management area were obtained from annual censuses conducted by National Park service at the beginning of each annual reproductive (rutting) period, which differs approx. one month between both species (September for red deer and October for fallow deer). During rutting, individuals of both species concentrate on open areas, which greatly facilitates counted.

Population data on domestic ungulates were obtained from the National Park service, through censuses undertaken during the (bi)annual animal-health controls (June-September). These data only refer to adults older than 12 months, since young of the year were not reported consistently throughout the study period. National Park regulations set a cap at the total number of domestic ungulates allowed at each management area, which is adjusted on yearly basis (see above). Hence, their (maximum) abundance is relatively independent of yearly fluctuations in environmental drives, and yearly values only show slight fluctuations relative to that year's cap.

In the national park livestock is raised in a low-management ranching system where animals are only herded once or twice a year for the extraction of part of the individuals (most often young-of-the-year) and for health control. Wild ungulates are, in principle, unmanaged. Both groups are allowed to move and feed freely across the whole area of each management unit. Fences separating management units cannot be crossed by livestock (unless temporarily damaged), but they are relatively permeable for wild ungulates – which are able to cross them on seasonal or even daily basis.

Based on all this information, we built a database reflecting the abundances (number of adult individuals) of each of the four ungulate species at each management unit (Figure 2). To correct for management unit size, we used these abundances to calculated population densities (number of individuals / ha). It is important to note that these values solely rep-resent mean values per management unit: within each unit, the spatial distribution of the different species will vary over space, across vegetation types and over time. We limited our data to 2000-14 because this is the time period for which consistent and reliable in-formation on wild ungulate and livestock abundances was available.

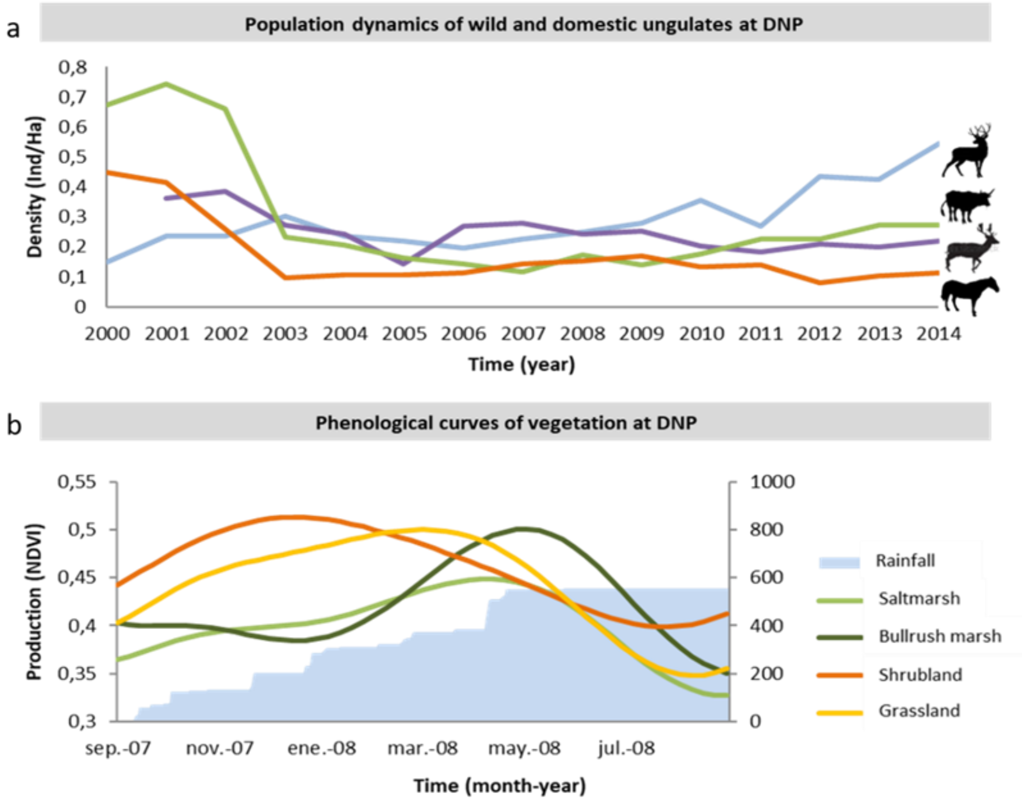

Figure 2: a) Evolution of the population density (individuals/ha) of the four species of ungulates present at Doñana National Park area during the study period. b) Phenological curves of the four vegetation types during 2007-08, a hydro-meteorological year whose levels of accumulated rainfall (blue bars) coincide with the average of the study period (2000-2014). Phenological curves were fitted to MODIS NDVI values aggregated per vegetation type (all management units merged), using the TIMESAT software.

2.6. Data analysis

To analyze plant production (peak NDVI per unit area), we used hierarchical generalized additive models (HGAM's) fitted separately to each vegetation type, using the "GAM" function available in the R mgcv package (Wood 2011). The models included production (peak NDVI) as response (dependent) variable; phenology (time of phenological peak, as number of days counted from September 1st), rainfall accumulated during the growth season (i.e., until the phenological peak), the interaction between phenology and rainfall, and the density (number of adults per unit area) of each of the four ungulate species, as independent, continuous covariates; and management areas as random factors. To account for temporal autocorrelation, we also included "year" as a continuous co-variate. All models used a gaussian error distribution and an identity link function. These models were subjected to automatic selection of covariates using the model argument "Select" (Wood et al., 2016).

The predictor variable ‘phenology’ (i.e., the day counted from the beginning of the hydrological year at which the phenological peak was observed in the NDVI curve) was taken to represent a surrogate of the evolution (i.e., the specific timing) of rainfall and temperature on that specific hydrological year. This variable was complemented with a second predictor variable, ‘accumulated rainfall’ (i.e., the amount of rainfall accumulated until the moment at which the phenological peak took place), taken to represent a surrogate of the water resources available during that year’s specific growth period. Hence, the combination of these two variables represents the time and water resources available during the period that preceded the peak NDVI value used as surrogate of plant production (i.e., as response variable).

The different timing of the (wild and domestic) ungulate censuses vs plant production estimates introduced a temporal uncertainty concerning which ungulate density values best reflect their impact on plant production. This uncertainty arises because plant production values reflect a biomass-accumulation process taking place from September to peak bio-mass, in late winter – spring (February-June); while ungulate density values during such period fall between measured values the previous year (before the onset of the growth period) and those at the end of the growth period (June-September). Because all births and most deaths take place primarily place during such period (during the summer, most animals are confined for animal-health control and artificially fed), we expected end-of-the-season density values to be more representative of ungulate impacts on vegetation than previous-season values. To objectively test for this assumption, however, we fit-ted separate models with either one of the other values, and selected the best-performing models based on the AIC score.

Residuals’ autocorrelation, if not adequately dealt with, may result in biases in parameter estimates and tests of significance. Spatial autocorrelation was dealt with by introducing the random factor “management unit”, which accounted for the spatial dependence of observations in both the dependent and independent variables. Temporal resolution was dealt with by (1) including the co-variate “year” in the model, and (2) computing estimates of the autocorrelation function of each model, using the Acf functions of R’s forecast package (Hyndman and Khandakar, 2007; Hyndman et al., 2020). These plots indicated that autocorrelation was adequately dealt with by the models - i.e., there was very low (and, in virtually all cases, non-significant) levels of residuals’ autocorrelation.

Finally, we used the function vis.gam in the mgcv package to produce contour plots of model predictions on primary production, for different combinations of ungulate abundance (only those with significant effects) and climatology (separate plots for rainfall and phenology). Based on these plots, we performed a visual comparison of historical data and climate change scenarios. These scenarios, represented by vertical lines in the prediction plots, showed the average values of accumulated rainfall or phenology (estimated separately for the average value of the other variable, respectively) as estimated from the historical series (1961-2000) and the MIROC RCP4.5 (2040-70) regional-scale climatic change scenarios provided by Andalucia's Environmental Information Network REDIAM at: https://kerdoc.cica.es/cc?lr=lang_es# (REDIAM, 2014). We chose the simulations based on the MIROC model for our study system, which tends to provide relatively drier estimates, because it is the one that best reproduces the current climate in this area (Errasti et al., 2014) and best represents the interannual fluctuations in rainfall (Nieto & Rodriguez-Puebla, 2006). Within it, we selected the RCP4.5 (or 'mitigation') scenario because it is based on a more realistic assumption of fossil fuel consumption (decreasing use of fossil fuels), thus providing a more conservative output than RCP8.5, which assumes a sustained fossil fuel use during the modelled time period (Van Vuuren et al., 2011).

3. Results

Models including end-of-the-season values of ungulate density performed systematically better than those including previous-season values (Table 2). Hence, we present only here the results from the first type of models (although we provide the results and diagnostic plots of the second type of models also in Table A1 and Figure A5, Appendix A). All models fitted nicely the data (R2>0.90, deviance explained >92%; Table 2) and fulfilled (or showed only slight departures from) the assumptions of residuals' normality and homoscedasticity. No model showed relevant signs of temporal autocorrelation (Figure A1, Appendix A).

Table 2: Summary table for the comparison between models based on ungulate censuses before or after the plant's growth season. Bold type indicates significantly better fits (ΔA-IC>2).

Time of ungulate census	**Saltmarsh**		**Bulrush marsh**		**Shrubland**		**Grassland**	
	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2
Start of growth season	-195.5	0.91	-231.1	0.90	-325.1	0.94	-228.5	0.90

End of growth season	-193.6	0.90	-256.7	0.93	-331.7	0.94	-227.1	0.89

Variation in the length of the phenological cycle (days until NDVI peak) and the rainfall accumulated by then was significantly associated with the production of all four vegetation types. These effects were only additive (main factors significant, interaction not significant) for one vegetation type (shrubland) and synergistic (significant factors and inter-actions) for the other three (Table 3). The two domestic ungulates differed strongly in their effects on different marsh vegetation types, which were always negative: saltmarsh pro-duction decreased significantly with horse density, bulrush marsh production decreased significantly with cattle density, and grassland production decreased significantly with both. Wild ungulate species had limited effects on vegetation production: red deer density was positively associated to bulrush marsh production, and fallow deer density showed a non-linear association with shrubland production.

Table 3: Significance tests and probability levels of the GAM models predicting plant production (peak NDVI), fitted separately for each vegetation type. Only the predictor variables included in the 'best' model are shown. 'Adjusted-R squared' and 'Deviance explained' refer to the results of the full model, including all variables (i.e., those with significant and with non-significant effects).

	Saltmarsh	**Bulrush marsh**	**Shrubland**	**Grassland**
Rainfall	**F(2.17,4)=6.32** **$P<1.6*10^{-6}$**	**F(3.09,4)=19.9** **$P<2*10^{-16}$**	**F(1.99,4)=5.91** **$P<4.2*10^{-5}$**	**F(2.27,4)=6.03** **$P<3.26*10^{-6}$**
Phenology	**F(1.5,4)=2.29** **P<0.0042**	**F(2.16,4)=9.59** **$P<8.3*10^{-7}$**	**F(1.02,4)=53.89** **$P<1.7*10^{-6}$**	**F(1.45,4)=6.69** **P<0.0074**
Rainfall*Phenology	**F(5.29,16)=1.33** **P<0.0021**	**F(1.26,16)=0.37** **P<0.019**	F(0.66,16)=0.09 P>0.12	**F(7.28,16)=2.54** **$P<8.51*10^{-5}$**
Horse	**F(1.37,4)=18.2** **P<0.0006**	F(1.45,4)=10.6 P>0.0835	F(0.40,4)=3.17 P>0.16	**F(0.72,4)=5.94** **P<0.043**
Cattle	F(0.43,4)=0.328 P>0.14	**F(0.97,4)=21.4** **$P<2*10^{-16}$**	F(0.46,4)=0.60 P>0.10	**F(0.68,4)=1.89** **P<0.027**
Fallow deer	F(0.35,4)=0.33 P>0.24	$F(1.5*10^{-6},4)<0.01$ P>0.92	**F(1.61,4)=30.79** **P<0.0145**	F(0.99,4)=1.82 P>0.067
Red deer	$F(1.9*10^{-5},4)<0.01$ P>0.71	**F(1.24,4)=30.18** **P<0.0016**	$F(7.40*10^{-5},4)<0.01$ P>0.54	$F(3.92*10^{-5},4)<0.01$ P>0.70

Space(manag.unit)	**F(3.94,4)=87.2** **$P<2*10^{-16}$**	**F(3.83,4)=35.2** **$P<2*10^{-16}$**	**F(3.97,4)=160.91** **$P<2*10^{-16}$**	**F(3.92,4)=44.96** **$P<2*10^{-16}$**
Time(year)	**F(4.82,12)=1.73** **P<0.00094**	F($2.8*10^{-6}$,12)<0.01 P>0.52	F($1.5*10^{-5}$,12)<0.01 P>0.80	F($9.9*10^{-6}$,12)<0.01 P>0.83
Adjusted R2	0.91	0.90	0.94	0.90
Deviance explained (%)	93.5	92.2	94.8	92.9

The responses of the different vegetation types to rainfall showed a common pattern – an asymmetric, concave downward function, whose maximum was situated at medium or relatively high values of rainfall. However, the location of the maximum and the strength of the response (i.e., the slope of the upward and downward parts of the curve) varied strongly among vegetation types (Figure 3). Saltmarsh production showed a pronounced increase at low rainfall levels, which started to saturate at ca. 400 mm, reached its maxi-mum at 510 mm and decreased moderately above it. Bulrush marsh production increased moderately at low rainfall, started to saturate around 600 mm, reached a maximum at 685 mm and decreased slightly above it. Shrubland production showed a weak response, which increased slightly until reaching a maximum at 593 mm and decreased slightly after it. Grassland production showed a fairly symmetrical concavity that increased strong-ly until reaching a maximum at 511 mm and decreased strongly at higher levels of rain-fall.

The association between the production of the different vegetation types and their phenology (time of phenological peak) showed also a common pattern, albeit with considerable differences in the intensity and shape of the response curve (Figure 3). Responses range from a linear decrease in shrubland, to an inverted sigmoid curve in bulrush marsh, to asymmetric concave curves (with early peaks followed by a prolonged decrease) in salt-marsh and grassland. As a consequence, production peaks take place at the lowest phenology value registered (ca. days 87 and 210, respectively) in the shrubland and bulrush marsh, and close to day 150 for the saltmarsh and grassland. (These days correspond to early December, April and February, respectively.)

The effect of rainfall and phenology was not merely additive (i.e., there was a significant interaction effect in the selected models) for three vegetation types: saltmarsh, bulrush marsh and grassland (Figure A3, Appendix A). The interaction effects add to the separate effects of both variables showing (i) declines in production at both low rainfall + late phenology and high rainfall + early phenology, for saltmarsh; (ii) a decline in production at low rainfall + early phenology, but an increase at high rainfall + late phenology, for bulrush; and (iii) an additional decline in production at the lowest rainfall levels, which coincide with early phenologies, for grassland.

The density of domestic ungulates showed always linear, negative effects on vegetation production (Figure 3). Cattle density showed a strong effect on bulrush marsh production, a moderate effect on grassland production, and non-significant effects on saltmarsh and scrubland production. Horse density showed a strong effect on saltmarsh production, a moderate effect on grassland production, and not-significant effects on bulrush marsh and scrubland production.

The density of wild ungulates had either neutral or fairly weak effects on vegetation production (Figure 3). Red deer density had non-significant effects on the production of three vegetation types (saltmarsh, scrubland and grassland) and showed a linear, positive association with bulrush marsh production. Fallow deer density showed non-significant effects on saltmarsh, bulrush marsh and grassland production; and non-linear effects (asymmetric concave curve peaking at a moderate density, ca. 0.13 adults/ha, and decreasing above it) on scrubland production. (Note that the relationship between shrubland production and fallow deer density is positive for most values included in the dataset – and the saturation and decrease of the curve only take place for four exceptionally high values included in it).

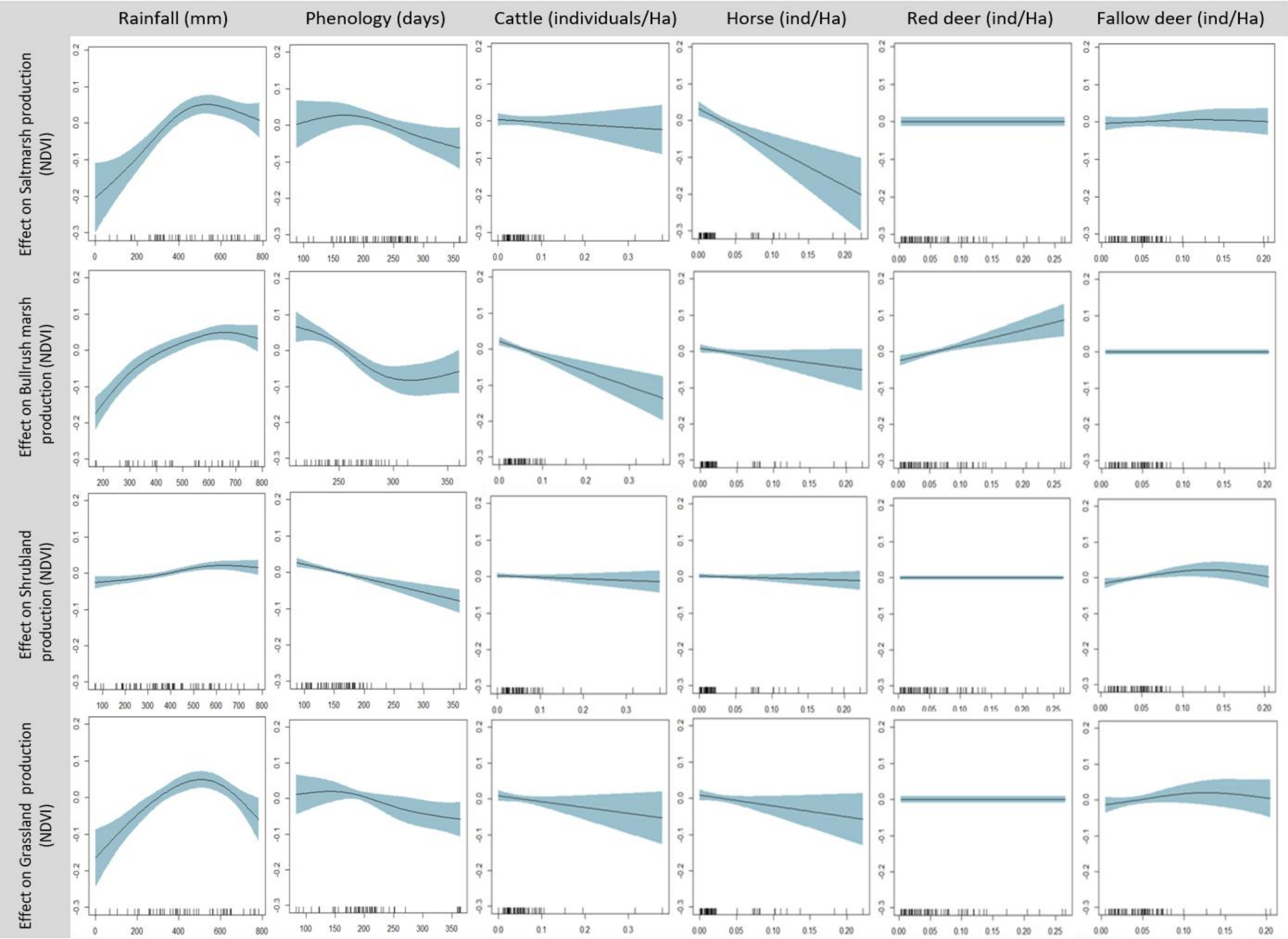

Figure 3: Predictor effects describing the effect of rainfall, phenology and herbivore density on the production of the four different vegetation types. Grey-blue bands are confidence bands representing the 95% confident intervals. The small black lines at the bottom of each plot indicate x-values of individual observations in the dataset. Y-axis represents the effect of each variable on the production of each vegetation type

3.1. Combined effect of rainfall and phenology

The non-linear relationships between production and both rainfall and phenology, and the positive association between the latter (which results in the absence of values at two types of combinations: early phenology with abundant rainfall, and late phenology with scarce rainfall) result in complex patterns that are best visualized using integrated inter-action plots (Figure 4). These plots show the combined effect of both variables (i.e., the sum of their main effects and their interaction) on the production of each of the four vegetation types, leaving blank the variable ranges where no observations are available. They are particularly useful in defining the actual ranges of both variables for which optimal, suboptimal and minimal production is predicted – which may differ considerable from those based on a direct extrapolation of the effect curves shown in Figure 3.

The plots show a general pattern for the four vegetation types: production tends to follow a 2D concave downward function, with a local maximum at intermediate values of rainfall and phenology, and decreasing production below and above them. The location of this optimum and the shape of the curve (i.e., whether the decrease is rapid or slow, and more or less asymmetric) varies strongly among vegetation types. Saltmarsh production reaches its maximum when intermediate phenological peaks (days 200-240, i.e., early March – mid April) coincide with medium-high levels of accumulated rainfall (500-650 mm); then de-creases strongly towards the lower part of the graph (i.e., at lower levels of rainfall, which take place at both early and intermediate phenologies); and decreases more softly at high-er rainfall levels (which coincide with delayed phenological peaks). Bulrush marsh pro-duction peaks also at medium-high levels of accumulated rainfall (500-650 mm) and early phenologies – which, owing to the delayed growth cycle of this type of vegetation, take place relatively late in the season (days 200-250, i.e., late March – mid May); and decreases strongly towards the lower (low rainfall) and more moderately the upper-right (high rain-fall and late phenology) parts of the graph. Shrubland production showed a flatter response, with peaks at medium-high levels of rainfall (450-550 mm) and early phenology (ca. day 120, i.e., early January, close to the earliest values recorded) and a smooth decrease at later phenologies, particularly in combination with increased rainfall. Grassland pro-duction peaked at intermediate levels of rainfall (420-440 mm) and early phenology (days 130-170 mm, i.e., early January – late February); it decreased strongly with decreasing rainfall, and decreased slightly for later phenologies and/or increased rainfall.

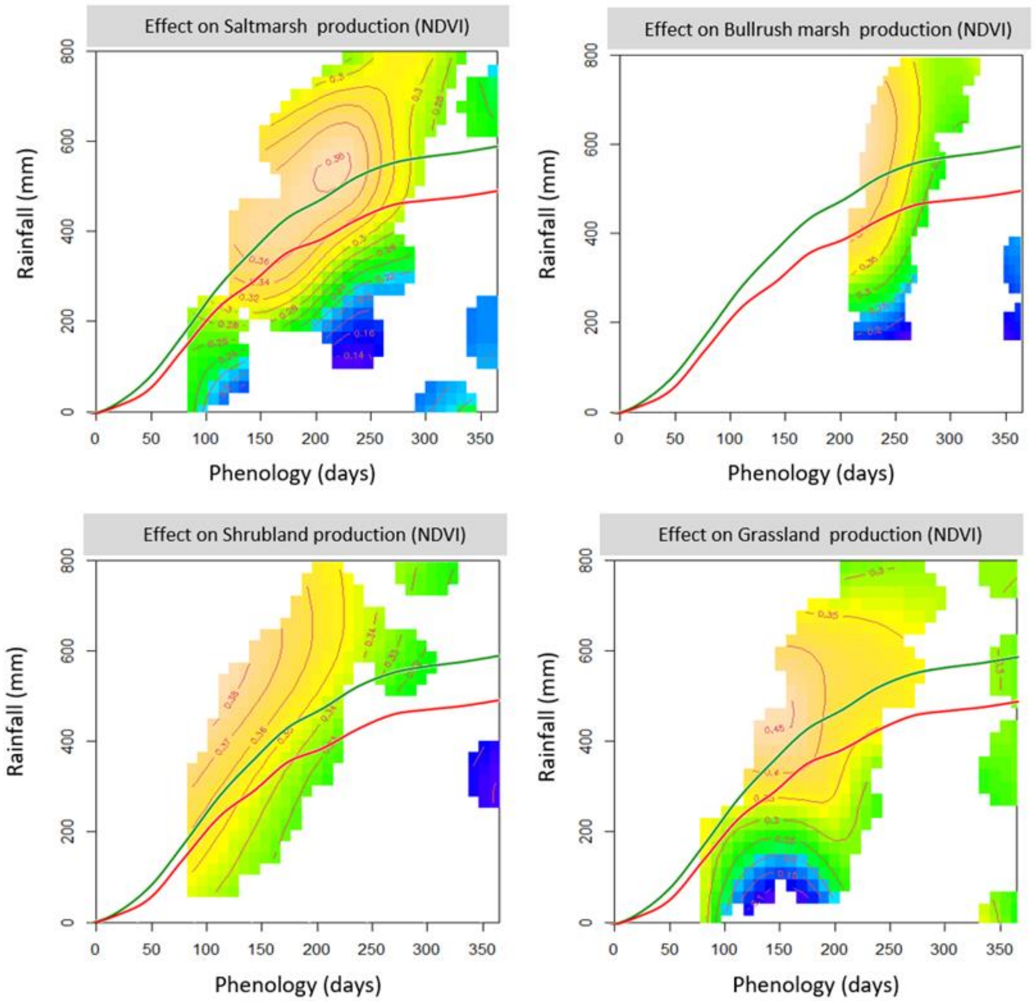

Figure 4. Bi-dimensional effect plots describing the joint effect of phenology (time of the NDVI peak; x axes) and water availability (rainfall accumulated until the phenological peak; y axes) on the production of four different vegetation types. The effects displayed in the graph included are sum of the main effects of both variables and their interaction. Note that the color palette varies among graphs – i.e., the same color does not necessarily indicate the same range of production values at all graphs, and information on production values must be extracted from the contour lines. Range of production values shown by contour lines are: 0.14-0.36 for saltmarsh, 0.2-0.4 for bulrush marsh, 0.2 - 0.38 for shrub-land, and 0.1–0.45 for grassland. Green and red lines indicate the observed (1996-2000) and predicted values (MIROC model: 2041-2070) of accumulated rainfall at all possible values of phenology (daily cumulative values, averaged across the aforementioned time series).

3.2. Model predictions

Plots of model predictions (Figure 5) show the combined effect of either rainfall or phenology, and the grazing pressure exerted by domestic ungulate species – including only those with significant effects on each vegetation type: horse for saltmarsh, cattle for bulrush marsh, cattle and horse (combined as ‘livestock’) for grassland. (Shrubland is not included, since there were no significant effects of domestic herbivores on it, and the effects of fallow deer were weak and dependent on 2-3 values of unusually high density). All plots show similar patterns: the decreases in primary production at lower rainfall levels or later phenological peaks is strongly accelerated at higher ungulate densities – reaching very low levels of plants production (<50% of the maximum), where they flatten out. Resilience to domestic ungulate grazing (showing as a vertical “crest” in the six panels) is relatively high at optimal rainfall and phenology – but a displacement away from these conditions (both towards the left or the right part of the plots) causes production to drop as soon as moderate (0.1 cattle/ha for bulrush marsh, 0.2 livestock/ha for grassland) or even low (0.2 horse/ha for saltmarsh) densities of domestic ungulates are reached.

The prediction plots also show that the medium-term changes (2041-2070) in the quantity and temporal distribution of rainfall predicted by the MIROC RCP4.5 climate change scenarios (REDIAM, 2014) will probably cause a strong decrease in plant production, whose impact would be exacerbated at medium to high levels of livestock density. The effect of decreased rainfall levels are relatively moderate for the Doñana vegetation, albeit particularly strong for saltmarsh type; but they will be compounded, however, by the pro-longed period required to achieve comparable levels of accumulated rainfall – i.e., by the strong delays in phenology required to attain them, whose strong impact on plant pro-duction will cause severe drops in plant productivity (NDVI<0.15, i.e. <50% of maximum values) at intermediate levels of livestock density. Altogether, the results indicate that the vegetation will face a combination of lower productivity and shorter phenological cycles, in turn causing lower biomass yields and shorter growth periods - thus, a strong decrease in food quantity and quality for herbivores.

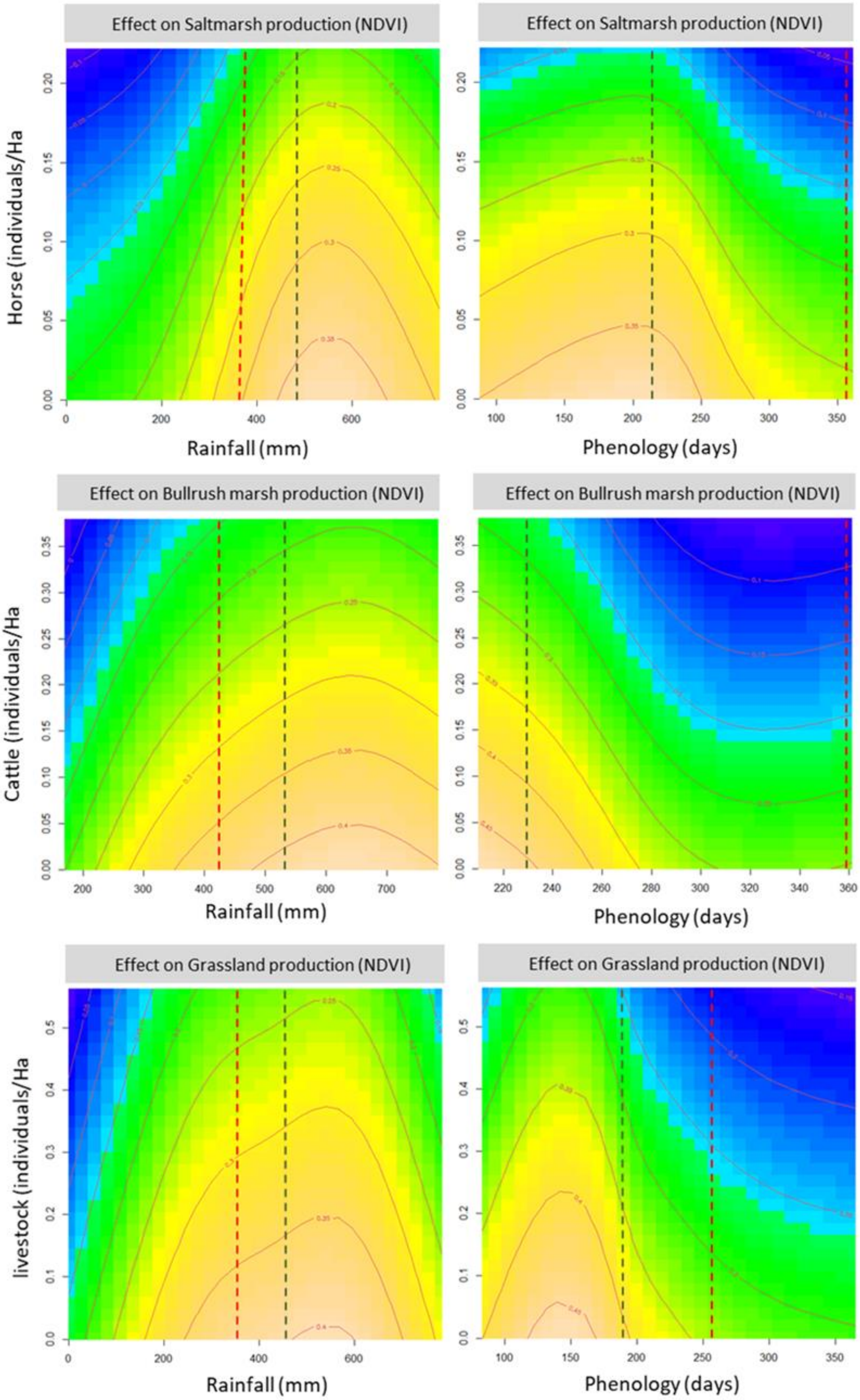

Figure 5: Model prediction plots describing the combined effect of climatology (either rainfall, left panels, or phenology, right panels) and grazing pressure exerted by domestic ungulate species – including only those with significant effects on each vegetation type. Note that the

color palette varies among graphs – i.e., the same color does not indicate the same range of production values (as indicated at the contour plots) at all graphs. Vertical dashed lines indicate the observed (green color; 1961-2000) and predicted (red color; 2041-2070, using the MIROC RCP4.5 scenario) values of accumulated rainfall and phenological peak (calculated, respectively, for the mean day of occurrence of the phenological peak or the corresponding value of accumulated rainfall in our 2000-2014 data series), obtained from REDIAM's ADVECRA (available at: https://kerdoc.cica.es/cc?lr=lang_es).

4. Discussion

The use of remote sensing imagery combined with field surveys of ungulates and meteorological data provided a powerful tool to model the factors determining vegetation production at Doñana National Park. Model results indicate that the four different vegetation types differed in their phenology (time of the NDVI peak), their productivity (NDVI peak value) and their response to inter-annual changes in rainfall levels. These differences reflect the spatiotemporal segregation among vegetation types and may increase ecosystem resilience to both climatological variability and grazing. Regarding the latter, model results also show important differences in the impact of wild and domestic species on vegetation production: the former have neutral, weak unimodal or even positive effects, while the later may have strong negative impacts on the production of most vegetation types (three out of four: saltmarsh, bulrush marsh and grassland). As a consequence, model prediction plots indicate that increasing livestock densities decreases vegetation resilience to decreased rainfall levels or delayed phenological peaks – thus exacerbating the impact of medium-term changes (2041-2070) in the quantity and temporal distribution of rainfall predicted by the climate change scenarios.

Our approach represents an attempt to simplify the modelling of plant production. In-stead of trying to incorporate the whole suite of different meteorological factors (average, max or min temperature; length of the coldest period temporal distribution of rainfall; etc.) and discriminate at which lag levels they operate, which would increase model complexity beyond the possibilities of a necessarily limited, we chose to use an indirect approach – in which two variables, “phenology” (the time of the NDVI peak) and ‘rainfall’ (the amount of rainfall accumulated until such moment) were introduced as surrogates of the integrated effect of climatology (the temporal sequence of rainfall and temperature) and water availability (from the start to the peak of the growth season) on plant production. The result was encouraging, because the fitted models, despite their relative simplicity (low number of parameters) were highly significant, explained a considerable proportion of the observed variation and provided useful insight into the operation of the constituent variables – including the effects of ungulate grazing. Detailed modelling of the ultimate, climatological causes of these effects, using a more extensive dataset, will however be necessary to derive more precise predictions and forecasts.

Three of the four vegetation types reach their maximum production at or close to the average rainfall levels of the historical series (ca. 500 mm), albeit marshland vegetation did best at higher rainfall levels (ca. 600 mm) and one type (grassland) did so at lower rainfall levels (ca. 400 mm). This convergence around average rainfall probably reflects the adaptation of the vegetation to local climate conditions, on which differences following the gradient of hygrophily (from the more xerophilous shrubland to the seasonally mesophylous bulrush marsh) gets overimposed. In addition, model results reflected the considerable phenological differences among the different vegetation types. These differences result in a complex spatiotemporal pattern of plant primary production, where the spatial mosaic of vegetation types is associated to seasonal differences in plant production that, in turn, vary among years. This allows for considerable resilience to variations in rainfall level and temporal distribution – inasmuch as these fluctuations do not depart extremely from average levels. On the one hand, rainfall levels ensuring optimal production for one vegetation type will result in suboptimal production for the other types, and vice-versa; on the other, the temporal sequence of production peaks along the xeric-mesic gradient will buffer the loss of production of any given vegetation type through the afore-mentioned increase in the production of other vegetation types, which not only increases the peak but also expands the breath of the phenological curves. Hence, ensuring a balanced access to the different vegetation types may hold the key to ensure a diverse set of forage resources able to meet the herbivore guild’s dietary needs (Provenza et al., 2003) – extending the availability of resources for herbivores, facilitating the maintenance of biodiversity, pat-terns and processes (Fuhlendorf et al., 2012) and increasing its resilience to climatic conditions predicted by climate change scenarios (Schneider & Kéfi, 2016). This may require, however, a wise choice of stocking rates, tailored to the productivity offered by each vegetation type – in particular, the most limiting one at each management unit (see below).

Model results indicated also that the impact of ungulate density (i.e., grazing pressure) on plant production differed strongly between wild and domestic species. These distinct effects may, at least partially, arise from the strong difference in stocking rates when expressed in terms of animal biomass. While population densities were comparable among the four different herbivores (averaging 10.15 and 8.58 individuals/km2 for wild and domestic ungulates, respectively), the body mass of cattle and horse is four to six-fold higher than the body mass of the two cervid species present in the study area – thus resulting in much larger biomass stocking rates of domestic ungulates (1.05 tons/km2 of cervids vs. 4.06 tons/km2 of livestock). This does not seem to be, however, the only reason behind this discrepancy – since both cattle and horse linear, negative effects on vegetation were there-fore exerted already at low densities (i.e., should responses would be comparable to those found for wild ungulates, non-linear effects with flat responses at low densities would be expected). Differences in foraging intensity, diet choice and behavior (including the pro-portion of non-consumptive plant damage, e.g., by trampling in soft soil) probably com-bine with higher consumptive rates (related to the larger body mass) to cause the negative impact of domestic, but not wild, herbivores on vegetation. As for the positive effects of wild ungulates on several vegetation types (either at all densities, or at the low-densities part of the concave downward curves) may result from facilitation mechanisms – (e.g., eliminating shading by less productive plant parts, removing apical dominance, favoring regrowth; (Stewart et al., 2016; Gill & Beardall, 2001)) or simply reflect indirect, non-causal effects (e.g., displacement away from areas grazed by herbivores with more severe impacts).

Within the domestic herbivores, cattle and horse showed similar effects (i.e., linear negative responses of similar slope) but affecting different vegetation types – probably indicating a trophic niche segregation between these two species. Both species caused similar, moderately negative effects on the grassland – the most suitable type of pasture for them. However, cattle showed strong negative effects on bulrush marsh vegetation, while horse did so for the saltmarsh vegetation. Preliminary data on habitat use and knowledge shared by local ranchers suggest that this difference may reflect different foraging choices by these two herbivores – with cattle being able to exploit extensively the bulrush marsh and horse feeding primarily in saltmarsh vegetation (both before bulrush emergence and after a few weeks of growth, when bulrush plants become unpalatable). Future work characterizing in detail these preferences, e.g., through the use of GPS collars, will be of key importance to adequately calculate stocking rates of the different herbivores, adjusting them to the type of vegetation exploited; and to optimize the design and management of management (thus, foraging) units.

The resilience of the vegetation to the combination of environmental stress (strong inter-annual fluctuations in rainfall and phenology) and grazing pressure will be further compounded by the expected impact of climate change. According to the model predictions, increasing livestock densities decreases vegetation resilience to decreased rainfall levels or delayed phenological peaks – thus exacerbating the impact of medium-term changes (2041-2070) in the quantity and temporal distribution of rainfall predicted by the climate change scenarios. Based on the predictions of a moderate scenario of the MIROC model, we may conclude that the END's vegetation will face increasingly constraining conditions for its development. Vegetation will face a 16.5% decrease in annual rainfall. This shortage is not homogeneous over time; hence, its effect is compounded by its temporal interaction with vegetation phenology. Should vegetation maintain its current pat-terns of phenological development, most types (all but the shrubland) will face a stronger decrease (17.8-18.8%) available during the growth period; and, should it adjust their development to the changes in rainfall distribution, it will have to delay severely their phenological peak to achieve the levels of rainfall at which their production peaks (ca. 60 days for grassland vegetation, Fig.4) – or they will not be able to achieve them , since they would exceed the end of the potential growth season, getting into the period of prolonged summer drought (saltmarsh and bulrush marsh vegetation, Fig.4). The latter trend is particularly worrying, since the delay in phenology necessary to achieve optimal rainfall will play against the general trend resulting from the concomitant increase in temperatures, i.e., an acceleration of vegetation phenology. Indeed, the observed phenological shift of vegetation in the northern hemisphere during the last decades reflects an advance of 0-12 days (Root et al., 2003; Menzel et al., 2006; Xu et al., 2019) – which would result in even lower levels of accumulated rainfall for the END's vegetation.

The moderate reduction in primary production caused by these changes in rainfall amount and patterns, especially in marshland vegetation (9-20% for the two upper panels of Fig.4), will become much stronger under a scenario of moderate to high herbivore pressure – which can be expected under current densities of domestic herbivores (e.g., 11-28% for densities of 0.15 individuals/ha in the two upper panels of Fig.4). The effect of moderate herbivore density is smaller in grassland vegetation, but it accelerates strongly at higher densities (lowest panel, Fig.4). The overall result is a strong decrease in the resilience of vegetation production to climate change in the presence of moderate to high domestic herbivore pressure. These effects will have, in turn, major consequences on the secondary production of livestock, whose profitability and sustainability would be thus compromised (Allred et al., 2014; Sloat et al., 2018). These results highlight the importance of considering local stressors in combination with predicted climatic conditions in order to better understand the com-plex evolution of specific habitats.

5. Conclusions

In summary, we have shown that environmental variability has strong consequences on primary production (Sneva & Hyder, 1962; Le Houérou 1980). However, the phenological alternation of different vegetation types and their differentiated responses to inter-annual variation in rainfall may increase ecosystem resilience to grazing pressure, buffering transient effects of climatic variability on grazing impact – inasmuch as excessive densities are not sustained over time. Unfortunately, under predicted climatic conditions, current herbivore pressure will represent a major stressor that may decrease vegetation resilience to inter-annual variability and extreme events, increasing the risk of reaching no-return degradation thresholds - which, once stabilized by complementary feed-backs, are likely to become irreversible (van de Koppel et al., 1997; Lohmann et al., 2012). Management strategies that take advantage of the aforementioned complementarities among vegetation types, designing management units and rotations to optimize their use by different herbivores, and adjusting stocking rate to the most sensitive vegetation types may alleviate these effects and allow for a sustainable management of these exploitations (e.g. [Allred et al., 2014; Fuhlendorf et al., 2017 and references therein]) – particularly those hosting habitats of high conservation value, such as our study system.

In addition, the use of remote sensing imagery processed with statistical models represents a powerful tool to improve the management of these systems (Booth & Tueller, 2003; Hunt et al., 2003). These tools could be used to both design long-term management strategies based on plant production/consumption scenarios, and develop (near) real time tools allowing for the rapid adjustment of herbivore stocking rates to observed vegetation production (e.g., through the displacement, enclosing and/or artificial feeding of livestock). For this purpose, we need to deepen our knowledge of the plant-ungulate interactions – in particular, the factors regulating both the spatial variation in plant production, and the space use and foraging pat-terns of herbivores. Further work in these areas may hold the key to preserve ranching activities in areas of high conservation value, by enhancing vegetation and ecosystem resilience to climate change.

Appendix A

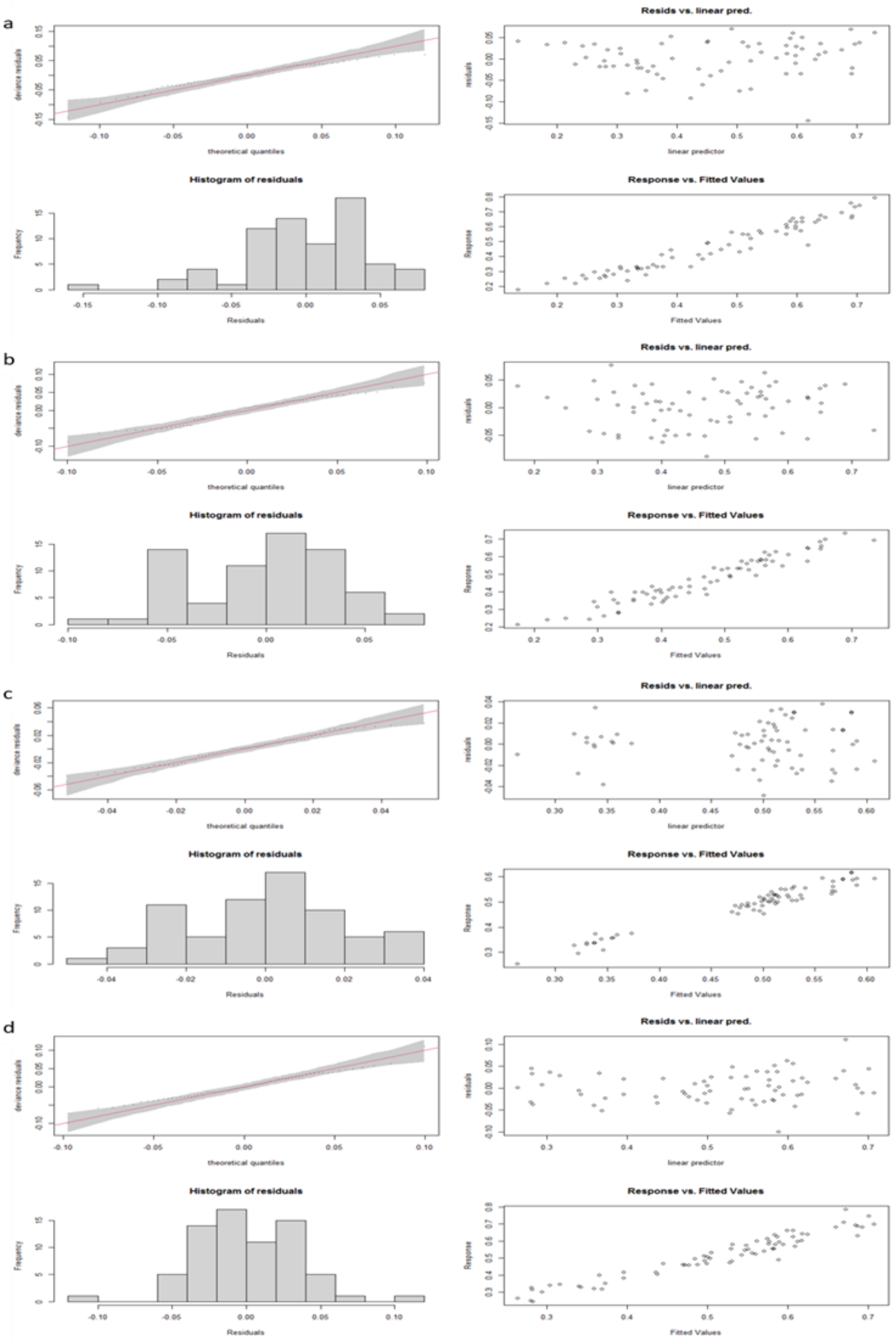

Figure A1: Diagnostic plots of the GAM models adjusted to the production (peak NDVI) of the four main vegetation types consumed by wild and domestic ungulates at the study area (Doñana National Park). Model for saltmarsh (a), bulrush marsh (b), shrubland (c) and grassland (d).

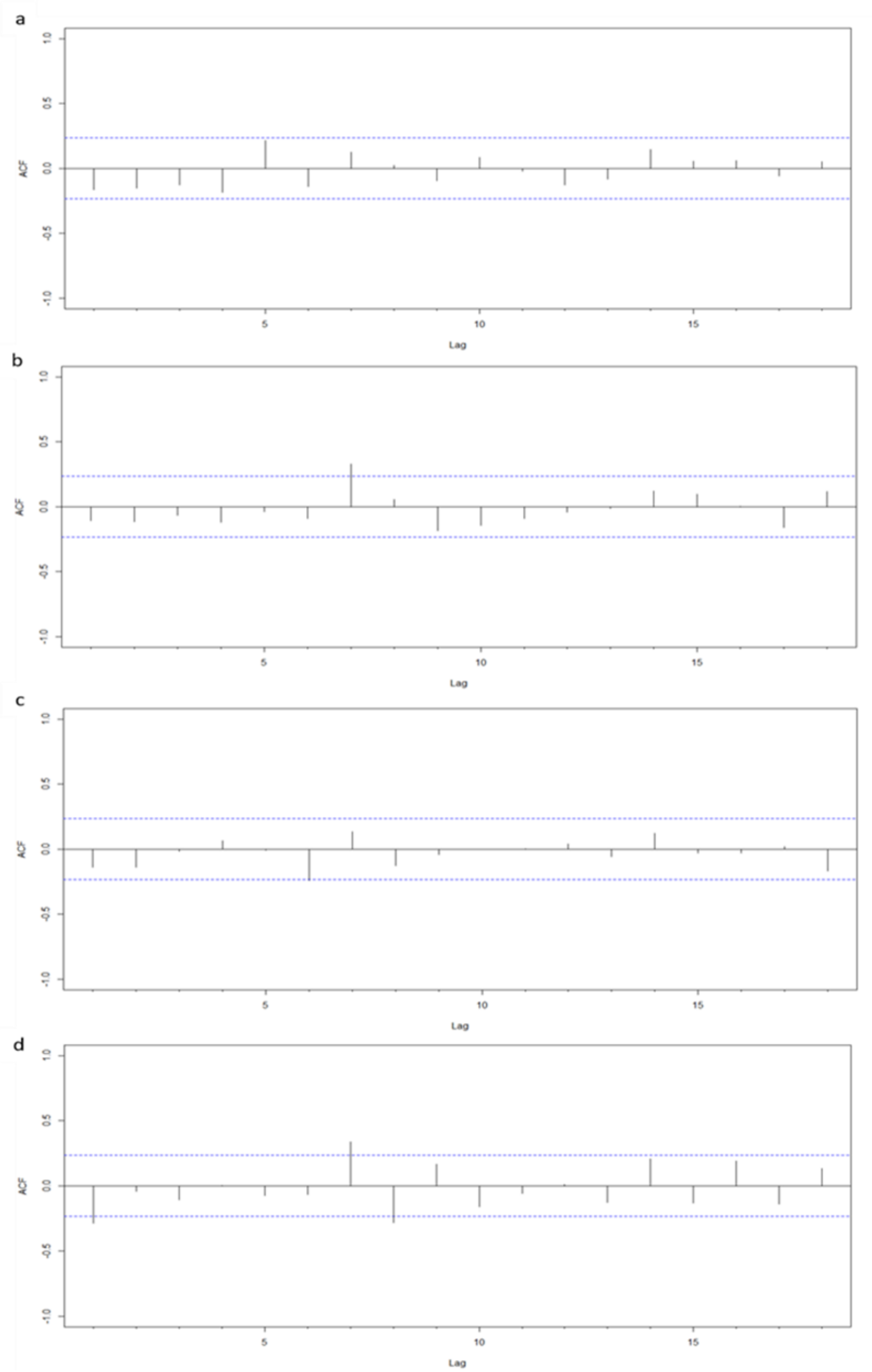

Figure A2: Autocorrelation plots of the residuals of the GAM models adjusted to the production (peak NDVI) of the four main vegetation types consumed by wild and domestic ungulates at the study area (Doñana National Park). Model for saltmarsh (a), bulrush marsh (b), shrubland (c) and grassland (d).

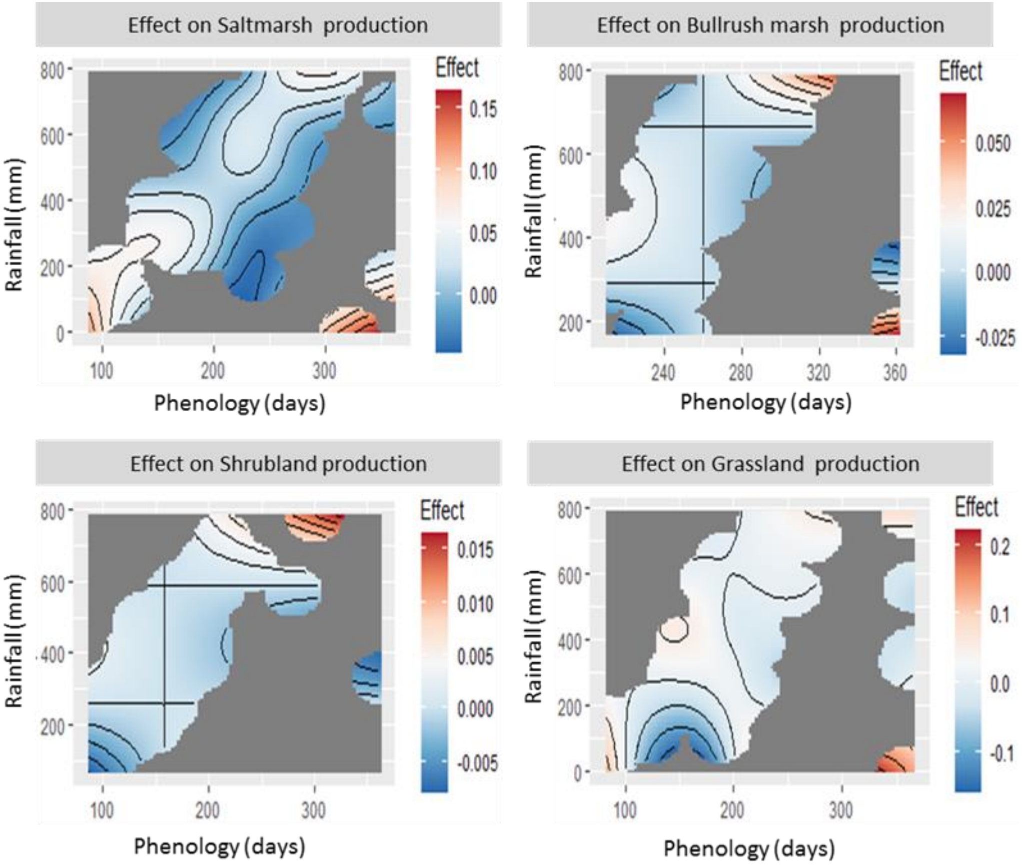

Figure A3: Effect of the interaction between rainfall and phenology in the GAM models adjusted to the production (peak NDVI) of the four main vegetation types consumed by wild and domestic ungulates at the study area (Doñana National Park). The plot differs from Fig.3 in showing the effect of the interaction factor without the effect of the main factors. Note that the color palette varies among graphs – i.e., the same color does not indicate the same range of production values (as indicated at the contour plots) at all graphs.

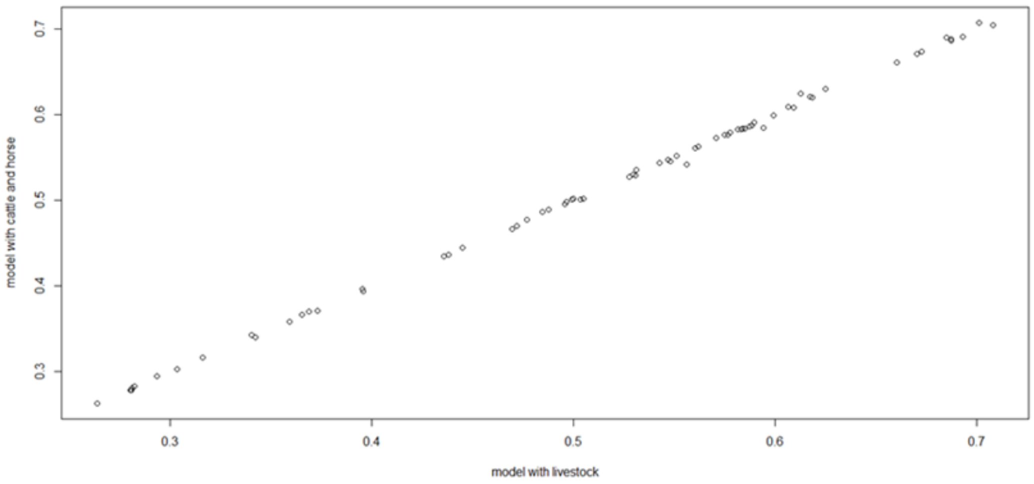

Figure A4: Correlation between the results (fitted values of grassland NDVI) of the models with separate variables for cattle and horse densities (whose results are shown in the main text) and those pooling these densities in a single variable named ‘livestock’ (used to produce the prediction plots shown in the lowest panels of Fig.5).

Table A1: Significance tests and probability levels of the alternative gam models -using the beginning-of-the-season values of ungulate census- predicting plant production (peak NDVI) fitted separately for each vegetation type. Only the predictor variables included in the 'best' model are shown.

	Saltmarsh	**Bulrush marsh**	**Shrubland**	**Grassland**
Rainfall	**F(2.38,4)=6.86** **P<5.35*10^{-7}**	**F(2.76,4)=12.5** **P<2*10^{-16}**	**F(2.61,4)=12.18** **P<0.0025**	**F(2.79,4)=10.54 P<7.56*10^{-7}**
Phenology	**F(1.7,4)=10.29** **P<0.00018**	F(6.69*10^{-1},4)=0.78 P>0.0522	**F(2.16,4)=117.7** **P<0.00012**	**F(8.81*10^{-1},4)=6.43** **P<0.0015**
Rainfall*Phenology	F(4.4*10^{-5},16)<0.01 P>0.467	**F(1.09,16)=0.99** **P<0.011**	F(6.19*10^{-5},16)<0.01 P>0.79	**F(5.88,16)=1.25 P<0.0442**
Horse	F(1.12,4)=2.44 P>0.322	**F(9.04*10^{-1},4)=46.6** **P<0.0017**	F(1.53*10^{-5},4)<0.01 P>0.78	F(3.94*10^{-1},4)=0.98 P>0.19
Cattle	F(2.4*10^{-5},4)<0.01 P>0.886	**F(9.2*10^{-1},4)=34.18** **P<0.00041**	F(3.97*10^{-5},4)<0.01 P>0.50	F(8.9*10^{-6},4)<0.01 P>0.89
Fallow deer	F(1.0*10^{-1},4)=0.032 P>0.267	F(6.4*10^{-5},4)<0.01 P>0.39	F(9.52*10^{-5},4)<0.01 P>0.35	F(4.07*10^{-5},4)<0.01 P>0.45
Red deer	**F(8.07*10^{-1},4)=8.81** **P<0.021**	F(9.4*10^{-5},4)<0.01 P>0.56	F(7.18*10^{-5},4)<0.01 P>0.59	F(4.56*10^{-5},4)<0.01 P>0.40
Space(manag.unit)	**F(3.91,4)=54.7** **P<2*10^{-16}**	**F(3.96,4)=132.5** **P<2*10^{-16}**	**F(3.98,4)=188.3** **P<2*10^{-16}**	**F(3.94,4)=55.25** **P<2*10^{-16}**
Time(year)	**F(6.18,12)=2.29** **P<0.0005**	**F(7.87,12)=3.69** **P<2.34*10^{-5}**	F(2.2*10^{-5},12)<0.01 P>0.83	F(9.26*10^{-6},12)<0.01 P>0.55
Adjusted R2	0.90	0.93	0.94	0.89
Deviance explained (%)	92.5	95.2	94.8	91.8

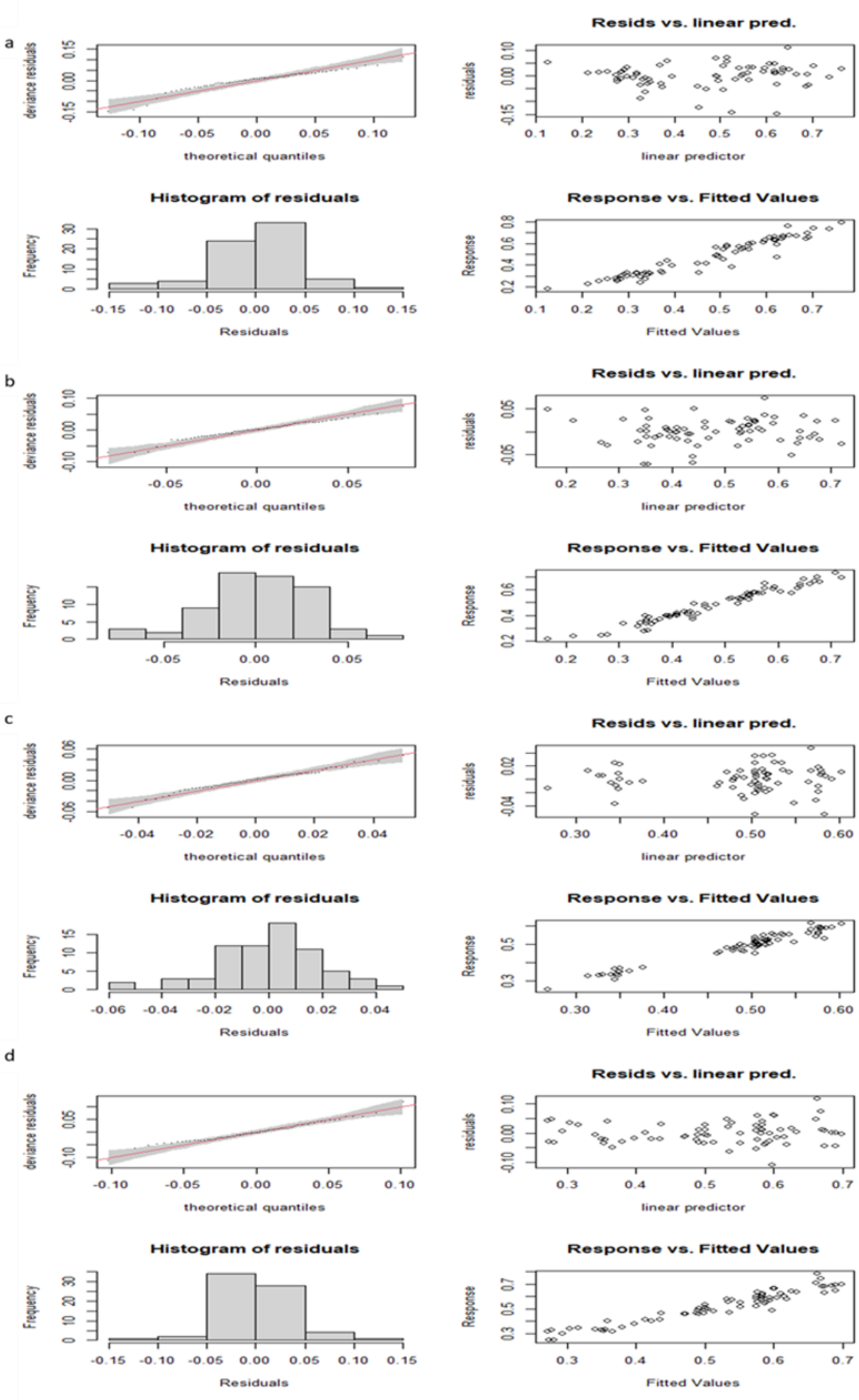

Figure A5: Diagnostic plots of the alternative GAM models -using the beginning-of-the-season values of ungulate census- adjusted to the production (peak NDVI) of the four main vegetation types consumed by wild and domestic ungulates at the study area (Doñana National Park). Model for saltmarsh (a), bulrush marsh (b), shrubland (c) and grassland (d).

Chapter 2

Functional and phenological complementarities resulting from vegetation heterogeneity increase resilience of ungulate populations to climatic variability in Mediterranean ecosystems

Giralt-Rueda, J.M.; Santamaria, L. Functional and phenological complementarities resulting from vegetation heterogeneity increase resilience of ungulate populations to climatic variability in Mediterranean ecosystems. *Submitted to Science of The Total Environment.*

Abstract

Mediterranean environments are characterized by strong intra- and inter-annual fluctuations in plant primary production, which are likely to regulate the carrying capacity and density-dependent responses of ungulate populations. These effects may, however, vary across spatial and temporal scales. Habitat heterogeneity, particularly when associated to differentiated phenological responses, may allow wild ungulates to mitigate temporal fluctuations in plant productivity by using different resources along the year. In this work, we use a 15-years dataset (including remote-sensing data on vegetation distribution, phenology and production, as well as ungulate population counts) to assess how temporal variability in plant primary production and livestock abundance influence the population dynamics of two wild ungulates: native red deer, *Cervus elaphus*, and introduced fallow deer, *Dama dama*. Results show that temporal alternation in the phenological cycles of the four different vegetation types increased plant production, thus food availability for ungulates, within each year. Furthermore, complementarity in the responses of different vegetation types to variations in the amount and timing of rainfall increased the predictability of food availability across different years. This complementarity effect was further increased by the contrasting responses of ungulate populations to variation in the production of different vegetation types. Furthermore, domestic ungulates had positive effects on wild ungulate density at low to intermediate abundances, but high livestock densities decreased ungulate density and constrained the resilience of the plant-ungulate system to the impact of climatic variation, particularly under climate change. Our findings deepen the knowledge on vegetation-ungulate interactions in Mediterranean areas, potentially contributing to develop better management strategies of ungulate populations and adapt them to ongoing climate change.

Keywords

Deer, primary production, phenology, livestock, heterogeneous landscapes, remote sensing, climate change.

1. Introduction

Understanding the influence of climate on terrestrial ecosystems represents a main challenge in ecology (Walther et al., 2002; Stenseth et al., 2003). As climate change and other anthropogenic impacts on ecosystems rapidly increase, such knowledge becomes crucial to develop adequate management strategies and tools. Semi-arid and Mediterranean rangelands are exposed to important levels of anthropic intervention and climatic variability (Gillson & Hoffman, 2007; Reynolds et al., 2007; Lohmann et al., 2012). Climatic variability (mostly regarding rainfall levels) are a key factor controlling ecosystems dynamics, which respond to it with large fluctuations in associated processes (such as plant and secondary production). Seasonal fluctuations in rainfall, with significant levels of precipitation in autumn and spring and dry periods in summer and winter, represent the main factor governing vegetation production and phenology (Carmona et al., 2013). This effect dependence is modulated by the strong, inter-annual variation in rainfall levels typical of semi-arid and Mediterranean climates. Floods and droughts represent recurrent disturbances with strong impacts on vegetation structure and function, and the subsequent recovery from them is frequently mediated by environmental or anthropogenic factors (Mayor et al., 2013). This complex source of spatio-temporal variation has fundamental impacts on herbivore populations, which usually cascade to other trophic levels of the ecosystem (Post et al., 1999; Katona & Coetsee, 2019; Ramirez et al., 2021).

Large herbivores such as ungulates are keystone elements playing important roles in ecosystems. They participate actively in nutrient cycles, regulate primary productivity and the specific composition of many vegetation types, mediate seed dispersal, and represent a fundamental resource for large predators and scavengers (Hobbs, 1996). The direct effects of primary production and phenology on their population, space use and behavior has been a recurring topic in ecology. In general terms, the carrying capacity of the (plant) system and the foraging behavior of large herbivores are the main factors driving their population dynamics, though their effects are modulated by density-dependence processes, (White, 1983). In particular, the alternation of wet and dry seasons results in cycles of vegetation growth and phenology that are reflected in cycles of food quantity and quality (Illius and O´connor 1999; Schwinning et al., 2004). Ungulates lose weight due to resource limitation during the dry seasons and their survival often depends on the body reserves accumulated during the wet season (Sinclair 1975, Fryxell 1987, Illius & O’Connor 2000).

To mitigate these effects, ungulates often show sophisticated behavioral responses, including dynamic patterns of space use and changes in diet preferences (Gordon & Illius 1989). Overlaying these processes is density dependence, an important factor in the dynamics of many populations (Brook and Bradshaw, 2006) that can occur in multiple life stages (e.g. Clutton-Brock et al., 1987; Ciannelli et al., 2004). In Mediterranean and semi-arid environments, ungulate populations are controlled mainly by density-dependent mortality in the dry season (Owen-Smith 1990). However, environmental factors modulate density limiting processes such as habitat selection or food availability (Brook and Bradshaw, 2006; Maunder and Deriso, 2011). Hence, the effects of environmental fluctuations on the population dynamics of Mediterranean and semi-arid ungulates are strong and multi-layered (Imperio et al., 2012) and they interplay with anthropogenic stressors through a complex set of feed-back loops whose operation and impact we are only beginning to understand (Jeltsch, Weber & Grimm, 2000; Vetter, 2005; Gillson & Hoffman, 2007, Lovari et al., 2007; Alves et al., 2014).

According to climate change models, Mediterranean and semi-arid environments are being subjected to important changes in the rainfall regime, characterized by decreased rainfall levels and shifts in its seasonal distribution (Ramos, 2001; Sumner et al., 2003; Scheiter & Higgins 2009; IPCC, 2014). However, our limited understanding on the interacting effects of such changes and other anthropogenic stressors on ecosystem functioning hinders our ability to develop effective management or conservation strategies for both the vegetation and the large herbivores feeding on it (Pettorelli et al., 2005; Tietjen & Jeltsch 2007). In the past, most environmental studies struggled with the difficulties involved in measuring and monitoring the spatio-temporal variability in patterns and processes at the required scales. Recent advances in remote sensing, however, facilitated greatly this task. In particular, the use of satellite-derived vegetation indices as a proxy of vegetation productivity allows researchers to approach long-term and high-resolution studies on vegetation dynamics and thus, forage availability (Kerr and Ostrovski 2003; Pettorelli et al., 2005; Duffy and Pettorelii 2012; Naidoo et al., 2012; Borowik et al., 2013). Recently, several studies have demonstrated its application to animal ecology studies, e.g. by linking vegetation patterns and processes with animal population dynamics, distribution (Borowik et al., 2013) and behavior (Remelgado et al., 2018).

In this work, we use a 15-years series (2000-2014) of satellite-derived data on vegetation dynamics (primary production and phenology), livestock stocking rates and wild ungulate population counts in an iconic protected area (the Doñana National Park, SW Spain) to quantify the effect of plant productivity, intra-guild competition and density-dependent processes on the population dynamics of two wild ungulates (the red deer *Cervus elaphus* and fallow deer *Dama dama*), and evaluate the role of landscape heterogeneity in modulating these processes. Specifically, we evaluate whether: (i) The intra- and inter-annual differences in production and phenology among the four main different vegetation types result in complementarity effects that increase resource availability for wild ungulates. (ii) The two different livestock species (horse and cattle) have positive (facilitative), neutral or negative (competitive) effects on wild ungulates. (iii) Livestock stocking rates modulate the resilience of wild ungulate populations to the reductions in vegetation production predicted under the extreme climatic fluctuations characteristic of these areas, which are expected to increase under climate-change.

2. Material and methods

2.1. Study area

The research is carried out in the Doñana National Park (DNP onwards), an iconic conservation area located on the southern tip of the Atlantic coast of the Iberian Peninsula. The region is characterized by a Mediterranean climate classified as dry sub-humid with marked seasonality (Siljeström et al., 2002). DNP is characterized by high landscape heterogeneity and temporal dynamism (Giralt-Rueda & Santamaria., 2021). It includes coastal dunes almost free of vegetation; forests and woodlands dominated by conifers (stone pine *Pinus pinea* and/or coastal juniper *Juniperus phoenicea*) and cork oaks (*Querqus suber*); a mosaic of dry ('monte blanco') and wet ('monte negro') shrubland; small patches of grassland in and around groundwater-fed depressions and ponds; and a more extensive grassland at the sand-marsh fringe, locally known as 'vera' (Novo, 1997; Munoz-Reinoso & Novo 2005; Munoz-Reinoso, Jordán & Tejada-Tejada 2020; see Table 1 for details). In the marshland, there are two main vegetation types: saltmarsh dominated by halophilous scrub ('almajar'), in shallower areas with higher salinity, and bulrush marsh hosting seasonal meadows of tall sedges, at deeper areas with lower salinity (Novo 1997; García-Murillo et al., 2007; see Table 1 for details).

The study area hosts populations of three wild ungulates, two native (the red deer *Cervus elaphus* and the wild boar *Sus scrofa*) and one introduced (the fallow deer *Dama dama*) species; as well as three domestic ungulates (cattle *Bos taurus*, horse *Equus ferus* and sheep *Ovis aries*) that are traditionally bred in different management units (MU hereafter) largely corresponding to land property units (Estates) or combinations thereof. MU are delimited by livestock-proof fences, restricting the movement of livestock but being relatively permeable for wild ungulates. We focused our work on five MU (Matas Gordas, Sotos-Algaida, Reserva Biológica de Doñana, Puntal and Marismillas; hereafter MAT, SOA, RBD, PUN and MAR), which together cover 40.27% of the National Park area, because each of them contains all four vegetation types included in the study (see below) and they differ greatly in the composition of the ungulate guild (Fig. 1). Our work focused also on the herbivorous ungulate species (thus leaving out wild boars) and excluded sheep (since they are not present in the five MU selected). The current density of these four species in the DNP is: 6.26 red deer/km^2, 6.01 cattle/km^2 (excluding MAT, where there is no presence of cattle since 2000), 3.89 fallow deer/km^2 and 2.49 horses/km^2 (excluding MAT, where there is no presence of horses since 2000). All together, they make 18.73 ungulates/km^2, of which 10.15 and 8.58 individuals/km^2 are cervids and livestock respectively.

2.2. Delimitation of vegetation types

Our analysis focused on the four vegetation types accessible to wild and domestic ungulates (i.e., excluding woodlands of pines, junipers and cork oaks) within the five MU mentioned above. These four classes were: saltmarsh, bullrush marsh, shrubland and grassland (see Table 1 for a detailed description).

Table 1. Description of the four vegetation types included in the study.

Vegetation type	**Description**
Saltmarsh	Halophilous scrub (‘almajar’) on floodplain/marine brackish mudflats, dominated by glaucous glasswort (*Arthrocnemun macrostachium*) and shrubby sea-blite (*Suaeda vera*), interspersed with halophilous grass meadows.
Bullrush marsh	Seasonal meadows of tall sedges (Fam. Cyperaceae) on floodplain/brackish marshes. Dominant or co-dominant species are saltmarsh bullrush (*Bolboschoenus maritimus*), blysmus bullrush (*Schoenoplectus litoralis*) and somerset rush (*Juncus subulatus*).
Shrubland	Shrub formations on stabilized dunes, sometimes interspersed with sandy grassland. These formations include a mosaic of two main types, respectively occupying more xeric and more mesic sites: dry scrubland (‘monte blanco’) dominated by *Halimium halimifolium, Cistus salvifolius, C. libanotis*, *Rosmarinus officinalis,* and *Lavandula stoechas*; and wet shrubland (‘monte negro’), dominated by heather (*Erica scoparia*, *E. umbellata*, *E. ciliaris*, *Calluna vulgaris*), *Rubus ulmifolius, Ulex minor* and *Ulex australis*.
Grassland	Grassland formations with great variability in their extent and species composition, dominated by the

association of *Galiopalustris* sp. with *Juncus maritimus*. Wet pasture formations include small patches of grassland in/around groundwater-fed depressions and ponds; and more extensive meadows at the sand-marsh fringe, locally known as ‘vera’.

To define the different vegetation types, we selected the corresponding classes of vegetation maps (Fig. 1) elaborated in 2014 by the long-term monitoring program (PSPN; Andreu et al., 2014, pp. 37-59) of Doñana’s Singular Scientific-Technical Facility (ICTS-RBD), and grouped into the four types described above (Fig. 1). First, in order to avoid erroneous measurements due to mixed signals from heterogeneous land features, all pixels partially or totally covered by dunes, bare soil, water or trees were removed from the map. Therefore, the resulting map only contained “pure” vegetation types. Subsequently, the polygons occupied by each of these types within each of the five management units were used to calculate their respective area and the variables derived from satellite-obtained NDVI Values (see below). These tasks were performed with the ArcGIS 10.1 software (ESRI 2011).

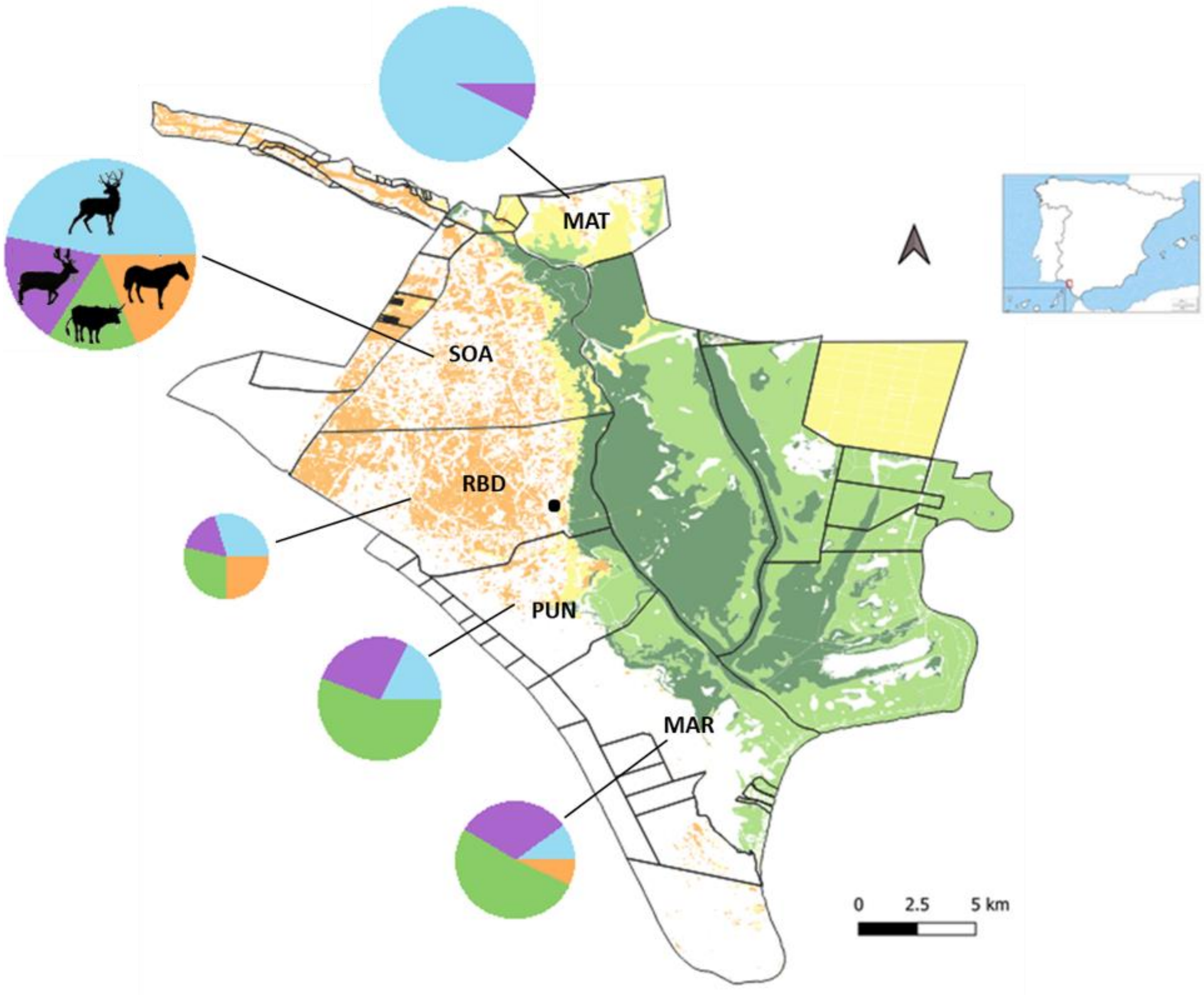

Fig. 1. Distribution of the four vegetation types used in this study within the Doñana National Park. Black lines represent different management units (largely coinciding with property boundaries). Shrubland is showed in orange, grassland in yellow, saltmarsh in light green and bulrush marsh in dark green. The acronyms refer to the names of the management units included in the study. The black dot indicates the location of the meteorological station. Pie charts indicate the total density of every ungulate species present in each MU. Cattle is shown in green, horse in orange, fallow deer in purple and red deer in blue. The size of the pie charts reflects the total density of ungulates in the corresponding MU.

2.3. Estimation of Plant primary production

Satellite information obtained from the Institute of Surveying, Remote Sensing and Land Information (IVFL) of the University of Natural Resources and Applied Life Sciences (BOKU), Vienna, was used to estimate the production of different vegetation types during the study period. This institution offers remote sensing products – smooth and continuous Normalized

Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) – from MODIS satellite images with different temporal resolution (From 16 to 7 days) from year 2000 to present. These products are the result of processing standard products from Terra and Aqua satellites, namely MODIS Level-3 16-day composite Vegetation Indices (VI) available at 250-m of spatial resolution. The combination of 16-day composites from these two satellites –Terra (MOD13 series) and Aqua (MYD13 series) – allows to obtain imagery at a temporal resolution of 7 days. Detailed information on the processes for creating such time series can be consulted in in Vuolo et al., (2012) and at BOKU's website (https://boku.ac.at/rali/geomatics).

For our study we use the Normalized Difference Vegetation Index (NDVI), a commonly used vegetation index that serves as a proxy of vegetation density and plant health (Gaitán et al., 2013). NDVI was demonstrated to reflect appropriately the vegetation response to rainfall variability (Helman et al., 2014) and extreme events (e.g. droughts) across different biomass around the world (Vicente-Serrano et al., 2013) and has been proven to correlate with plant biomass at the study area (Lumbierres et al., 2017). We use the long-term series of NDVI values with the highest temporal resolution available (every 7 days) for the study period (January 2000 – August 2014). For each vegetation type and within each management unit, we extracted the average NDVI value at each observation date (i.e., every 7 days) of the study period, using the Zonal Statistics function available in ArcGIS 10.1 (ESRI, 2011). The resulting data series provided the phenological curves at each observation unit (N=75 per vegetation type, arising from a combination of 15 years x 5 management units). We then used the TIMESAT software (Jönsson and Eklundh, 2004) to estimate the date and value of each annual NDVI peak, which we interpret as surrogates of the vegetation's phenology and production on each given growth period (referring, hereafter, to hydro-meteorological years, running from 1 September to 31 august). Production of each vegetation type at each given MU was calculated as the average of all pixels' values at that MU, multiplied by the area covered by this vegetation type and then divided by the total MU area– hence, it represents the average production of that given vegetation type per pixel.

2.4. Ungulate density

Data on the abundance of wild ungulates (red deer and fallow deer) at each management unit were obtained from annual censuses conducted by National Park service at the beginning of each annual reproductive (rutting) period, which differs approx. one month between both species (September for red deer and October for fallow deer). During rutting, individuals of both species concentrate on open areas, which greatly facilitates counting.

Population data on domestic ungulates were obtained from the National Park service, through censuses undertaken during the annual animal-health controls (June-September). These data only refer to adults older than 12 months, since young of the year were not reported consistently throughout the study period. National Park regulations set a cap at the total number of domestic ungulates allowed at each management area, which is adjusted on yearly basis. Hence, their (maximum) abundance is relatively independent of yearly fluctuations in environmental drivers, and yearly values only show slight fluctuations relative to that year's cap.

Based on all this information, we built a database reflecting the abundances (number of adult individuals) of each of the four ungulate species at each management area (Fig. 2). To correct for management area size, we used these abundances to calculated population densities (number of individuals / ha).

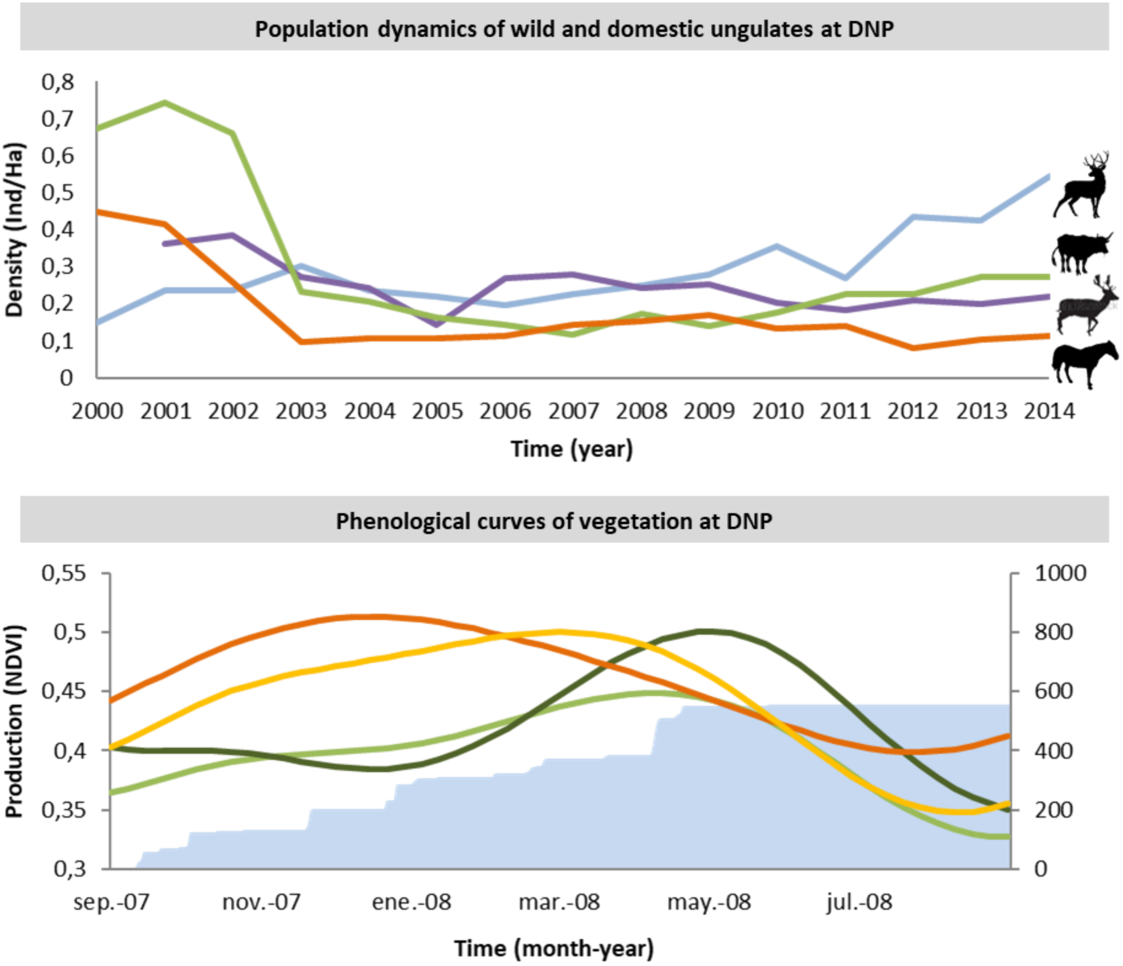

Fig. 2. Upper panel: Evolution of the population density (number of adult individuals / ha) of the four species of ungulates of the Doñana National Park for the period of 2000-2014. Lower panel.: Phenological curves of the four main vegetation types (shrubland in orange, grassland

in yellow, saltmarsh in light green and bullrush marsh in dark green) during a year with average levels of rainfall (shown in blue) at the DNP.

2.5. Data analyses

Data on wild ungulate density were analyzed by means of hierarchical generalized additive models (HGAM), using the GAM function available in R’s mgcv package (Wood, 2011). Full models included wild ungulate density (either ref deer or fallow deer) as response variable; its previous year’s density as continuous covariate (to account for the density dependence); the densities of other ungulates (separately for cattle, horse and the other wild ungulate), as well as the value and time of the annual NDVI peak (referred to as primary production and phenology hereafter) of each vegetation type, as continuous covariates; management unit as random factor, to account for spatial autocorrelation; and year as continuous covariate, to account for temporal autocorrelation. These models were subjected to automatic selection of covariates using the model argument “Select” (Wood & Säfken, 2016). This argument adds an additional penalty to all smooth functions in the model, affecting perfectly smooth terms and shrinking linear effects back to zero effects so that they can be removed from the model. This is the appropriate method for variable selection among a group of covariates in GAM models (Marra & Wood, 2011). We only report on the ‘best’ model, as selected by this argument.

Models were fitted using a Poisson distribution with a log link function, after expressing ungulate densities as individuals/10km^2 and rounding them to integers. We used this distribution because it improved model fits, in terms of residuals’ normality and homoscedasticity (visualized with the GAM.check function from the mgcv package), as compared with those using the gaussian or gamma distributions. Temporal autocorrelation was evaluated by computing estimates of the autocorrelation function and evaluating their significance, using the Acf function available in the Forecast package (Hyndman & Khandakar, 2007; Hyndman et al., 2020).

A common problem for these types of multivariate models is the impact of multi-collinearity on parameter estimates, significance levels and model predictions. An adequate treatment of this kind of effects is important for a correct interpretation of the relationships involved in the processes modeled – in particular, whether a given relationship with an independent variable is partly attributable to the confounding effect of other variables included in the model. To evaluate (and correct for) this potential problem, we estimated the correlations (before model fitting) and the concurvities (after model fitting, only for the ‘best’ reduced model) between all pairs of independent variables included in the model. Concurvity is the analogue to co-linearity for smooth terms and it can lead to unstable estimates (Wood, 2006). While GAM models are designed to deal with concurvity between independent variables, it may affect the reliability of the results (Wood, 2008). Multiple, pairwise concurvity measures between covariates was estimated using the vis.concurvity function of R's mgcv package (Wood, 2011). If high concurvity values were detected, we assessed the robustness of the selected model by running identical analyses (HGAMs with model selection) departing from two additional full models, respectively obtained by removing each one of the two variables showing a high pairwise concurvity value (above 0.7). The results of the initial model ('best' reduced model selected from a full model with all the covariates) was then compared with those of these submodels ('best' models after removing one of the two variables with high concurvity), in terms of (i) having the lowest AIC and best residuals' distribution, and (ii) having robust effects (i.e., we avoided the introduction of variables whose incorporation caused large changes if other variables' effects). Moreover, the interpretation of the selected model took into account the information on the concurvity and the correlations among the independent variables included in it and those excluded from it (see below). Concurvity and autocorrelation plots are provided in the appendix (Fig. A1, A2, A3 and A4).

Finally, we used the function vis.gam in the mgcv package to produce contour plots of model predictions of wild ungulate (either red deer or fallow deer) densities, based on different combinations of domestic ungulate density (only those with significant effects) and production of the four different vegetation types. Based on these plots, we performed a visual comparison of the impact of climatic variation, using the range of vegetation production estimates observed in our time series.

3. Results

3.1. Vegetation complementarity in phenology and production

The phenological curves of the four vegetation types showed a clear pattern of seasonal complementarity, whereby the increasing delay in the phenological peak of more mesic vegetation types (from the more xeric type, the shrubland, to the most mesic one, the bulrush marsh) spanned a total of approx. 200 days – increasing food availability for herbivores able to feed on them. This seasonal pattern, which is very distinct in 'average' years (i.e., when rainfall is ca. 500 mm/year), varies strongly among years. In dry years, the productivity of more mesic vegetation types (specially the saltmarsh and bulrush marsh) drops severely, reducing food availability in spring (from day 230 onwards, i.e., after mid-April). In wet years, the delay of all phenological peaks (which peak after day 185-230, corresponding to early March – mid April) reduces considerably food availability during winter (Fig. 3).

An examination of the patterns of variation along the time series (Fig.3, middle and lower panel) exemplifies further these patterns. In the driest years (2005 and 2012), the broad spread in the phenological peaks of the four vegetation types provided for an extended foraging season, although the drop in productivity in most vegetation types (all but the shrubland) limited this compensation effect. Similarly, in the wettest years (2004 and 2010), the decreased production and delayed phenology of the saltmarsh and bulrush marsh vegetation was alleviated by the availability of shrubland (and, to a lower extent, grassland) vegetation, which showed smaller changes in both parameters. In both cases, the shrubland provides a key element of resilience for herbivores who can resort to browsing.

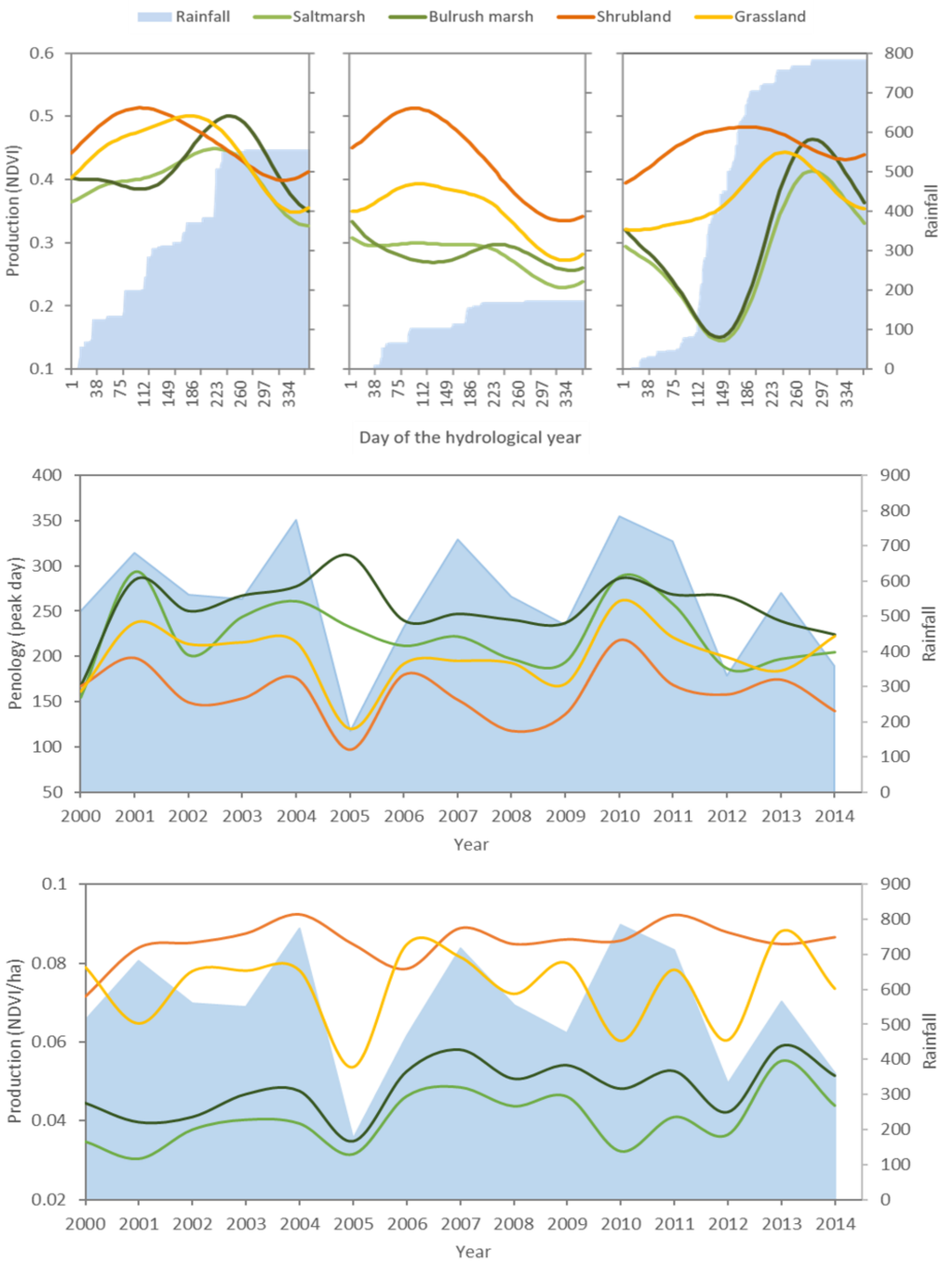

Fig. 3. Upper panel: Examples of phenological curves of the four vegetation types (using the average NDVI value considering all MU) at years with average (2007-2008, 556.3 mm), low (2004-2005, 173.0 mm) and high (2009-2010, 784.2 mm) annual rainfall (left, middle and right plot respectively). Middle panel: Interannual variation in the phenological peak (time of the NDVI peak, in days since September 1st) of the four vegetation types. Lower panel: Interannual variation in the primary production (peak NDVI) of the phenological peak of the four vegetation types. Shrubland is showed in orange, grassland in yellow, saltmarsh in light green and bulrush marsh in dark green. Note that the upper row shows values of NDVI per pixel of each given vegetation type; while the lower panel shows NDVI per pixel of the study area, thus incorporating already the variation in cover among different vegetation types (as used in the statistical analyses below).

Complementarity effects can be also detected in the multiple correlations plot (Fig. 4), which are based on the values per management unit. Positive correlations among the production and/or the phenology of different vegetation types indicate similar and/or synchronous responses to inter-annual variation in environmental conditions, amplifying environmental variability; while negative correlations indicate opposing responses, which may result in complementarity effects. Production showed a predominance of complementarity, with negative correlations between all pairs of vegetation types except two (saltmarsh-grassland and bulrush marsh-shrubland, which showed weak positive correlations). These negative correlations were particularly strong for two pairs of vegetation types: saltmarsh-shrubland and saltmarsh-bullrush marsh. Amongst the phenological responses, correlations were scarcer, with positive correlations between two pairs of vegetation types: shrubland vs. grassland, and saltmarsh vs. bullrush marsh. In summary, complementary differences in productivity among vegetation types may provide resilience to inter-annual variation in rainfall – adding to the seasonal complementarity provided by intra-annual differences in phenology.

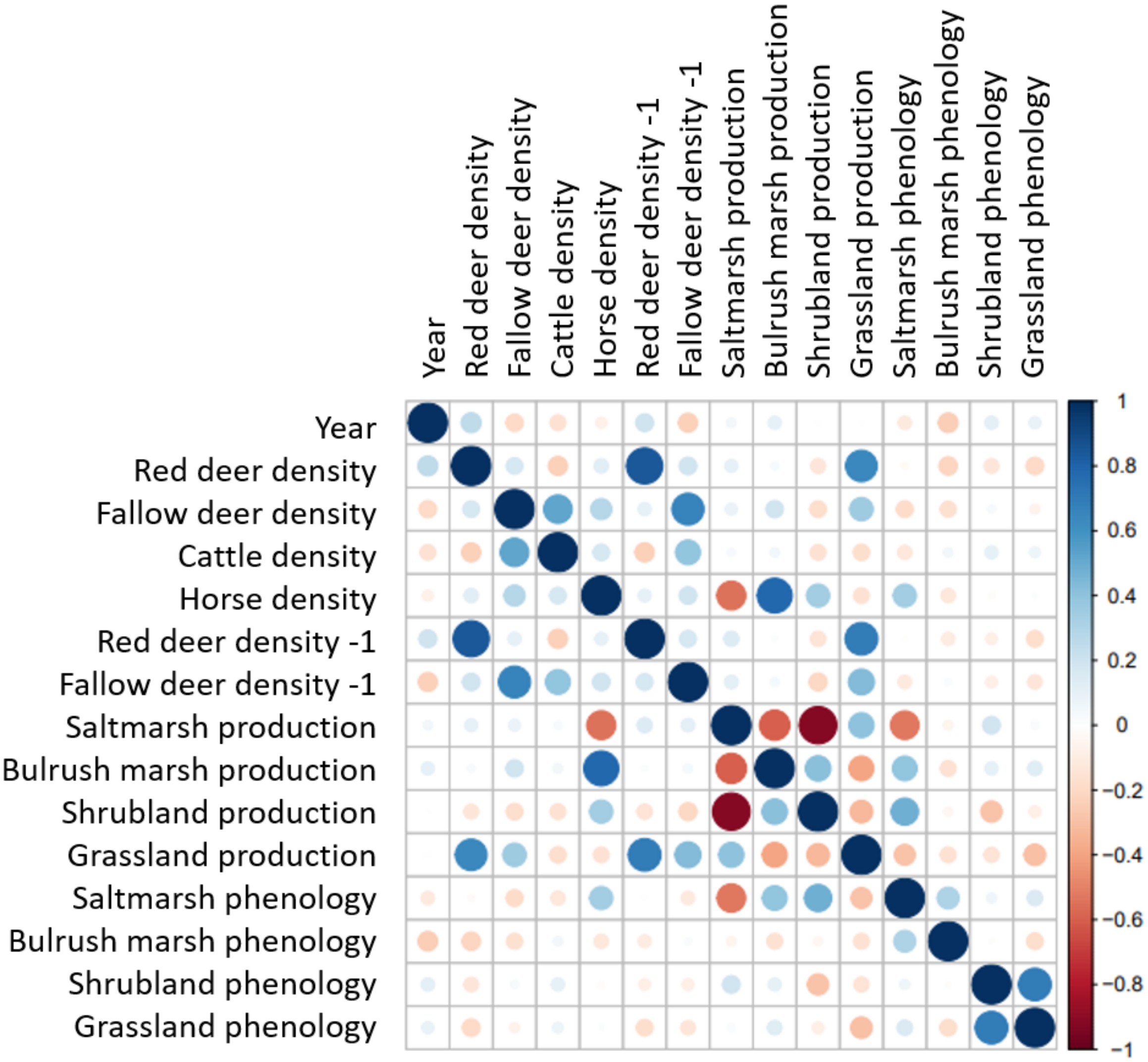

Fig. 4. Multiple correlations between all independent variables included in the models predicting the densities of red and fallow deer.

3.2. Predictor effects on ungulate density

Statistical models predicting red and fallow deer density fitted nicely the data (R^2>0.84, deviance explained >90%; Table 2) and fulfilled (or showed only slight departures from) the assumptions of residuals' normality and homoscedasticity (Fig. A5 and A6). Both models predicted adequately the temporal structure of the dependent variables – whose residuals showed no relevant signs of temporal autocorrelation (Fig. A3 and A4).

Table 3. Summary table showing approximate significance of the smooth terms for the models with red deer and fallow deer as response variables. Significant effects are highlighted in bold.

	Red deer	**Fallow deer**
Saltmarsh production	**F(2.64,4)=29.71 P<2*10^{-16}**	**F(0.983,4)= 60.81 P<2*10^{-16}**
Saltmarsh phenology	**F(3.70,4)=44.50 P<2*10^{-16}**	**F(2.93,4)= 55.97 P<2*10^{-16}**
Bullrush marsh production	**F(2.76,4)=95.86 P<2*10^{-16}**	**F(3.34,4)= 41.22 P<2*10^{-16}**
Bullrush marsh phenology	**F(3.66,4)=62.21 P<2*10^{-16}**	F(1.21*10^{-5},4)<0.01 P>0.73
Shrubland production	F(0.92,4)=1.77 P>0.776	**F(3.15,4)=58.44 P<2*10^{-16}**
Shrubland phenology	**F(3.15,4)=42.32 P<2*10^{-16}**	**F(3.70,4)=68.05 P<2*10^{-16}**
Grassland production	**F(2.91,4)=92.83 P<2*10^{-16}**	F(3.98*10^{-5},4)<0.01 P>0.45
Grassland phenology	**F(0.91,4)=10.10 P<0.0001**	**F(3.85,4)=59.17 P<2*10^{-16}**
Horse density	**F(2.73,4)=72.44 P<2*10^{-16}**	**F(3.65,4)=60.54 P<2*10^{-16}**
Cattle density	**F(2.40,4)=28.43 P<2*10^{-16}**	**F(1.96,4)=19.15 P<1.62*10^{-6}**
Fallow deer density	F(0.85,4)=1.56 P>0.069	**-**
Red deer density	-	**F(1.96,4)=12.01 P<0.00031**
Fallow deer density previous year	-	F(4.90,4)<0.97 P>0.14
Red deer density previous year	**F(3.70,4) =178.08 P<2*10^{-16}**	-
Space (management unit)	F(8.72,4)<0.01 P>0.65	F(7.32*10^{-6},4)<0.01 P>0.85
Time (year)	**F(8.01,12)=113.75 P<2*10^{-16}**	**F(5.16,12)=70.61 P<2*10^{-16}**
Adjusted R^2	0.96	0.85
Deviance explained (%)	96.8	90.6

The best model predicting red deer density showed significant effects of the phenology of all vegetation types and the production of three of them (all except shrubland; Table 3). The effect of primary production varied strongly among vegetation types (Fig. 5). Bulrush marsh showed the strongest effect, with red deer density increasing slightly at low productivity (up to 0.03 NDVI) and decreasing strongly at medium to high ones. Saltmarsh production showed an S-shaped effect, with a rapid increase in red deer density at moderately high (0.06-0.09 NDVI) production. Grassland production showed a concave downward shape, with maximum red deer densities at intermediate values (0.17 NDVI). In contrast, the effects of phenology were more consistent, with red deer density increasing with delayed phenology for the two 'highland' vegetation types (saltmarsh, within the marsh, and shrubland, within the stabilized dunes) and decreasing with delayed phenology of the two 'lowland' vegetation types (bullrush marsh, within the marsh, and grassland, within the stabilized dunes). The effects of livestock density showed a concave downward shape, with maximum red deer densities at moderately high (0.1 cattle/ha and 0.12 horses/ha) densities, preceded by a positive response to livestock density and followed by a negative response to it. In contrast, fallow deer density had a non-significant effect on red deer density. Density dependent effects (red deer density in the previous year) was highly significant, with a strong, positive effect at low densities (up to 0.10 individuals/ha) that saturated at higher densities.

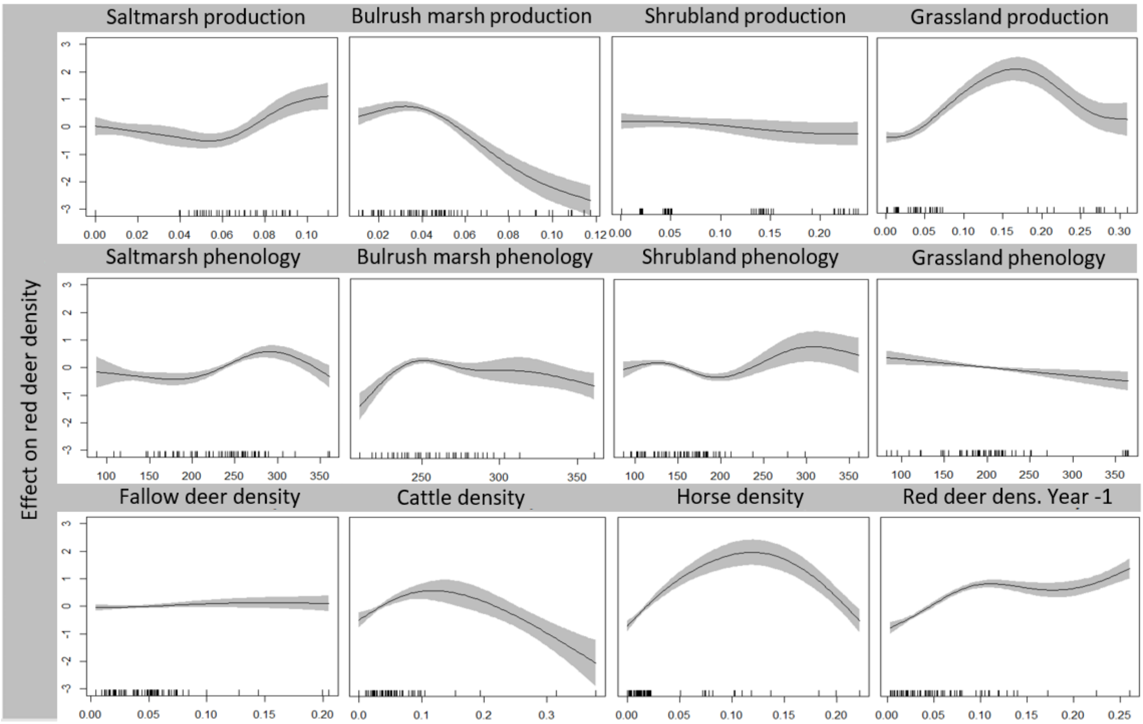

Fig. 5. Predictor effect plots describing the effect of productivity, phenology and herbivore density on red deer density. Units for the horizontal axes are: NDVI for the production plots (Upper panel), day of the hydro-meteorological year for the phenology plots (middle panel) and individuals/ha for the ungulate density plots (lower panel)

The best model predicting fallow deer density showed significant effects of the production of three vegetation types (all but the grassland) and the phenology of three vegetation types (all but the bullrush marsh; Table 3). The effect of primary production varied strongly among vegetation types (Fig. 6): fallow deer density increased linearly with saltmarsh productivity, decreased non-linearly with bullrush marsh productivity, and showed an asymmetric, concave downward shape with a maximum at moderately high (0.15 NDVI) for shrubland productivity. In contrast, the effects of phenology were more consistent, with fallow deer density showing two distinct peaks at early (day 100-150, equivalent to early December – late February) and late (day 280-300, equivalent to mid-late June) phenological peaks, and a ‘valley’ at intermediate ones (day 200-220, equivalent to early April; Fig. 4). The second peak is, however, based on 2-3 extreme values for two of the three vegetation types (saltmarsh and shrubland), so it should be considered with caution. The effects of livestock density on fallow deer showed (as for red deer) a concave downward shape, although maximum fallow deer densities were attained at higher densities of cattle (0.15 adults/ha) than horses (0.07 adults/ha). In contrast, neither the density of red deer nor density-dependence (fallow deer density in the previous year) resulted in significant effects.

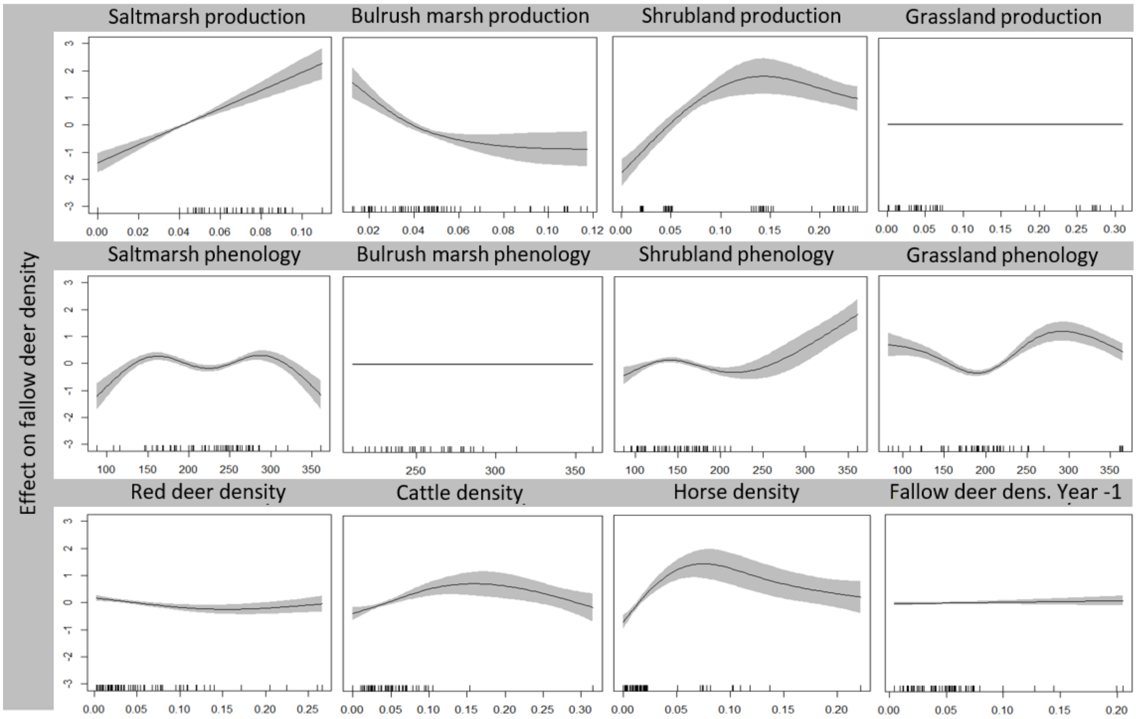

Fig. 6. Predictor effect plots describing the effect of productivity, phenology and herbivore density on fallow deer density. Units for the horizontal axes are: NDVI for the production plots (Upper panel), day of the hydro-meteorological year for the phenology plots (middle panel) and individuals/ha for the ungulate density plots (lower panel)

The potential complementary of the effects of vegetation production and phenology on wild ungulate densities can be best appreciated by calculating the estimated effects of these two variables over the different years of the data series (Fig. 7). These effects reflect the combined contribution of the vegetation's phenological and functional complementarity, described in the previous section, and the direction and strength of their relative effects on ungulate density (which may reinforce or weaken the aforementioned complementarity); and (different from Fig.3, which shows total values, averaged across all MUs), they incorporate the contribution of spatial variation in vegetation composition across MUs. For red deer, opposing changes (i.e., negative correlations) in the effect values of different vegetation types, reflecting complementary effects, take place only between the production of grassland and that of the saltmarsh (r=-0.85, P<0.0001) and bulrush marsh (r=-0.76, P<0.0015); while positive correlations, reflecting reinforcing effects, are found between the production values of saltmarsh and bulrush marsh (r=0.85; P<0.0001). For fallow deer, complementary effects occur between the production of saltmarsh and bulrush marsh (r=-0.84, P<0.0002) and between the phenology of saltmarsh and grassland (r=-0.76, P<0.0017). Access to both stabilized dunes (grassland/shrubland) and marshland is therefore a key factor in the capacity of the landscape to buffer the impact inter-annual variation on wild ungulates through vegetation complementarity; while access to both saltmarsh and bulrush marsh provides additional complementarity for one of the species, the fallow deer. Note that the very low availability of some of these vegetation types in some management units (saltmarsh in SOA and RBD, grassland in MAR; Fig.1) constrains severely these potential complementarities.

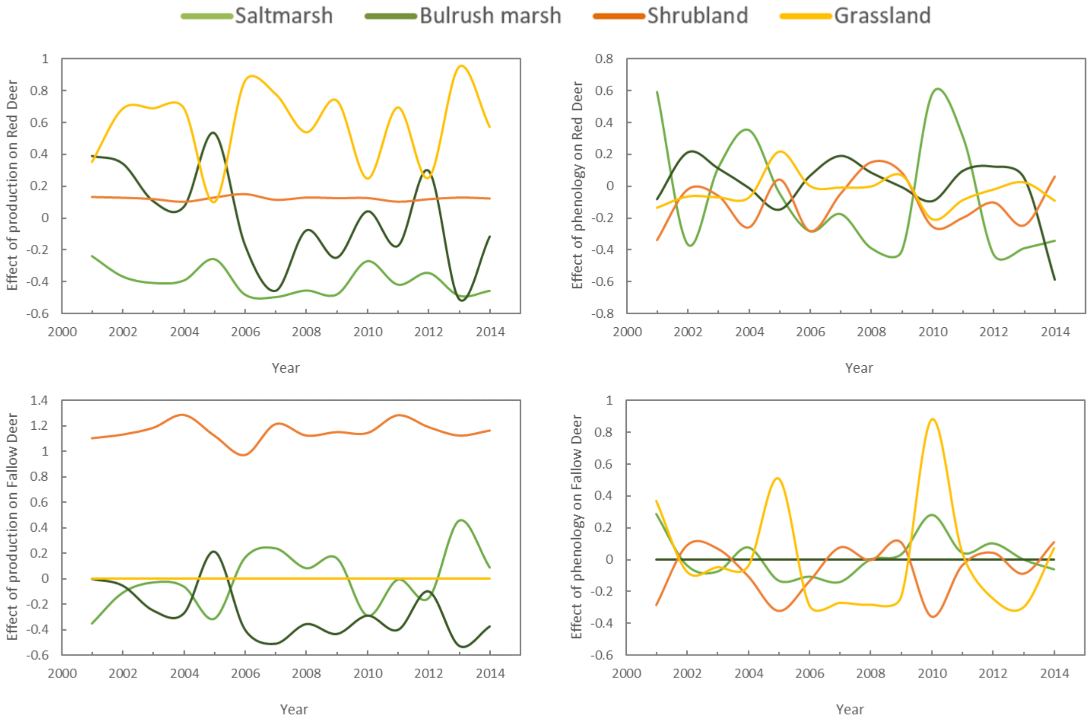

Fig. 7: Inter-annual variation in the estimated effects of the production (left panels) and phenology (right panels) of different vegetation types on red deer (upper panels) and fallow deer (lower panels) density. Lines with opposing peak patterns show complementary effects, while those with similar peak patterns show reinforcing effects. Shrubland is showed in orange, grassland in yellow, saltmarsh in light green and bulrush marsh in dark green.

3.3. Model predictions

Plots of model predictions show the combined effect of the primary production of different vegetation types and the density of domestic ungulates on the abundance of red and fallow deer. All plots show similar effects for both red and fallow deer densities, stressing the positive effects of intermediate densities of both cattle and horse. For all vegetation types except the shrubland, resilience to grazing pressure decreases with suboptimal production conditions – i.e., the range of livestock densities associated to high densities of wild ungulates becomes increasingly narrower as saltmarsh production decreases, bullrush production increases or, for red deer, grassland production becomes too high or too low.

According to these prediction plots, the optimal conditions for red deer include medium-low densities of livestock (0.05-0.20 and 0.08-0.15 individuals/ha for cattle and horse, respectively) in combination with high production of saltmarsh (>0.08 NDVI), intermediate production of grassland (0.12-0.20 NDVI) and low production of both bullrush marsh and shrubland (<0.07 NDVI). For fallow deer, optimal conditions include intermediate densities of both domestic species (0.08-025 and 0.05-0.12 individuals/ha for cattle and horse, respectively) and high production of saltmarsh (>0.09 NDVI), intermediate production of shrubland (0.10-0.19 NDVI) and low production of bullrush marsh (<0.03 NDVI).

The impact of mobility constrains on these effects are best exemplified by plotting the vegetation production values of the most extreme (driest and wettest) years of our data series (red and blue horizontal lines in Fig.4). These lines represent the mean production of each vegetation type, averaged across the five management units; hence, they also represent a scenario of full ungulate mobility across management units. These values show that inter-annual variation had a limited impact on reed and fallow deer densities under optimal livestock densities, but they have a much stronger impact, reaching minimum values at moderately high livestock densities – particularly, for the impacts of saltmarsh and bullrush marsh on both red and fallow deer.

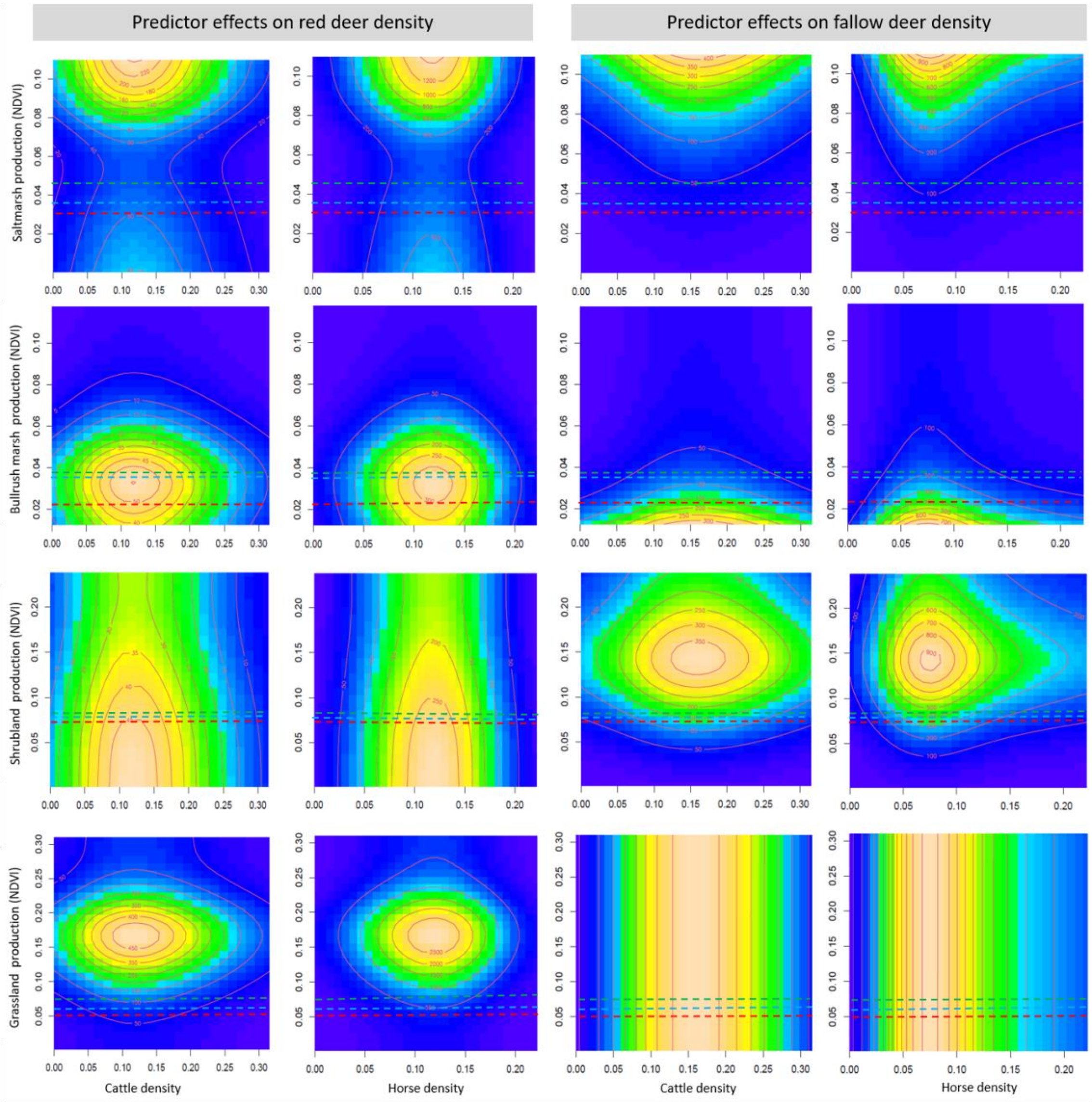

Fig. 8. Model prediction plots describing the combined effect of plant productivity (NDVI) and livestock (individuals/ha) on red deer and fallow deer density (individuals/10 km^2). Note that the color palette varies among graphs – i.e., the same color does not indicate the same range of deer density values (as indicated at the contour plots) at all graphs. Horizontal broken lines indicate mean vegetation production (averaged across the five management units) in an average year (2008; green), as well as in the driest (2005; red) and wettest (2010; blue) years of the time series (2001-2014).

4. Discussion

According to our results, complementary differences in the responses of the phenology and production of four different vegetation types to intra- and inter-annual variation in climatic conditions increase the availability and predictability of key food resources for wild ungulates (red and fallow deer), thus enhancing the resilience of their population dynamics to such variation. Furthermore, moderate livestock densities had a positive effect on wild ungulate density. However, at high livestock densities, negative effects on both vegetation production (Giralt-Rueda & Santamaría 2021) and wild ungulate densities will severely restrict the resilience of the plant-herbivore system, thus threatening ecosystem stability in the absence of compensatory management interventions.

The high levels of habitat heterogeneity observed within the study area (Doñana National Park) resulted in high functional and phenological variation in plant production. This variation resulted in seasonal complementarity of both phenological responses and productivity to inter-annual variation in rainfall, whereby the negative effects of high or low rainfall on certain vegetation types were mitigated by simultaneous, positive effects on other vegetation types.

Within years, differences in the phenological curves of the four vegetation types resulted in seasonal complementarity that, following the existing gradient from xeric to mesic vegetation types, extended the period of food availability for herbivores up to 200 days in an ‘average’ year (i.e., a year with average rainfall levels). Intra-annual complementarity was particularly strong in dry years, when the broad spread in the phenological peaks of the four vegetation types provided for an extended foraging season despite the drop in productivity of most vegetation types (all but the shrubland). In contrast, it was strongly reduced in wet years, when the delay of all phenological peaks reduced considerably food availability during winter.

Phenological complementarity within years was reinforced by the functional complementarity of different vegetation types among years. In particular, shrubland maintained the most stable production levels in both wetter and drier years, providing a key element of resilience for herbivores who can resort to browsing. Furthermore, complementary effects were particularly strong for two pairs of vegetation types (saltmarsh-shrubland and saltmarsh-bulrush marsh), indicating a key role of marshland vegetation. Overall, results from multiple correlation plots suggest that phenological complementarities may help ungulate populations to cope with intra-annual variation in plant production, while functional complementarities may increase their resilience to inter-annual variation in plant production. Taken together, these effects indicate potential management possibilities regarding the design of foraging areas and/or management units. In particular, increasing the functional heterogeneity of management units, e.g. by including a more diverse and balanced representation of vegetation types, will likely enhance the resilience of the plant-ungulate system. This is particularly important since, in our study case, several management units included fairly small proportions of key vegetation types, such as saltmarsh or grassland.

Wetland vegetation (in and around marshland, sandy lakes and ponds) provide green forage throughout the dry seasons when other areas offer only scarce, dry and usually poor-quality forage (Prins 1996; Hopcraft et al., 2010; Fynn et al., 2015; Fyn et al., 2019). Access to these forage resources by wild ungulates ensures the availability and predictability of food quantity and quality during resource-lacking periods (dry season or extreme climatic events; Prins 1996; Owen-Smith 2002; Hopcraft et al., 2010; Fynn et al., 2015; Fyn et al., 2019). Designing optimal management units will require, however, detailed knowledge of the requirements of the different herbivores (including both livestock and wild ungulates) and the ability of different vegetation types to supply these. Ungulates are known to track across the landscape and seasons the areas of high forage quantity and palatability, as well as those with higher nutrient concentration (Murray 1995; Grant and Scholes 2006; Prins and van Langevelde 2008; Fynn, 2019). High-quality forages usually appear seasonally in less productive areas where pastures are shorter and more palatable; and they contain higher concentrations of minerals that are fundamental for ungulates, mostly for pregnant and lactating females (e.g., Murray 1995; Grant and Scholes 2006; Fynn et al., 2014; Fynn et al., 2019). The concentration of specific minerals is not equally distributed across the landscape and ungulates may search for the specific areas of high nutrient concentration.

Models predicting the effects of vegetation production and phenology, as well as livestock density, represent a key contribution to such knowledge. Vegetation production had significant albeit complex, non-linear effects that varied strongly among vegetation types – including predominantly positive (saltmarsh) or negative (bulrush marsh) responses, as well as concave downward curves with a central optimum (grassland for red deer, shrubland for fallow deer). Phenology had even more complex effects, often with bimodal responses peaking at both high and low values. These results probably reflect the feeding preferences of both species of wild ungulates, with a clear preference for short, palatable vegetation (particularly saltmarsh, but also low-density grassland and tender bulrush); as well as a decrease in such preference when vegetation becomes too tall, dense and therefore unpalatable (thus the negative responses to high-density grassland and bulrush marsh).

The impact of consumption by other herbivores, such as livestock, thereupon results in a dynamic template of food resources to which wild ungulates must continuously adapt. Indeed, the impact of livestock density was similar for both deer species, which responded positively to increasing livestock density at low values of the range, but showed negative responses when livestock densities rose above intermediate values (0.1-0.15 cattle/ha and 0.05-0.15 horse/ha, respectively). Facilitation effects of large ungulate species on medium-small ones are well known, and they are generally related to increased access to higher-quality pasture in moderately grazed areas. Grazing by cattle and horse eliminate old and poor-quality vegetation, facilitating grass regrowth with higher nutritional content (Vesey-FitzGerald 1960; Fornara and du Toit 2007; Odadi et al., 2011; Fynn et al., 2019) and helping wild ungulates to improve its body condition (Gordon 1988; Odadi et al., 2011; Fynn et al., 2019). Competitive effects at high livestock densities, on the other hand, are broadly reported and generally related to resource competition, owing to depletion of plant production by livestock grazing and interference effects of both livestock individuals and the human activities associated to ranching (Schieltz & Rubenstein 2016; Gordon 2018).

Given the complexity of the effects of vegetation production and phenology on wild ungulates, further guidance can be derived from an estimation of effects of these two variables over the different years of the data series (Fig.7). These effects, which reflect the contribution of the vegetation's phenological and functional complementarity as mediated by the effect of vegetation phenology and production on ungulate density, confirmed that a balanced access to the different vegetation habitat types (inland and marshland) is a key factor in the capacity of the landscape to buffer the impact inter-annual variation on wild ungulates through vegetation complementarity. Furthermore, access to both saltmarsh and bulrush marsh provides additional complementarity for one of the species, the fallow deer. Prediction plots (Fig.8) illustrated how a virtuous combination of management measures may enhance such resilience: while a combination of moderate livestock densities and high wildlife connectivity among management units (indicated by the horizontal lines, representing the narrowed range of variation in vegetation production when averaged across such units) results in small changes in wild ungulate abundances, high livestock densities and/or landscape fragmentation in smaller management units cause strong decreases in ungulate abundances. Given that the driving force for the subdivision of Doñana's National Park area in management units is actually livestock ranching, the unavoidable conclusion is that the maintenance of inadequate, largely outdated ranching practices may represent a major constrain for the Park's management – particularly when facing the trends towards decreasing rainfall and increased frequency of extreme events already caused by climate change. These practices include other interventions that may either benefit or compromise ecosystem resilience. These include the provision of supplementary feeding during resource-limited periods (e.g. droughts or floods), which may reduce temporarily the grazing impact on vegetation but it is likely to increase grazing pressure after such periods, leading to land degradation (Perevolotsky & Seligman, 1998; Kerven et al., 2003, Kerven, 2004., Vetter 2009); re-stocking livestock populations to achieve a rapid recovery after such periods (Vetter, 2005), increasing grazing pressure before vegetation recovery; and using artificial watering points that interfere with the natural regulation of population densities and behavior (e.g., spatial foraging patterns), particularly during drought periods.

This should not be taken to mean that livestock ranching necessarily has a negative effect on wild ungulates. Positive effects of moderate livestock densities detected in our analyses suggest that, under an adequate combination of management measures, the coexistence of livestock and wild ungulates may be achieved. These measures may include several options: (1) Holding more conservative stocking rates (according to the resources of the most limiting period), at the cost of under-exploiting all the available forage during average to wet years (which will probably result in significant costs for ranchers, see e.g., Gilles, 1982, Sandford, 1983; Behnke and Scoones, 1993; Vetter, 2005). (2) Flexible management, adjusting stocking rates to early-season rainfall levels, which allows for increasing herd numbers in optimal years and ensures population survival in unfavorable ones, but may require the design and operation of alternative stocking areas (Toulmin, 1994; Vetter, 2005). (3) Optimizing the use of the spatio-temporal heterogeneity, taking advantage of its buffering effects against climatic variability (Ash et al., 2002) by enhancing the mobility of herds and facilitating their access to different forage resources, thus reducing the concentration of grazing on the same resources (Coughenour, 1991; Ellis et al., 1993; Stafford Smith, 1996; Vetter, 2005) and reducing herd mortality (Homewood and Lewis, 1987; Scoones, 1990; Oba, 2001; Vetter, 2005). Further work is needed to integrate information on the specific requirements, foraging and consumption patterns of the different herbivores into optimal management scenarios, building on the complementarities among different vegetation types identified here.

Homogenization is a common strategy in intensively managed rangelands and its use has increased during the last decades in many natural areas (Fuhlendorf et al., 2017) – or as a consequence of intensive ranging regimes, which applied over several years tends to erase spatial mosaics (Archibald et al., 2005; Hobbs et al. 2008). However, according to our results, it has important conservation implications for vegetation and wildlife. In particular, vegetation functional heterogeneity provides spatiotemporal complementarities that help buffering the negative impact of climatic variability on the vegetation-herbivore system. Our results suggest that, in our study site and comparable Mediterranean areas, it is crucial to introduce adaptive measures focused on avoiding excessive grazing - particularly during dry years and in highly sensitive areas, such as the vegetation around temporal lakes and ponds that maintain water during the summer months (whose number is increasingly reduced due to groundwater overexploitation; Munoz-Reinoso 2001).

The maintenance of high stocking rates during drought periods may threaten the stability and sustainability of the system, with important impacts on the ungulate-vegetation interactions. Besides its impact on wildlife (such as wild ungulates), the economic benefits of maintaining a strategy of high stocking rates during and after droughts are likely to be rapidly offset by the ensuing decreases in livestock production, owing to the high risk of land degradation caused by overgrazing. More importantly, it will entail even larger substantial costs in the long run, associated to the reduction in vegetation heterogeneity. In contrast, our results showed that low to moderate livestock densities are associated with positive responses in wild ungulate populations – which adds to their low impact on vegetation production (Giralt & Santamaría 2021) and heterogeneity.

The impact of stocking rates is modulated by the spatiotemporal patterns of grazing by both livestock and wild ungulates. Facilitating the access of herds to diverse forage resources and increasing their mobility, so that they can take full advantage of the vegetation's functional and phenological complementarities, may eliminate the concentration of grazing impacts on some specific areas of the landscape for long periods of time – or alleviate such impact when it is inevitable, e.g., in more fertile areas or those nearby water sources during droughts. The spatial design of ranching exploitation should also consider the susceptibility to degradation of the different landscape units, as well as their conservation value (e.g., endangered or protected flora, grazing within conservation areas). Alternatively, or complementarily, the use of flexible stocking rates (adapted to each year's rainfall levels) and ranching strategies that not only encourage the mobility of herds but guides them through the spatio-temporal mosaic to optimize its use, guided by spatially-explicit plant-herbivore models, may represent a complex yet necessary management strategy in highly sensitive areas of key conservation value – such as the DNP itself.

5. Conclusions

Production and phenological complementarities resulting from habitat heterogeneity increased the resilience of wild ungulate populations to climatic variability and grazing pressure. By combining data on plant production, phenology and census on wild and domestic ungulate populations we provide evidence that functional heterogeneity plays a pivotal role in the stability of the plant-ungulate interactions, by buffering the impact of climatic variability on wild ungulates. While low-medium livestock densities might reinforce such buffering effect, high densities may represent a potential risk for the plant-ungulate system.

The results revealed potential management strategies that may enhance the conservation of both vegetation and wild ungulates in Doñana and other, comparable areas. These include the use flexible livestock stocking rates, increasing the mobility of herds, redistributing the management units and facilitating the access of livestock to key forage resources. These measures should be complemented with vegetation management interventions aimed at maintaining or increasing habitat heterogeneity. This work contributes to deepen our understanding on the effects of functional and phenological complementarities (resulting from habitat heterogeneity) on wildlife and might help to design and implement better management strategies in Mediterranean and semiarid rangelands.

6. Appendix

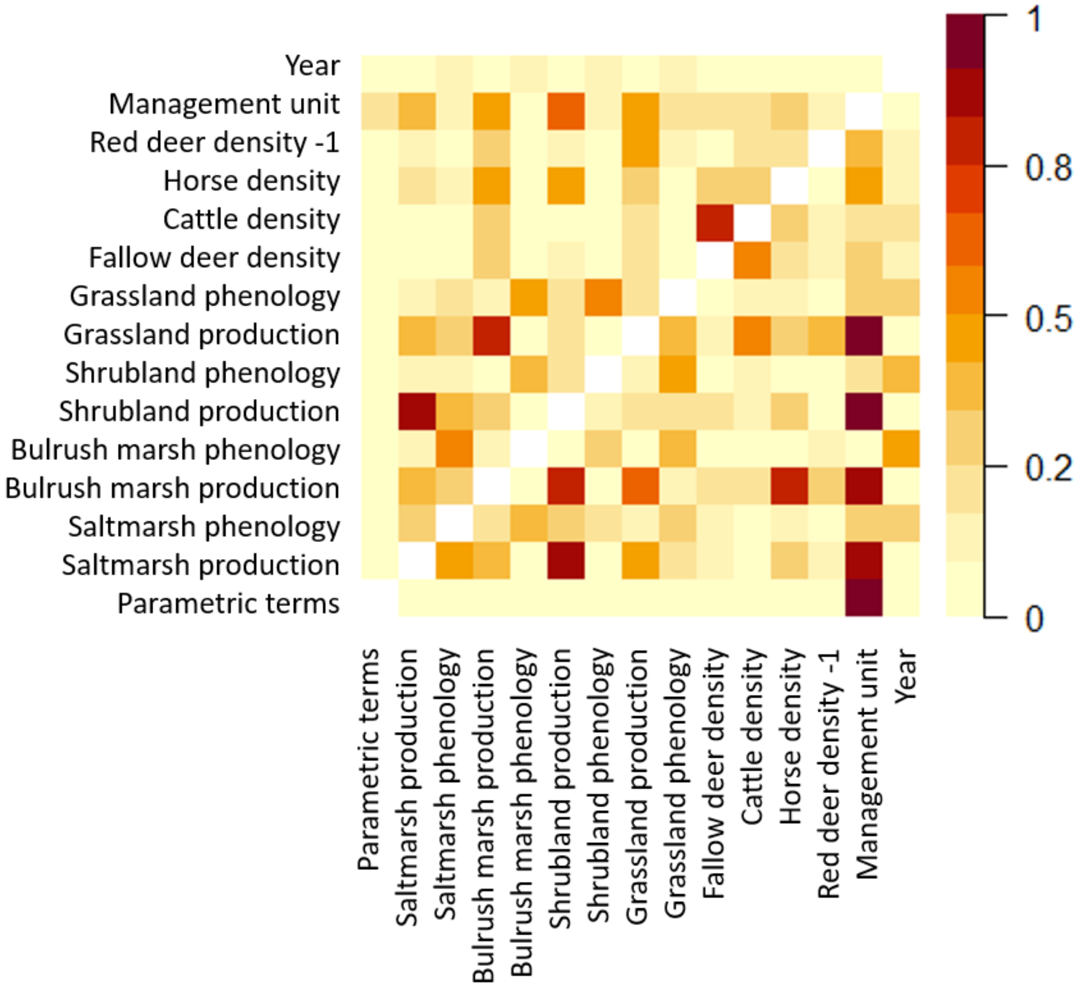

Fig. A1. Concurvity plot of the generalized additive model (HGAM) fitted to red deer density data.

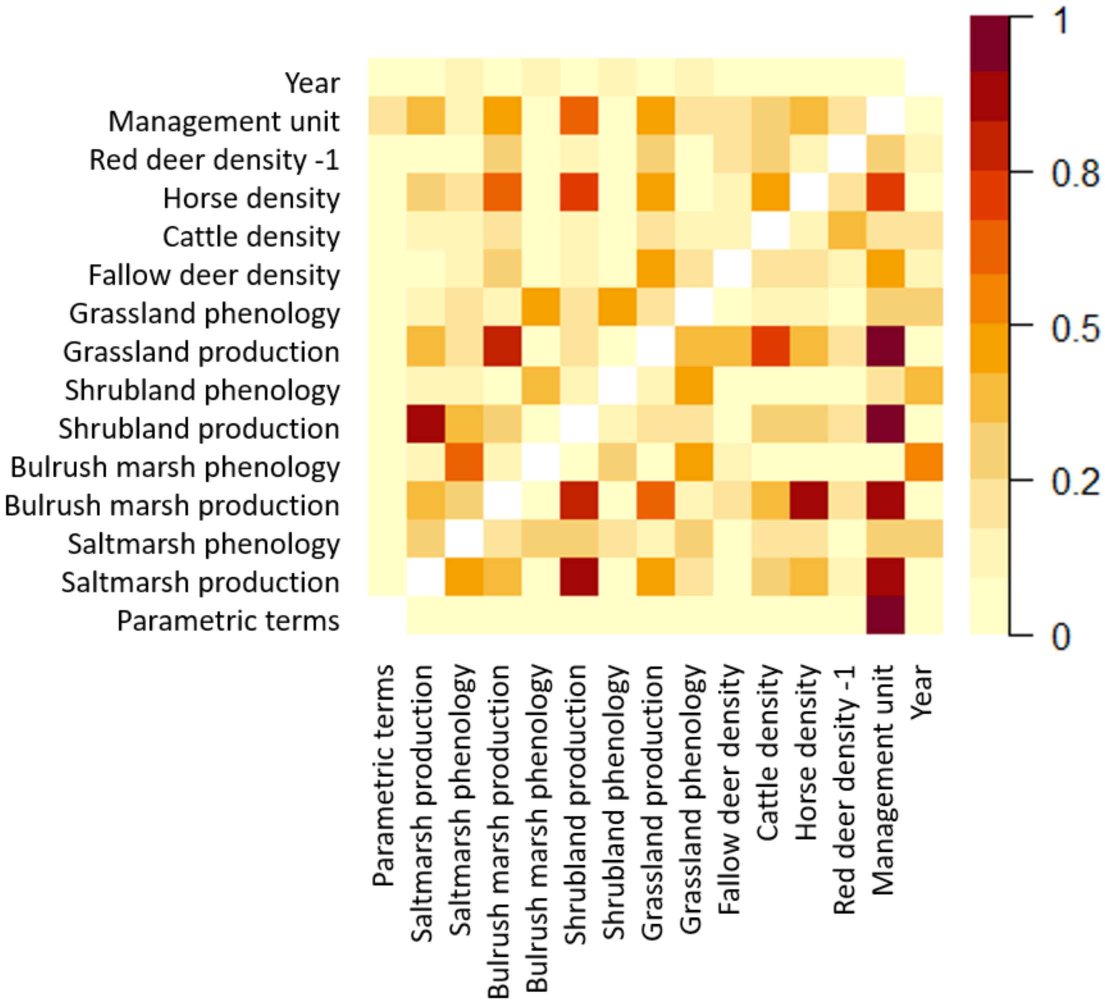

Fig. A2. Concurvity plot of the generalized additive model (HGAM) fitted to fallow deer density data.

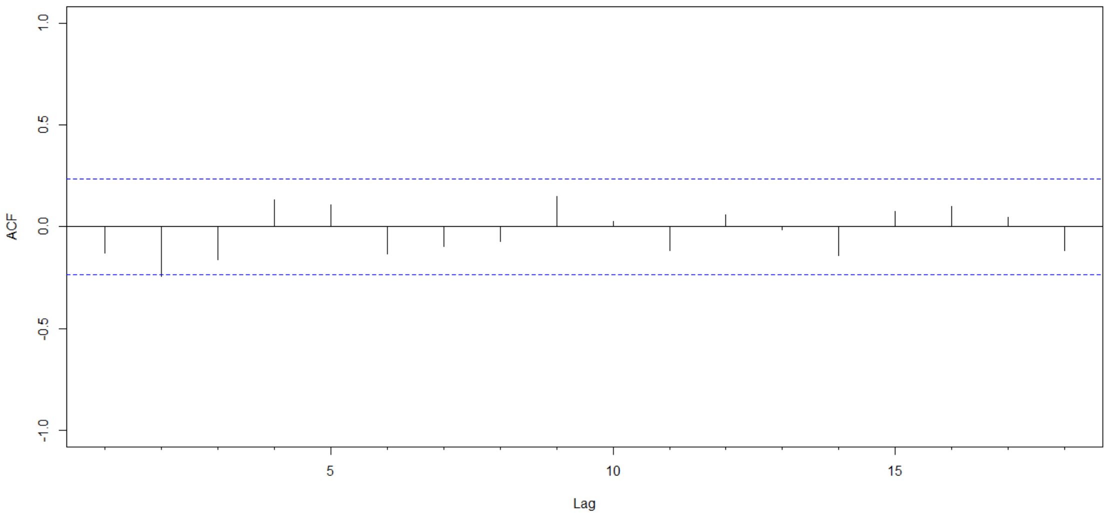

Fig. A3. Autocorrelation plot for the residuals of the generalized additive models (HGAM) fitted to red deer densities.

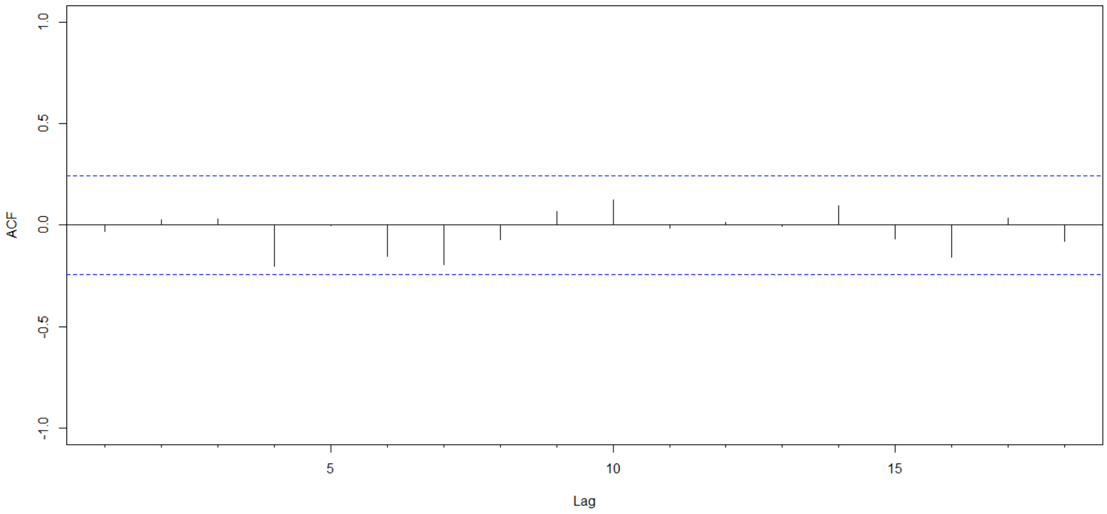

Fig. A4. Autocorrelation plot for the model for the residuals of the generalized additive models (HGAM) fitted to fallow deer densities.

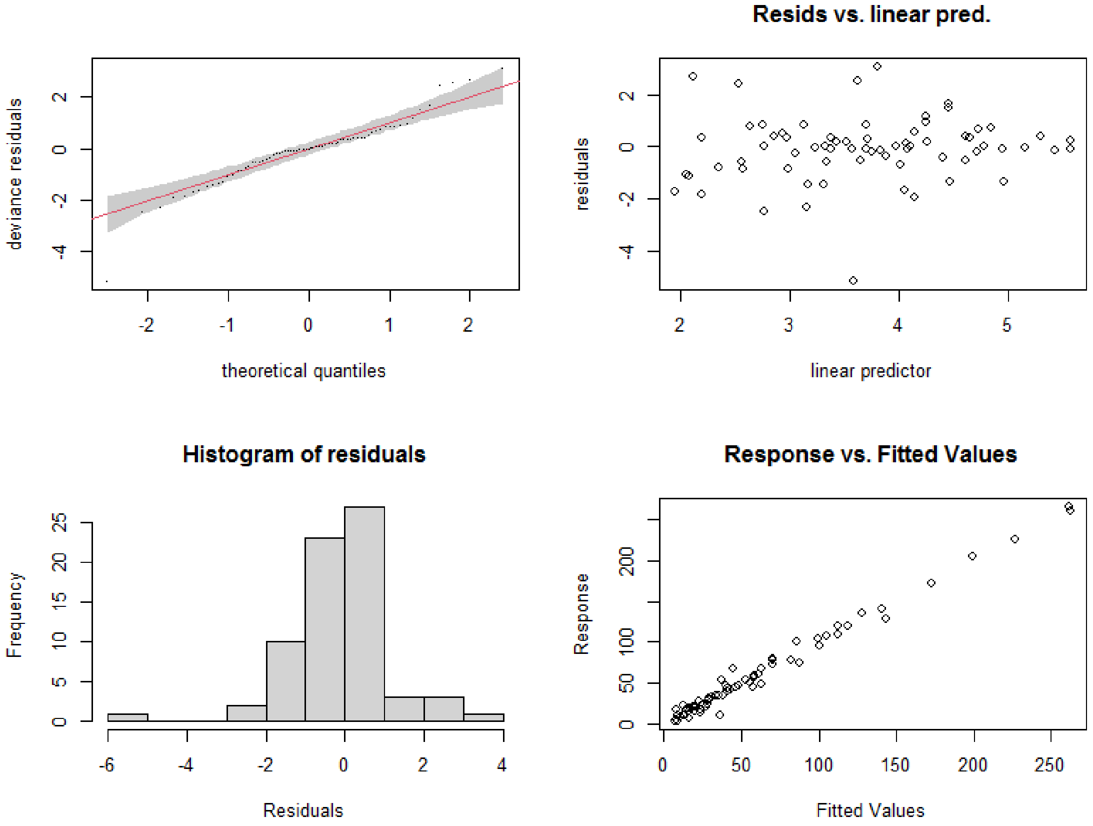

Fig. A5. Diagnostic plots of the generalized additive models (HGAM) fitted to red deer density data.

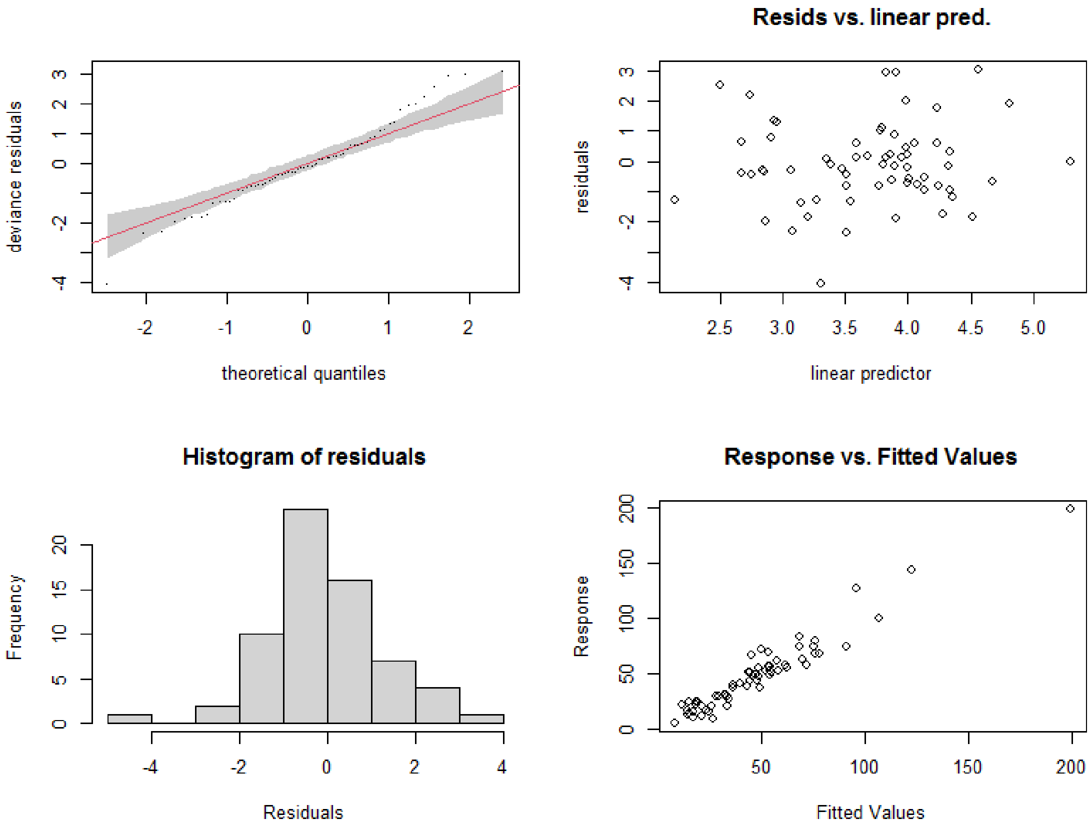

Fig. A6. Diagnostic plots of the generalized additive models (HGAM) fitted to fallow deer density data.

Chapter 3

Resource selection by domestic ungulates in heterogeneous Mediterranean landscapes

Giralt-Rueda, J.M.; Santamaria, L; Francisco Carro. Resource selection by domestic ungulates in heterogeneous Mediterranean landscapes. *In prep.*

Abstract

Understanding the influence of the environment on wildlife is a major challenge in ecology. In semi-arid and Mediterranean environments, the high variability in rainfall and habitat heterogeneity entail complex vegetation responses which both drive and interplay with herbivore populations. Ungulates are keystone elements of the ecosystems and provide multiple ecosystem services. In areas where wild ungulates coexist with livestock, the effects of herbivory and its feedback on ungulate performance is essential for management and conservation. We used information on the space use (derived from GPS location data) by two domestic ungulates (cattle and horse), satellite-derived data on vegetation production (NDVI) and composition, and distance to water sources at an iconic protected area, the Doñana National Park (SW Spain), to characterize the resource selection patterns of both species, identify their main environmental drivers and quantify their spatiotemporal variation. Our results indicate that both herbivores show strong seasonal variation in the relationship between vegetation composition, plant production and distance to water and space use. Space use increased with increasing plant production at areas with palatable vegetation types and at food-scarcer seasons, and showed the opposite pattern in food-richer seasons. Space use also decreased with increasing plant production of unpalatable vegetation types, although the type of vegetation involved varied between ungulate species. These effects were modulated by the proximity to water sources, with increasing use nearby water sources in high plant-production periods (winter and spring) and decreased use nearby water sources in low plant-production periods (summer and fall). Our results suggest that an increased connectivity and/or an improved spatial design of the MUs may allow a higher behavioral flexibility of herbivores in response to the spatiotemporal variation in resource availability, reducing grazing impacts on vegetation productivity, increasing the functional heterogeneity for the herbivore guild, and enhancing the plant-herbivore system's capacity to adjust to the impact of climatic variation and climate change.

Keywords

Functional heterogeneity, livestock, resource selection, water availability, grazing

1. Introduction

Rangelands are subjected to important natural or human-induced disturbances (MA, 2005). One of the major challenges in rangeland ecology is to understand how wild and domestic animal populations are affected by such changes and what are the consequences of such interactions (Fynn et al., 2019). That is the case of ungulate populations, whose behavior and population dynamics directly depend on the intra- and inter-annual fluctuations in primary production (Owen-Smith, 2004; Sianga & Fynn, 2021).

Habitat selection is a fundamental process in animal ecology. This behavioral process allows animals to choose the most suitable locations, i.e., those that maximize their performance (Fretwell & Lucas, 1969). Hence, understanding habitat selection is of major importance in management and conservation (Morris, 2003). Understanding how grazing pressure exerted by livestock is distributed across the landscape is essential for an effective rangeland management (Homewood, 2008; Liao, 2018a; Turner et al., 2014). In Mediterranean and semiarid environments, the strong spatiotemporal fluctuations in resource availability associated to variation in rainfall levels and phenology, together with the important levels of habitat heterogeneity, represent a continuous challenge to which herbivores must continuously adjust to cover their dietary needs (Niamir-Fuller, 1999; Liao et al., 2018). In such context, the complexity of ungulate-vegetation interactions is often oversimplified by the available theoretical models (Frank et al. 2012; Liao et al., 2018), which usually predict high concentrations of individuals and intense space use around waterbodies (resulting in piospheres; Lange, 1969) and free distributions throughout the landscape. Limited knowledge on livestock space use and resource selection, particularly when considering seasonal changes in heterogeneous landscapes, constrain current conservation and management actions (Liao et al., 2018).

The increasing degradation of extensive rangeland systems in Mediterranean and semiarid environments has received increasing scientific attention (MA, 2005). Factors such as extreme climatic events (e.g., droughts), fixed stoking rates uncoupled from forage availability, and inadequate management practices (such as reduced management areas or supplementary feeding) have been reported to cause important impacts on rangelands worldwide (Briske, 2017). These impacts might be mitigated by habitat heterogeneity, which plays an important role in ecosystems, maintaining diverse plant communities and landscapes, and buffering against climatic variability and the consequent variations in primary production (Fryxell et al., 2005; Wang et al., 2006). To capture such spatiotemporal variations in primary production over large spatial and temporal scales, researchers are resorting to using Earth Observation proxies, such as NDVI - a proxy of forage biomass and quality. The application of satellite-derived indices such NDVI in ungulate studies is increasingly robust (Pettorelli et al., 2011) and changes in NDVI have been shown to correlate with the body mass and nutritional condition (Couturier et al. 2009; Hamel et al., 2009), habitat use and movements (Sawyer & Kauffman, 2011) and population dynamics (Hurley et al., 2011; Fauchald et al., 2017) of multiple ungulate species.

Recent advances in Global Positioning Systems (GPS) and Geographical Information Systems (GIS) have increased our capacity of studying habitat selection processes, often through the application of Resource Selection Functions (RSFs). Resource selection functions are usually estimated in a use-availability design (Johnson et al., 2006), where environmental covariates (e.g., plant productivity and vegetation types) are extracted at a representation of the locations used and unused by the animals within the area which is considered as available for selection (usually each individual’s home range; Manly et al., 2002; Johnson et al., 2006) and then compared to predict the probability of selection of each location based on the values of the aforementioned covariates.

We investigated the seasonal patterns in resource selection of two free-ranging ungulates (cattle and horse) used for extensive livestock farming in the Doñana National Park (SW Spain). Using GPS-collar based location data of individual movements of both species during a complete hydrological year, we aimed at quantifying its relation to habitat heterogeneity (different vegetation types), primary production (satellite-based NDVI) and water availability (distance to water sources, which include both natural waterbodies and human-made drinking points); as well as the seasonal variation thereof. We hypothesized space use to increase with increasing plant production, particularly at food-scarcer seasons (summer and autumn) and for more palatable/nutritious vegetation types (e.g., grassland); and to decrease with increasing plant production for unpalatable vegetation types (e.g., shrubland, bulrush marsh), particularly for ruminants (cattle). We also expected these effects to be modulated by the proximity to water sources, with increasing use nearby water sources in high plant-production periods (where water availability becomes the main driver of space use) and decreased use nearby water sources in low plant-production periods (owing to overgrazing nearby such water sources). The information derived from these analyses was further use to estimate resource selection patterns across the different management units, and to derive recommendations for improved management regimes – regarding, in particular, the current trend towards decreased rainfall levels caused by climate change.

2. Methodology

2.1. Study area

The research was carried out in the Doñana National Park (DNP onwards), a protected area located on the Atlantic coast of the southwest of the Iberian Peninsula. The region is characterized by a Mediterranean climate, classified as dry sub-humid with marked seasonality. Doñana is also characterized by high landscape heterogeneity. Inland areas include bare-soil dunes interspersed with coastal vegetation; woodlands dominated by conifers (*Pinus pinea* and *Juniperus phoenicea*) and cork oaks (*Querqus suber*); extensive scrub formations structured as a mosaic of xeric ('monte blanco') and more mesic ('monte negro') scrub; as well as grasslands around temporary ponds, in topographical depressions, and at the edge of the marsh (the so-called 'vera', which forms an ecotone in which groundwater discharges maintain soil moisture throughout the year). Marshland areas include two main habitat types: saltmarsh, with shorter flooding periods, covered by halophilous scrub ('almajar') interspersed with halophilous grass meadows (Table 1); and bulrush marsh, flooded for longer periods, hosting seasonal meadows of tall sedges (Fam. Cyperaceae). These habitats host three species of wild ungulates, red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*), which coexist with three species of livestock (cattle, horse and sheep).

Livestock management is organized in different Management Units (MU hereafter) that generally follow the limits of the different (state-owned, communal and private) properties (Fig.1). Management units are delimited by livestock-proof fences, limiting the movement of domestic ungulates but being relatively permeable for wild ungulates. For this study, we used location data from livestock collared at four management units ('study area' hereafter; see Fig.1 and Section 2.3.). Accounting for all herbivorous ungulates, the total density on the whole National Park is 18.73 individuals/km^2 (10.15 and 8.58 individuals/km^2 for cervids and domestic livestock respectively), although the density of the different species varies largely among MU (Fig.1).

2.2. Environmental covariates

2.2.1. Delimitation of vegetation types

For the study were considered four main classes of vegetation, chosen because they represent in an understandable and approachable way the variability of vegetation of the study area. These classes are: saltmarsh, bulrush marsh, shrubland and grassland. We also used a fifth class, ‘other’, representing the small portions of bare soils, dunes, forest stands, and mixed vegetation cover present in the study area. The main vegetation types grouped in each class and their main characteristics are shown in Table 1.

Table 1. Vegetation classes, name of their variables in the model and description of the main vegetation types merged within each vegetation class.

Vegetation type	Description
Saltmarsh	Halophilous scrub (‘almajar’) on floodplain/marine brackish mudflats, dominated by glaucous glasswort (*Arthrocnemun macrostachium*) and shrubby sea-blite (*Suaeda vera*), interspersed with halophilous grass meadows.
Bullrush marsh	Seasonal meadows of tall sedges (Fam. Cyperaceae) on floodplain/brackish marshes. Dominant species are saltmarsh bullrush (*Bolboschoenus maritimus*), Blysmus bullrush (*Schoenoplectus litoralis*) and somerset rush (*Juncus subulatus*), which may be dominant or co-dominant.
Shrubland	Shrub formations on stabilized dunes, sometimes interspersed with sandy grasslands. These formations include a mosaic of two main types, respectively occupating more xeric and mesic sites: dry scrubland (‘monte blanco), dominated by Halimium *halimifolium, Cistus salvifolius, C. libanotis*, *Rosmarinus officinalis,* and *Lavandula stoechas*; and wet shrubland (‘monte negro’), dominated by heather (*Erica scoparia*, *E. umbellata*, *E. ciliaris*, *Calluna vulgaris*)*, Rubus ulmifolius, Ulex minor* and *Ulex australis*.
Grassland	Grassland formations with great variability in their extent as well as in their specific composition.

	Wet pasture formations usually spatially associated with lagoons and in the ecotone that form the marsh and inland areas, usually called "la vera". Dominated by the association of *Galiopalustris* sp. with *Juncus maritimus.*
Other	Bare soils, dunes, water bodies, forest stands and mixed vegetation cover (when any of the previous vegetation types did not cover at least 75% of the pixel)

To define the different vegetation types and to group them into the corresponding classes, vegetation maps offered by the Long-Term Monitoring Program of Doñana's Singular Scientific-Technical Facility (ICTS-RBD) (ESPN, 2021) were used. To avoid erroneous measurements due to mixed signals from heterogeneous land features, all pixels partially or totally covered by dunes, bared soils, water or trees were grouped into a miscellaneous class called "other". Therefore, all other vegetation classes represented "pure" vegetation types (i.e., pixels where the nominal class represented >75% of the area). For each management unit considered in the study, each vegetation type was extracted and grouped into the five main classes (Figure 1). Subsequently the vector layer of vegetation cover was transformed into a raster layer with a spatial resolution of 250 * 250 m in order to match the resolution of NDVI images (see below). To this end, the vegetation type in the vector layer with the largest area within the pixel yielded the attribute to assign to the pixel. These tasks were performed with the ArcGIS 10.1 software.

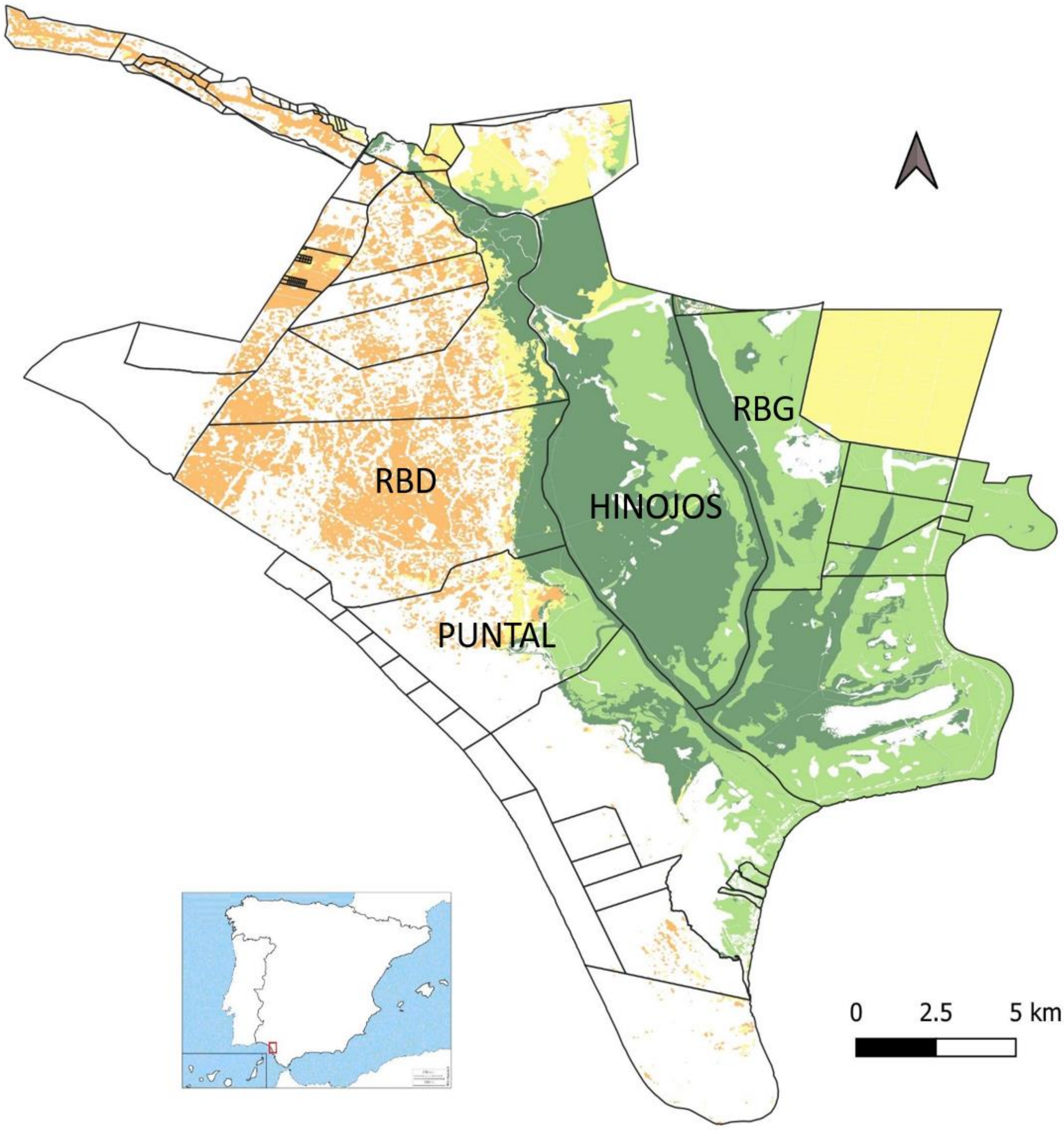

Figure 1. Map of the vegetation classes in the National Park of Doñana. shrubland is showed in orange, grassland in yellow, saltmarsh in light green and bulrush marsh in dark green.

2.2.2. Primary production

Satellite information obtained from the Institute of Surveying, Remote Sensing and Land Information (IVFL) of the University of Natural Resources and Applied Life Sciences (BOKU), Vienna, was used to estimate the productivity of different vegetation classes during the study period. This institution offers remote sensing products from MODIS satellite images with different temporal resolution. Information on the processes for creating such time series can be found in https://boku.ac.at/rali/geomatics.

For this study we used the Normalized Difference Vegetation Index (NDVI), a commonly used vegetation index that serves as a proxy of real biomass production of the vegetation. We used long-term series of NDVI values with the highest temporal resolution available (every 7 days) for the period from September 1st of 2018 to August 31st of 2019. Using all available images for every season, we calculated average NDVI values per season at every (250*250 m) pixel of the study area using the "cell statistics" tool in ArcGIS 10.1. This resulted in four different raster layers reflecting the NDVI values of all pixels of each vegetation type and for each season.

2.2.3. Distance to waterbodies

The layer representing 'distance to the closets water source' (hereafter, 'distance to water') was obtained by merging two different layers, respectively representing 'flooded areas' and 'artificial water points'. Flooding data were obtained from the Long-Term Monitoring Program of Doñana's Singular Scientific-Technical Facility (ICTS-RBD), which provides raster images created by using Landsat images at 30m spatial resolution (ESPN, 2021). The location of artificial water points was provided by the National Park Office. To combine these two data sources, we first searched for the available flooding layers for the different seasons and we selected the images whose date of capture was the closest to each mid-season date, resulting in four different layers reflecting the flooded areas during each season. These four raster images were transformed into vector layers and each of this layer was merged with a separate layer representing the artificial water points. Finally, we used these four vector layers to create four different raster layers (one per season) representing the Euclidean distance to waterbodies using the "Euclidean distance" tool in ArcGIS 10.1. These four layers representing 'distance to water sources' were resampled to a 250m spatial resolution using the "resample" tool (bilinear method) available in ArcGIS 10.1.

2.3. Location data

This study was restricted to domestic ungulates, since they allowed for the relatively large sample size required (at least 8 individuals within each of the 4 management units). Sheep were excluded they study, since they are only present in one of the MU and occupy a relatively small area within it. Collaring of wild ungulates was attempted but we did not reach a sufficient number of animals to allow for the kind of analyses presented here.

A total of 38 horses and 49 cows were tagged during summer (between June and September depending on the management unit) in 2018 using global positioning systems (GPS) collars (Digitanimal, Madrid, Spain: 265 g). These GPS devices used the Sigfox LPWAN and were configured to send its location every half hour, although part of the locations was lost due to limited reception – e.g., when animal stayed in dense vegetation or behind topographical barriers. For the study, we used data collected during the hydrological year 2018/2019 (from September 1st 2018 to 31st August 2019). We split the dataset into four different seasonal periods (three months each) which, combined with the two species, resulted into eight different datasets (separately, cattle and horse locations during fall, winter, spring and summer). The number of individuals of each species varied slightly among seasons (Table 2), since new animals were being collared during the study period and some of the GPS devices loss their battery power before the end of the hydrological year.

Table 2. Surface area of every management unit and number of individuals of both species collared with GPS devices in each management unit in different seasons.

MU	**Area (ha)**	**Fall**		**Winter**		**Spring**		**Summer**	
		Cows	**Horses**	**Cows**	**Horses**	**Cows**	**Horses**	**Cows**	**Horses**
RBD	6138	7	1	8	9	8	7	6	7
PUN	3217	9	0	8	0	9	0	7	0
RBG	3281	7	9	6	9	1	7	0	0
MAH	7944	12	16	10	15	8	12	3	12

For each individual and season, we used all locations to calculate the individual home range using the local convex hull method. We chose this method because it has been demonstrated to be more accurate than kernel density estimations for mammalian herbivores (Chirima & Owen-Smith, 2016). We used the function “hr-locoh”, available in R’s “amt” package (Signer, Fieberg & Avgar, 2019). In order to reduce potential autocorrelation, we subsampled the total number of available locations to keep a final sample of 500 points per kernel (i.e., per individual and season). Individuals with less than 500 locations within a season were excluded for the analysis for that specific season.

We then generated 5000 random points within each individual home range, and used both the random and the observed locations to extract the environmental variables (see table 1). With these values, we generated a new dataset containing, for each individual of the two species and for each of the four seasons, a total of 5500 locations (5000 ‘unused’, randomly selected locations and 500 ‘used’, observed in the GPS data, ones) and the corresponding values of environmental covariates from each location.

2.4. Statistical analyses

First, we evaluated the datasets for potential collinearity among predictor variables. For this purpose, we computed the correlation matrix between all predictor variables using the function “cor” from R package “stats” (R Core Team, 2013) and then plotted the results using the “corrplot” function available in R “corrplot” package. Final datasets were used to fit generalized mixed effects models (GLMM) using the binomial family (logit link) of the “mixed_model” function available in R “GLMMadaptive” package (Rizopoulos, 2022). The binomial variable “Used” (a qualitative variable coding whether each location was used or unused) was included as response variable. The fixed factors vegetation type and management unit, the continuous variables plant production (NDVI) and distance to water, and the random factor individual were included as predictors. The model also considered the first- and second-order interactions between plant production, vegetation type and season; as well as the first-order interaction between plant production and distance to water.

Since one of the assumptions of mixed models is the normal distribution of random intercepts, we tested it by plotting random intercepts (Figures A1 and A2) using the function “ranef” and “dotplot” available in R “lme4” and “lattice” packages, respectively (Bates et al., 2015; Sarkar, 2008). We also computed the Shapito-Wilk Normality Test to confirm the plot results (Table A1). We then tested the significance of each predictor variable using the function “joint-test” available in R “emmeans” package (Lenth, 2019). Finally, beta estimates resulting from the models were inserted into resource selection function equations:

$$w(x) = \exp(\beta_0 + \beta 1 X_1 + \cdots + \beta_i X_i) \qquad [1]$$

where $w(x)$ is the relative probability of a pixel being selected, β_0 is the intercept, and β_i (with I = 1 to n) is the estimated coefficient for variable X_i. $\beta_i>1$ indicates a preference for that specific habitat or resource, while $\beta_i<1$ indicates avoidance thereof.

We validated the accuracy of our models using the k-fold cross validation approach proposed by Boyce et al. (2002). The procedure involves calculating the correlation between RSF ranks and area-adjusted frequencies for a withheld sub-sample of data, using a k-fold partitioning of the original samples. Hence, for each of the two species, we divided the dataset using a quantile classification that splits the dataset into five groups that contain the same number of values; and evaluated the correlation between ranks and frequencies using the Spearman-rank correlation test using the function cor.test in the R package “stats” (R Core Team 2013), (Table A12 and Figures A3 and A4).

To evaluate the relative effect of (i) the primary production of each different vegetation type and (ii) the distance to water, on the resource selection by cattle and horse at each of the four different seasons, we plotted the effects of these predictors using the function “predictorEffect” available in R “effects” package (Fox & Weisberg, 2019). For each individual slope (i.e., at every level of the covariates’ interactions with categorical factors vegetation type and season), we tested their significance (i.e., whether there are significantly different from zero) (Tables A4 to A11) using the function “emmtrends” available in R “emmeans” package (Lenth, 2019).

We also used the coefficients fitted by the resource selection models to create maps displaying the relative probability of selection by, respectively, cattle and horse. Maps were created using ArcGIS 10.1 Raster Calculator (ArcGIS, 2011). Following Boyce et al.’s (2002) and Morris et al.’s (2016) recommendation that the mapping procedure should be aligned with the method used to test the model, we classified the continuous range of relative probability values in the maps into 5 quantiles, in accordance with the 5-fold cross validation method used previously.

3. Results

Results of the generalized mixed models showed significant effects of all model terms and their interactions for both cattle and horse (Table 3) except for plant production (NDVI), which was only marginally significant (P<0.10) in the horse model – albeit all its interactions were significant. The model including the mixed factor ‘management unit’ did not converge for horse; hence, we excluded this term from the model.

Table 3. Significance of effects of all the terms included in two models predicting, respectively, resource use by cattle and horse. N.I.: Factor not included in the model, owing to lack of convergence of the model including it.

			Cattle		Horse	
Model term	df1	df2	F.ratio	P	F.ratio	P
Plant production	1	Inf	12.298	0.0005	2.904	0.0884
Vegetation type	4	Inf	25.403	<.0001	4.724	0.0008
Season	3	Inf	3.568	0.0134	5.030	0.0017
Distance to water	1	Inf	35.919	<.0001	8.986	0.0027
Management Unit	3	Inf	7.213	0.0001	N.I.	N.I.

Plant.production:Veg.type	4	Inf	25.403	<.0001	5.593	0.0002
Plant.production:Season	3	Inf	3.568	0.0134	5.741	0.0006
Veg.type:Season	12	Inf	10.869	<.0001	4.761	<.0001
Season:Distance	3	Inf	20.213	<.0001	35.112	<.0001
Plant.production:Veg.type:Season	12	Inf	10.869	<.0001	6.609	<.0001

In both models, the effect of plant production (NDVI) varied significantly among vegetation types and seasons; and the effect of distance to water varied significantly among seasons (Table 3, Figs.2 and 3). Cattle tended to select areas with low plant production in bulrush marsh (with the strongest effect in summer), shrubland (strongest effect in fall) and saltmarsh (only in fall). In grassland, they selected areas of high plant production in summer and fall, and areas of low plant production in winter (Fig.2).

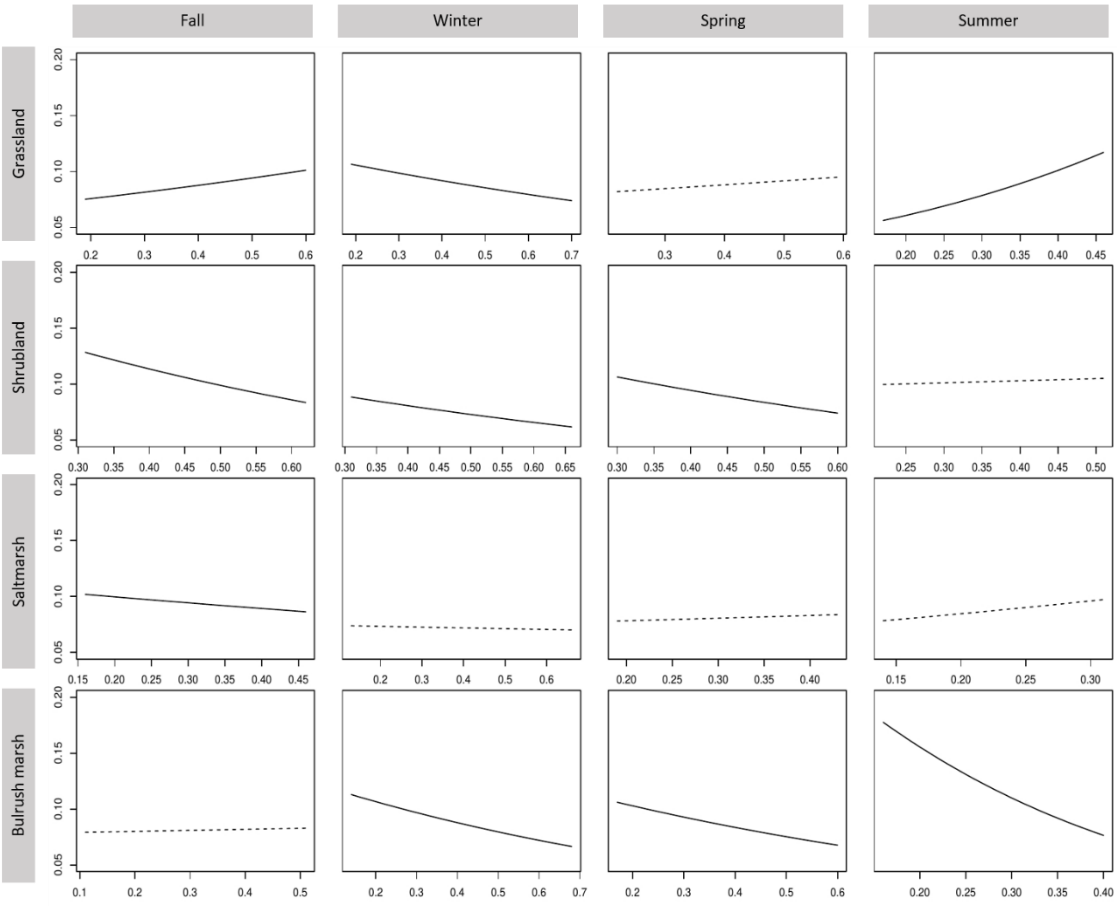

Figure 2. Effect of plant production (NDVI) on selection probabilities by cattle at different vegetation types (rows) and seasons (columns). Continuous line indicates significant relationships, dashed lines non-significant ones. Note that, both within rows and within columns, different panels have different X-axis value ranges.

In contrast, horses tended to select areas with high plant production in grassland (only in fall) and bulrush marsh (weak effects, strongest in fall). They also selected areas of low plant production in shrubland (strongest effect in summer). In saltmarsh, the effects were weaker and more variable, with two significant associations with plant production: positive in spring and negative in fall (Fig.3).

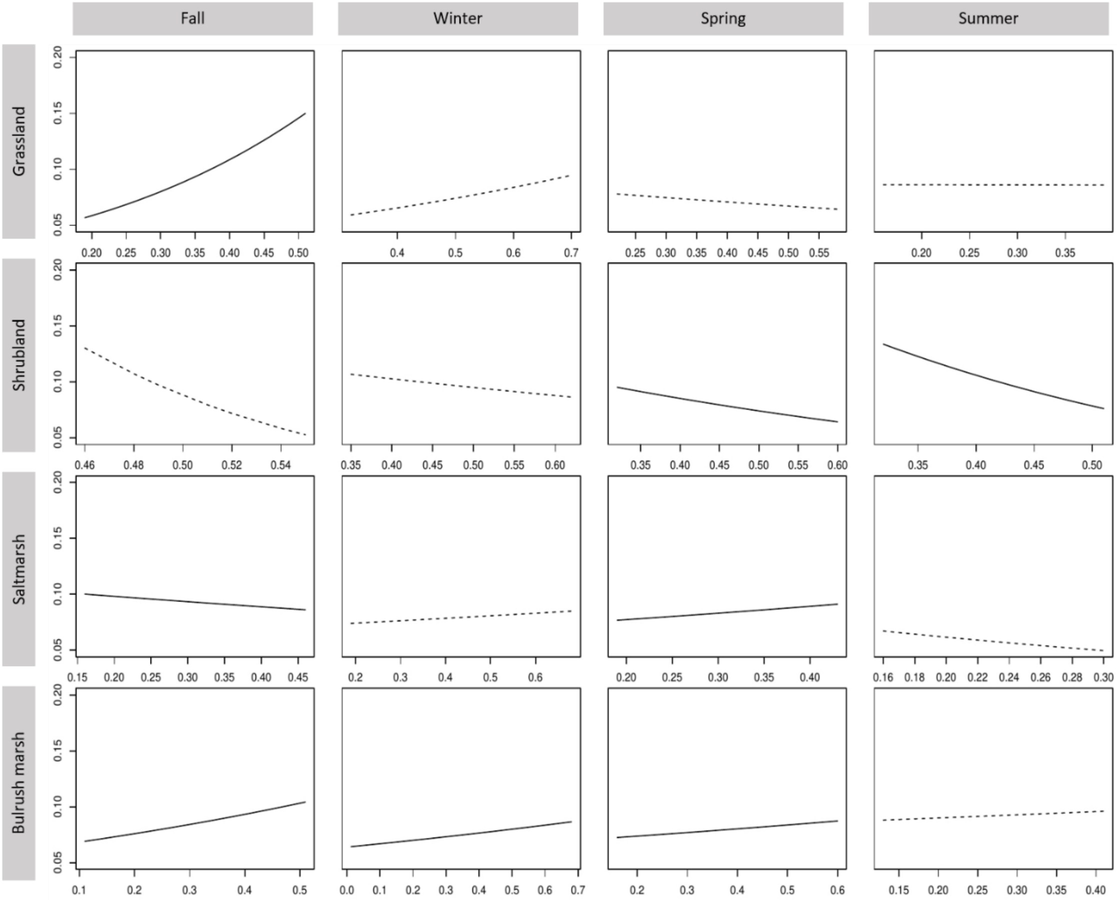

Figure 3. Effect of plant production (NDVI) on selection probabilities by cattle at different vegetation types (rows) and seasons (columns). Continuous lines indicate significant relationships, dashed lines non-significant ones. X-axis: plant production (NDVI). Y-axis: probability of selection (dimensionless, from 0 to 1). Note that, both within rows and within columns, different panels have different X-axis value ranges.

Distance to water showed significant effects for both species and in all seasons. Cattle selected areas closer to water sources in all seasons except fall, when they selected areas away from waterbodies. Note that the range of distances increased from winter (up to 1100 m) to spring (up to 2000 m) to summer (up to 8000 m) and decreased again during fall (up to 4000 m). Horses selected areas near water sources during the flooding seasons (moderately in winter, strongly in spring) and avoided such areas in the dry seasons (strongly in summer and moderately in fall). As before for cattle, the range of distances increased from winter (up to 900 m) to spring (up to 2700 m) to summer (up to 7000 m) and decreased again during fall (up to 4000 m).

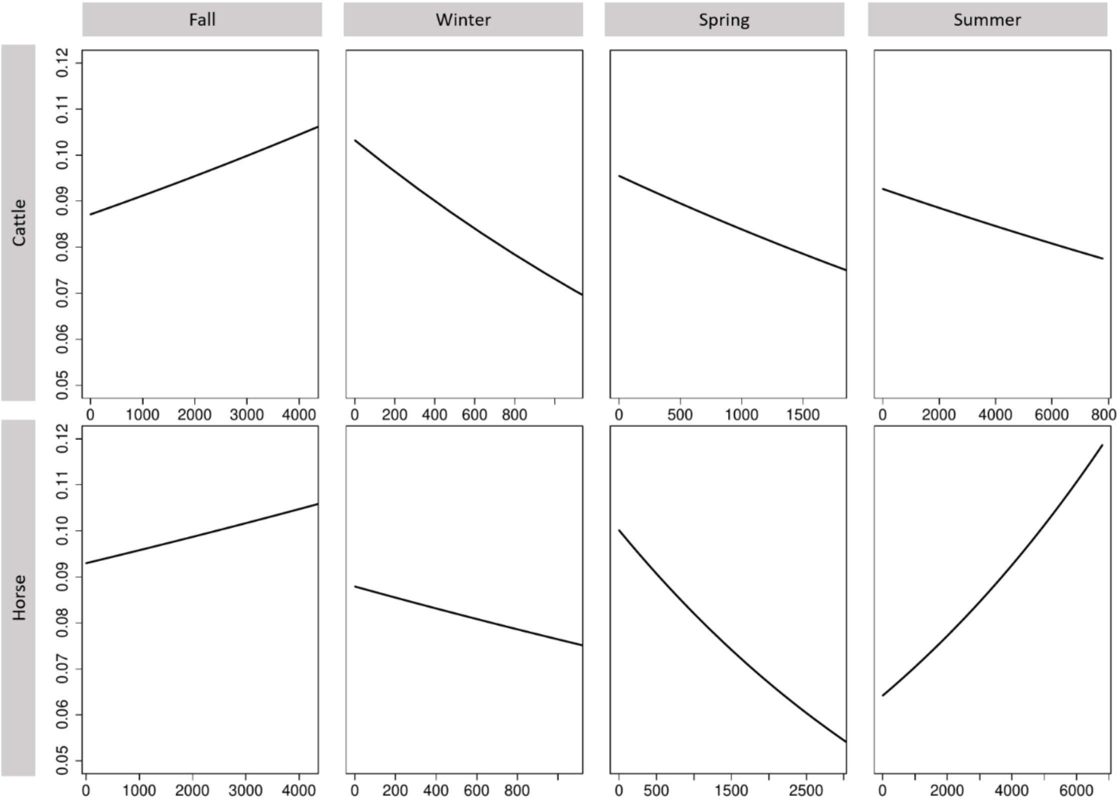

Figure 4. Effect of distance to water sources (X axis, in meters) on selection probabilities by cattle (upper row) and horse (lower row) at different seasons (columns). Continuous lines indicate significant relationships, dashed lines non-significant ones. Y-axis: probability of selection (dimensionless, from 0 to 1). Note that, both within rows and within columns, different panels have different value ranges.

To map resources selected by livestock in the different management units, we projected the top five bins of relative preference of selection onto the study area. Maps for both species show a strong seasonal variation in landscape use, with contrasting patterns between the two main types of management units: those of only almost exclusively marshland (Hinojos and RBG) and those including comparable areas of sandy mainland and marshland (Puntal and RBD). In the first group (only marshland), both herbivores tended to select the topographically higher areas with palatable saltmarsh pastures in autumn and winter; while during spring they started to avoid these areas and, in summer, they show contrasting preferences: cattle tend to select the lowland areas of bulrush marsh and horse return to the saltmarsh areas. In the second group (mainland-marshland mixture), the most striking pattern is the preference for shrubland in summer and its avoidance in autumn, for both herbivores; while, in winter and spring, they show a fine mosaic of preference that is likely related to the local productivity of the shrubland, grassland and saltmarsh vegetation – although horses seem to maintain a higher preference for shrubland throughout these two seasons.

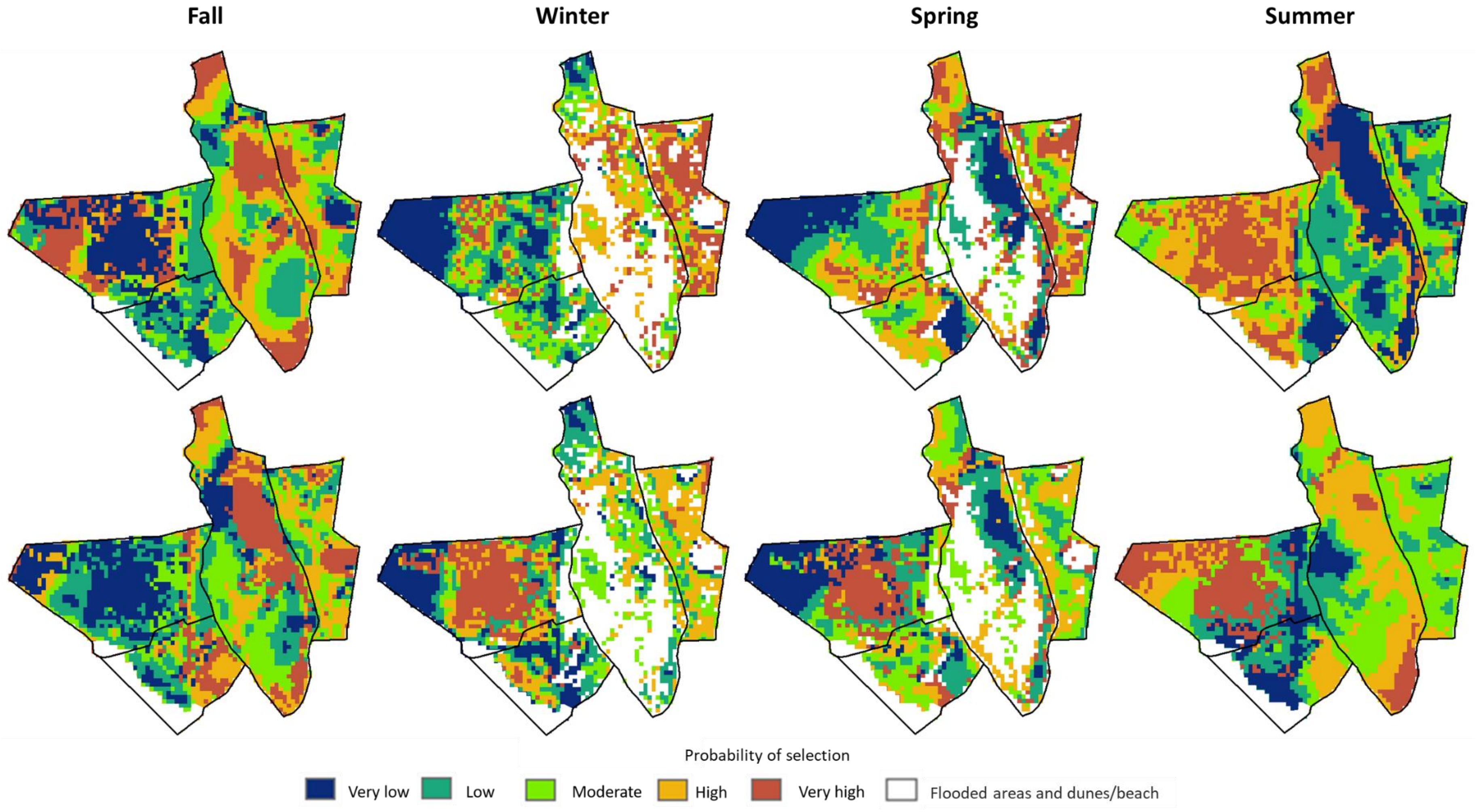

Figure 5. Predicted relative probability of resource selection by cattle (upper row) and horse (lower row) at the four seasons (columns), in four management units of the Doñana national Park (SW Spain). The 5 equal area bins are depicted. White pixels represent dunes/beach and flooded areas, where no prediction was made (buy extremely rare use is expected).

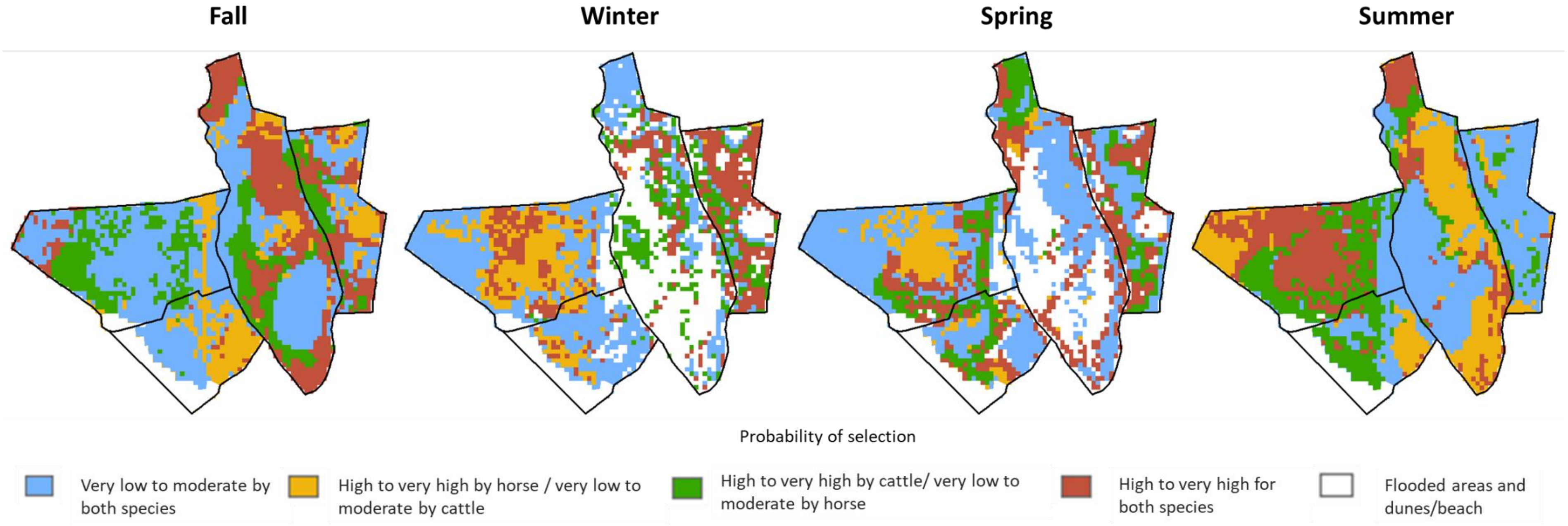

Figure 6. Overlap between the relative probability of resource selection by cattle and horse, at the four seasons (columns), in four management units of the Doñana national Park (SW Spain). White pixels represent dunes/beach and flooded areas, where no prediction was made (buy extremely rare use is expected).

Patterns of shared and complementary resource use can be visualized in Figure 6. On the one hand, areas selected by both species (in red) represent important landscape elements hosting resources of key importance for them (e.g., highly palatable pastures of the eastern marshland of Hinojos and RBG during fall and winter, central areas of shrubland at RBD during summer). Inter-specific competition is likely to be highest at these areas, whenever resources become scarcer (e.g., in dry seasons or years). On the other hand, areas in green and yellow are strongly selected by one species and avoided by the other. Hence, they provide landscape complementarity and reduced inter-specific competition. The clearest example is the dissociation of selection preferences between horse and cattle at the marshland areas of Hinojos (and, to a lower extent, RBG) during summer – with horse sticking to the topographically higher saltmarsh areas (which are intensively used in the previous seasons) and cattle selecting the lower areas of bulrush marsh.

To explore further how the patterns shown in these maps relate to the distribution of the different vegetation types and the subdivision of the area in management units, we calculated the proportion of pixels assigned to each of the 5 different equal area bins within each vegetation type (all MUs pooled; Fig.7) and within each MU (all vegetation types pooled; Fig.8). Note that these patterns depend on the specific production of each vegetation type at each MU and season. As described for the maps, selection of different vegetation types (Fig.7) show contrasting strong seasonal patterns for both ungulate species. Cattle selects strongly a large proportion of areas of saltmarsh in fall and spring; and, as this preference decreases in summer and autumn, selection of grassland and bulrush marsh peaks in summer, and selection of shrubland peaks in winter. Horse shows a similar preference for saltmarsh and grassland in fall; and a weaker preference for these two vegetation types, accompanied by a strong preference for shrubland, in winter, spring and autumn. Predicted selection for grassland differs from other vegetation types, because it tends to have either very-high or very-low scores in most seasons, particularly in winter and summer (when rainfall is lowest). As a consequence, overlap of predicted resource selection by both species is maximal for saltmarsh in fall, and decreases progressively until summer (when it is minimal); while it shows the opposite pattern in shrubland, and peaks in spring for bulrush marsh.

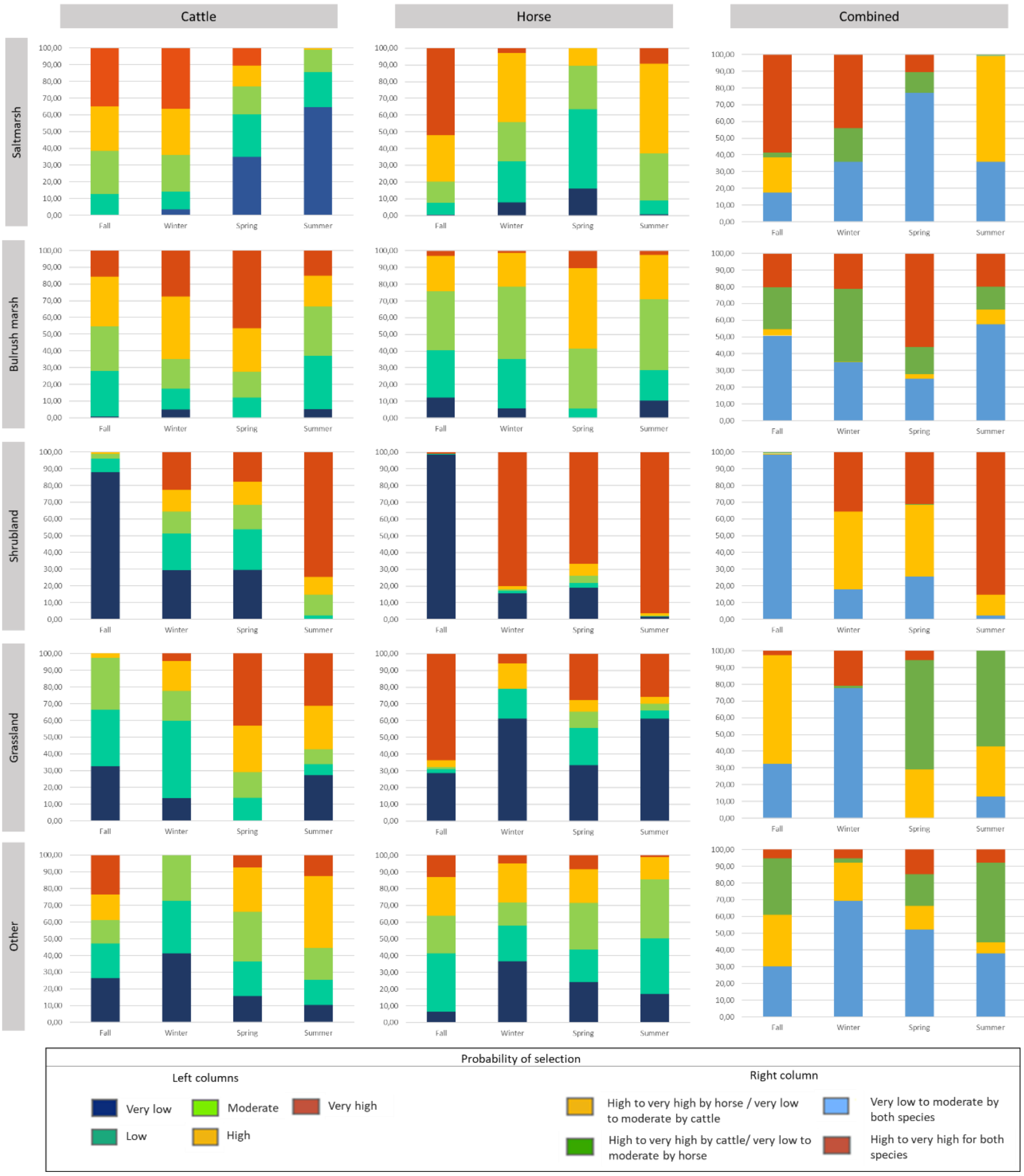

Figure 7. Distribution of the five categories (corresponding to equal area bins) of predicted relative probability of resource selection within each vegetation type (rows) by cattle (left column), horse (middle column) and combined (right column) at the four different seasons. “Combined”: overlap between the relative probability of resource selection by both species.

Selection of the different MUs (assuming free circulation of livestock) varied also strongly among seasons (Fig.8). As a general pattern, cattle tend to select preferentially areas in the two mixed MUs (i.e., those including marshland and mainland: RBD and Puntal) as they progress from fall/winter to summer; while they show the opposite pattern in these of pure marshland (RBG and Hinojos). For horse, patterns are less clear, besides an increase in the preference for one of the mixed MU (RBD) from fall to summer. As a consequence, the overlap between the resource selection preferences of both ungulates decreases from fall to summer in the pure marshland MUs (RBG and Hinojos) and shows the opposite pattern in the mainland MUS (particularly at RBD).

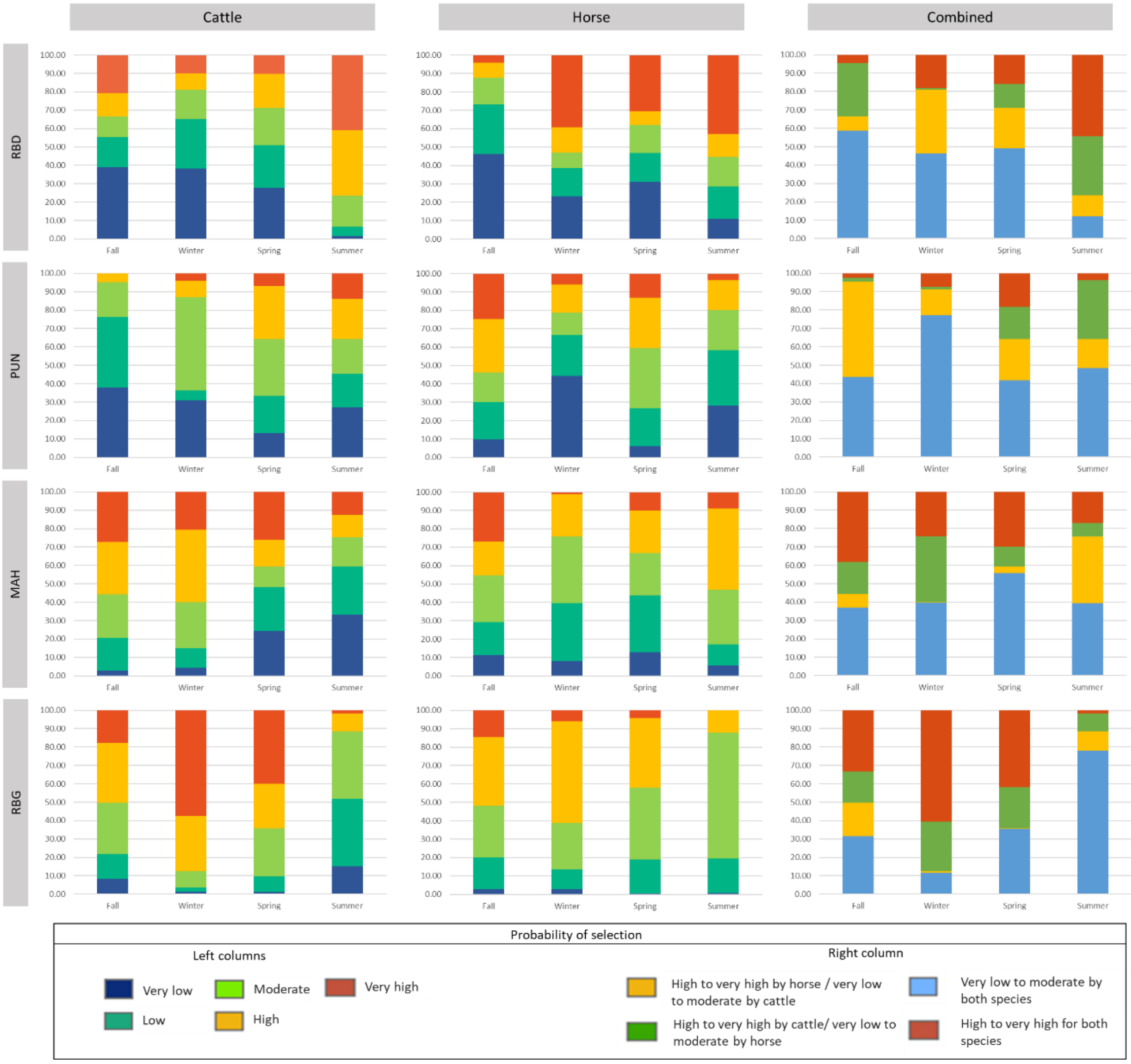

Figure 7. Distribution of the five categories (corresponding to equal area bins) of predicted relative probability of resource selection within each management unit (rows) by cattle (left column), horse (middle column) and combined (right column) at the four different seasons. “Combined”: overlap between the relative probability of resource selection by both species.

4. Discussion

Our results show that the space use by livestock was strongly influenced by plant production, habitat heterogeneity and water availability; and these patterns varied strongly between both livestock species. In particular, the effect of plant production (using NDVI as a proxy) varied among species, vegetation types and seasons; and the effect of distance to water varied among seasons. As hypothesized, space use increased with increasing plant production at areas with palatable vegetation types and at food-scarcer seasons (e.g., grassland in fall for both species, also in summer for cattle); although it showed the opposite pattern in food-richer seasons (e.g., grassland in winter for cattle). As hypothesized also, space use decreased with increasing plant production of unpalatable vegetation types, although the type of vegetation involved varied between species: bulrush marsh in summer for cattle, shrubland in fall for horse. These effects were modulated by the proximity to water sources, with increasing use nearby water sources in high plant-production periods (winter and spring) and decreased use nearby water sources in low plant-production periods (summer and fall).

Ungulates therefore tracked the spatiotemporal gradients of plant availability and palatability derived from habitat heterogeneity in order to meet their dietary needs. Certain vegetation types probably acted as key resources during food-limited periods, and this resulted in differences in space use among management units (MUs) – albeit modulated by seasonal variation in plant production and water availability. Indeed, resource selection maps resulting from fitted RSF models showed both clear differences between the two main groups of management units (marshland MUs: RBG and Hinojos; and mixed MUs: RBD and Puntal). These differences were driven by seasonal vegetation responses to rainfall and flooding. In fall, early rain causes saltmarsh and grassland production and palatability to increase rapidly, and they are simultaneously exploited by both cattle and horses. In the MUs dominated by marshland vegetation, winter/spring flooding forced both species to feed on the saltmarsh vegetation available at higher (i.e., shallower) areas; while in spring, when water levels diminish and bulrush marsh emerges in lower (i.e., deeper) areas, cattle and horse broadened their ranging areas. Later on, in summer, after flooding receded completely and did not hinder any longer the access to the deepest areas of the marshland, cattle selected bulrush vegetation while horse maintained their preference for saltmarsh and grassland. Such differences in the selection patterns of cattle and horse are probably driven by their feeding preferences and digestive strategies, which are known to be important drivers of foraging behavior. Compared with grazing ruminants (such as cattle), the higher rates of food intake of hindgut fermenters (such as horses) overcompensate their lesser ability to digest plant material. Hence, they are more efficient processing (sufficiently abundant) low quality resources than ruminants and its feeding preferences usually rely on them (Duncan et al., 1990; Illius & Gordon, 1992). In summer, when both species had full access to all resources, saltmarsh vegetation had ended the growth season and had a low palatability and nutrient concentration; hence, horse preference for this low-quality resource probably reduced trophic competition with cattle.

In the MUs with mixed vegetation, in contrast, both species select shrubland vegetation during summer. This reflects the importance of this vegetation when other resources are lacking. A close inspection of the locations occupied by both species shows that they are associated to the most humid parts of the scrubland mosaic, i.e., the mesic ‘monte negro’ – which occurs in terrain depressions, around temporary ponds and in the mainland-marshland ecotone (‘vera’). This area includes a mosaic of shrubs and pastures that have a prolonged growth season (i.e., it remains green vegetation during late spring and early summer) owing to the proximity of the water table. Furthermore, as summer season progresses, the reduction of the water levels in some of these temporary ponds allow herbivores to access to green forage. Thus, this vegetation represents a key resource (sensu Illius & O’Connor, 2000) in mainland MUs. This pattern changed sharply during fall, when both species avoided shrubland and showed contrasting selection patterns: both species selected the limited amount of saltmarsh available, but horse selected also grassland, while cattle selected “other vegetation types” (which, since this category is dominated by wooded vegetation, may be related to food availability in the understory or to its use as resting areas during the hotter hours of the day). During winter and spring, both species show a mosaic-like pattern of selection including patches of grassland, saltmarsh and shrubland; although horse shows a stronger selection for shrubland. In Doñana, these three vegetation types usually reach their phenological peak between late winter and early spring in years (Giralt-Rueda & Santamaria, 2021). Therefore, they provide abundant and high-quality food, which represents an important forage resource shared by both ungulates (See below).

These patterns of resource use result in spatial patterns of shared and complementary resource selection (Figs. 7 and 8) with important potential implications for livestock and vegetation management. On the one hand, areas simultaneously selected by both species (e.g., saltmarsh in fall and winter, shrubland in summer) represent key elements of the landscape, which provide essential resources for them during such specific seasons. Inter-specific competition and grazing pressure is likely to be higher in these areas in resource-limited periods (e.g., dry seasons or drought years); hence, they area also key areas to identify the occurrence of overgrazing and introduce measures to mitigate it. On the other hand, the availability of areas with complementary selection (i.e., selection by one species and avoidance by the other) will reduce inter-specific competition. These patterns took place, e.g., in summer/autumn, when horse selected saltmarsh vegetation avoided by cattle (Hinojos and Puntal), while cattle selected bulrush marsh avoided by horse; or in spring, when cattle selected grassland avoided by horse. These results suggest that heterogeneity is fundamental to reduce the impact of grazing on vegetation, particularly in the presence of multiple ungulate species (Schweiger et al., 2015).

Our results also show the importance of flooding at the marshland, where it determines the availability of bulrush and saltmarsh vegetation. Bulrush needs flooding for its development and it emerges at mid-spring; hence, it is only available to for herbivores by ten, when flooding recedes. Our study year (2018/19) was relatively dry (427 mm, as compared to a 549 mm average during the last 40 years; ESPN, 2021). In wetter years, bulrush development is delayed further, and even the saltmarsh and grassland growing at higher areas may show a reduced or delayed growth caused by temporary flooding - thus reducing further the forage availability for ungulates. Hence, resource selection in the marshland is mediated by flooding and forage availability in fall and winter, when selection of saltmarsh by cattle and horse is highest and trophic competition is probably strong; while, once palatable bulrush vegetation becomes available in spring, the different feeding preferences of both species results in the segregation of their foraging areas. The selection of bulrush marsh during spring is however constrained by the evolution of its palatability, which decreased rapidly over late spring and summer (Giralt-Rueda & Santamaria, 2021); although in later summer and early fall, the lack of alternative resources forces both species to feed on the fresh patches of bulrush available in the deepest areas, where flooding lasted for longer periods.

A contrasting seasonal pattern is found in the mainland MUs, where both species show a high affinity for shrubland vegetation in summer, particularly at the RBD. (In Puntal, the absence of such pattern probable reflects the higher habitat heterogeneity, which hosts a more balanced representation of vegetation types, with a higher proportion of grassland and saltmarsh.) Hence, while the area of interspecific overlap (i.e., high selection by both species) is largest at the wettest seasons (fall/winter) in marshland-dominated MUs, it peaks at the driest one (summer) at the MUs with mixed (mainland + marshland). These results suggest that an increased connectivity and/or an improved spatial design of the MUs may allow a higher behavioral flexibility of herbivores in response to the spatiotemporal variation in resource availability, thus reducing grazing impacts on vegetation productivity, increasing the functional heterogeneity for the herbivore guild, and enhancing the plant-herbivore system’s capacity to buffering the impact of climatic variation – all of it with potential positive implications for both wildlife conservation and livestock production.

The contrasting effect of plant primary production at different vegetation types and seasons, for both livestock species, revealed the importance of vegetation phenology on herbivore resource selection. The negative effects of plant production on the selection of some vegetation types at certain different seasons probably reflect the effect of the low palatability vegetation of certain vegetation types at late phenological stages. Large herbivores are known to track forage with high quality, digestibility and nutrient concentration across the landscape (Murray, 1995; Grant & Scholes 2006; Prins & van Langevelde, 2008; Fynn, 2019). Forage of high quality is fundamental for ungulates (principally for lactating females) and it is usually characterized by short and more palatable pastures, which occur at the earlier parts of the growth season and in low productive areas with higher mineral concentration (e.g., Murray, 1995; Grant & Scholes 2006; Fynn et al., 2014; Fynn et al., 2019). Indeed, herbivore selection patterns were strongly related to plant phenology and forage quality (similar to Laycock and Price, 1970). Changes in primary production occurring at early stages of the growing season are directly related to peaks in plant crude protein content and palatability (Crawley, 1983), which decrease rapidly with the plant's maturation. Herbivores tend to track this "green wave" (the early increase in primary production) at different spatial scales (e.g., Bischof et al., 2012; Van Moorter et al., 2013), while avoiding highly productive areas of unpalatable or unsuitable vegetation (see also Giralt-Rueda & Santamaria, 2022). During the dry season, however, less palatable vegetation may become an important resource that limits weight loss and reduces mortality, especially in highly seasonal and/or unpredictable environments (Selebatso et al., 2018). In summary, pasture palatability and nutrient concentration probably interplayed with livestock physiological needs, digestive strategies and feeding preferences to determine the foraging behavior observed for both species.

Heterogeneity can mitigate the effect of climatic variation on ungulate populations (Giralt-Rueda & Santamaria., 2021) by decoupling the relationship between ungulate performance and rainfall levels (Allred et al., 2014). The use of flexible grazing management taking into account spatiotemporal patterns derived from resource heterogeneity is probably essential to facilitate livestock adaptation to the spatial and temporal variability in forage quantity and quality, reducing overgrazing impacts and facilitating the recovery of vegetation after dry seasons and/or years (Fynn, 2012). An improved design of management units, carefully adjusted to facilitate the access of wild and domestic ungulates to the highest possible levels of functional heterogeneity, may help mitigating grazing impacts and increasing animal performance, providing a virtuous combination of food security (stability and profitability of secondary production), wildlife conservation and ecosystem resilience. More research is required to advance in the implementation of strategies focused on alleviating the effects of climatic variability, which seek to harmonize long-term economic sustainability and conservation goals (Espeland et al., 2020).

An additional factor for optimal ungulate management is related to the availability of water sources. Our results indicated that space use increased nearby water sources in high plant-production periods (winter and spring) and decreased nearby them in low plant-production periods (summer and fall). Although the extensive availability of water probably relaxes such pattern during winter and spring, the patterns observed during summer and fall probably reflect the decrease in foraging resources nearby water points characteristic of piosphere conditions (Lange, 1969). In particular, the limited number of water points in the marshland MUs tends to generate strong piosphere patterns, and livestock spend an increasing amount of time as these two seasons progress walking back and forth from the foraging areas to the water points – often under conditions on intense heat. Reduced water inflows caused changes in the incoming streams (in the marshland) and by the increases in water abstractions for irrigated crops (in the mainland) are leading to increasingly xeric conditions – as indicated, e.g., by the substitution of mesic communities by more xerophytic ones (Muñoz-Reinoso, 2001; Serrano & Zunzunegui, 2008). Such a reduction in water resources, and the associated changes in vegetation, are likely to exacerbate the aforementioned piosphere patterns and processes, thus reducing functional heterogeneity for wild and domestic ungulates, limiting the availability of key resources during droughts and increasing grazing pressure on sensitive areas, with major implications for wildlife conservation and livestock production.

5. Conclusions

We show evidence of the pivotal role of functional heterogeneity on the ungulate foraging behavior in environments characterized by strong climatic variability. Ungulates tracked the complex spatiotemporal dynamics of resources resulting from habitat heterogeneity and water availability in order to meet their dietary needs. Results reveal the importance of plant phenology and water availability on the space use of both livestock species which is also driven by inter-specific differences in feeding preferences and digestive strategies. The results regarding shared and complementary resource selection patterns highlight how an increased access to higher levels of functional heterogeneity will help ungulates to deal with spatiotemporal variation in resource availability, reducing grazing impacts on vegetation and enhancing the resilience of the plant-herbivore system to the impact of climatic variation and climate change.

6. Appendix

Table A1. Results of the Shapiro-Wilk normality test for models with cattle and horse.

Model	W	p-value
Cattle	0.97954	0.7011
Horse	0.95165	0.1376

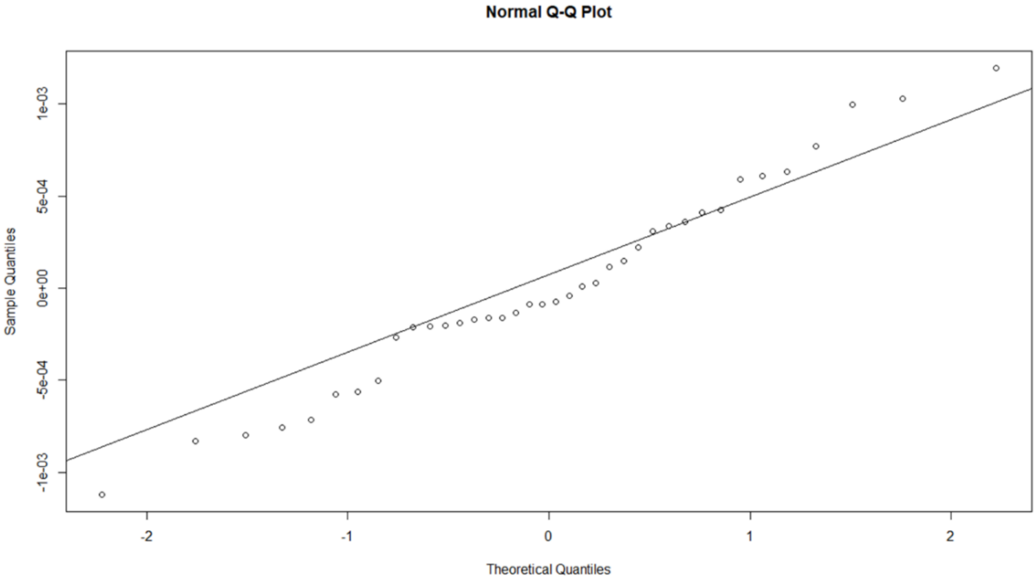

Figure A1. Normality of intercepts. Model with cattle.

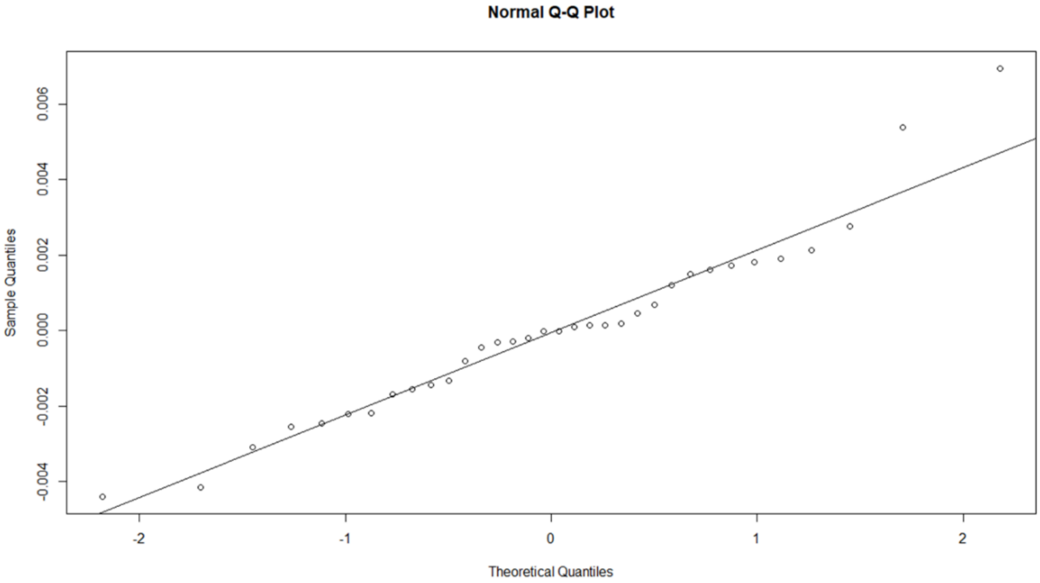

Figure A2. Normality of intercepts. Model with horse.

Table A2. Summary of model with cattle.

	Estimate	Std.Err	z-value	p-value
(Intercept)	-24.523	0.0366	-670.236	< 1e-04
scale(ndvi)	0.0144	0.0376	0.3823	0.70221038
vegfactorGrassland	0.0869	0.0513	16.925	0.09054968
vegfactorOther	0.1259	0.04	31.503	0.00163109
vegfactorSaltmarsh	0.0824	0.0412	20.021	0.04527831
vegfactorShrubland	0.3325	0.0634	52.416	< 1e-04
seasonspring	0.0005	0.0434	0.0107	0.99147398
seasonsummer	-0.1471	0.0686	-21.458	0.03189232
seasonwinter	0.0554	0.0635	0.8717	0.38335448
scale(distance)	0.043	0.0112	38.344	0.00012586
man_unitGuadiamar	0.0812	0.02	40.561	< 1e-04
man_unitHinojos	0.0569	0.0151	37.806	0.00015647
man_unitReserva	0.0339	0.0171	19.860	0.04703276
scale(ndvi):vegfactorGrassland	0.0774	0.0592	13.073	0.19109473
scale(ndvi):vegfactorOther	0.0677	0.04	16.929	0.09047285
scale(ndvi):vegfactorSaltmarsh	-0.0849	0.0482	-17.608	0.07827751
scale(ndvi):vegfactorShrubland	-0.1939	0.0627	-30.941	0.00197391
scale(ndvi):seasonspring	-0.1471	0.0431	-34.157	0.00063613
scale(ndvi):seasonsummer	-0.4777	0.0623	-76.664	< 1e-04
scale(ndvi):seasonwinter	-0.1391	0.0461	-30.164	0.00255827
vegfactorGrassland:seasonspring	-0.0009	0.0599	-0.0146	0.98832285
vegfactorOther:seasonspring	0.0393	0.047	0.8355	0.40343635
vegfactorSaltmarsh:seasonspring	-0.0635	0.0837	-0.7588	0.44799849
vegfactorShrubland:seasonspring	-0.2026	0.0727	-27.854	0.00534693
vegfactorGrassland:seasonsummer	0.3391	0.0955	35.510	0.00038381
vegfactorOther:seasonsummer	0.0036	0.0762	0.047	0.96250412
vegfactorSaltmarsh:seasonsummer	0.4027	0.243	16.575	0.09741976
vegfactorShrubland:seasonsummer	0.0688	0.0896	0.7678	0.44262726
vegfactorGrassland:seasonwinter	-0.0325	0.0767	-0.424	0.67159984
vegfactorOther:seasonwinter	-0.1384	0.0548	-25.260	0.01153615
vegfactorSaltmarsh:seasonwinter	-0.2817	0.0522	-54.000	< 1e-04
vegfactorShrubland:seasonwinter	-0.4259	0.0949	-44.892	< 1e-04
seasonspring:scale(distance)	-0.1651	0.0362	-45.664	< 1e-04
seasonsummer:scale(distance)	-0.0644	0.0146	-44.118	< 1e-04
seasonwinter:scale(distance)	-0.3673	0.0611	-60.128	< 1e-04
scale(ndvi):vegfactorGrassland:seasonspring	0.1054	0.0713	14.783	0.13933102
scale(ndvi):vegfactorOther:seasonspring	-0.0022	0.0493	-0.0436	0.96522076
scale(ndvi):vegfactorSaltmarsh:seasonspring	0.2547	0.0796	31.992	0.00137788
scale(ndvi):vegfactorShrubland:seasonspring	0.1725	0.0754	22.882	0.0221267

scale(ndvi):vegfactorGrassland:seasonsummer	0.7065	0.103	68.606	< 1e-04
scale(ndvi):vegfactorOther:seasonsummer	0.3111	0.0699	44.499	< 1e-04
scale(ndvi):vegfactorSaltmarsh:seasonsummer	0.7101	0.1441	49.264	< 1e-04
scale(ndvi):vegfactorShrubland:seasonsummer	0.681	0.0901	75.588	< 1e-04
scale(ndvi):vegfactorGrassland:seasonwinter	-0.0439	0.0745	-0.5894	0.55557028
scale(ndvi):vegfactorOther:seasonwinter	0.0058	0.0515	0.1126	0.91037465
scale(ndvi):vegfactorSaltmarsh:seasonwinter	0.1975	0.0561	35.226	0.0004273
scale(ndvi):vegfactorShrubland:seasonwinter	0.19	0.0866	21.947	0.02818199

Table A3. Summary of model with horse.

	Estimate	Std.Err	z-value	p-value
(Intercept)	-22.742	0.0287	-792.134	< 1e-04
scale(ndvi)	0.1382	0.0281	49.251	< 1e-04
vegfactorGrassland	0.1707	0.0745	22.909	0.0219673
vegfactorOther	0.0183	0.0671	0.2727	0.78504962
vegfactorSaltmarsh	-0.0545	0.0297	-18.362	0.06632212
vegfactorShrubland	10.295	0.6164	16.703	0.09485944
seasonspring	-0.1645	0.0368	-44.749	< 1e-04
seasonsummer	0.0284	0.0509	0.5568	0.57767879
seasonwinter	-0.2164	0.0756	-28.615	0.00421698
scale(distance)	0.036	0.0146	24.656	0.01367706
scale(ndvi):vegfactorGrassland	0.2767	0.0725	38.145	0.00013646
scale(ndvi):vegfactorOther	-0.0548	0.061	-0.8991	0.36858998
scale(ndvi):vegfactorSaltmarsh	-0.2062	0.0427	-48.283	< 1e-04
scale(ndvi):vegfactorShrubland	-14.953	0.7569	-19.756	0.04820365
scale(ndvi):seasonspring	-0.0817	0.033	-24.744	0.01334526
scale(ndvi):seasonsummer	-0.0964	0.0442	-21.796	0.02928785
scale(ndvi):seasonwinter	-0.0791	0.037	-21.363	0.03265419
vegfactorGrassland:seasonspring	-0.307	0.093	-33.005	0.00096508
vegfactorOther:seasonspring	0.0283	0.0767	0.3695	0.71173963
vegfactorSaltmarsh:seasonspring	0.1703	0.0476	35.780	0.00034621
vegfactorShrubland:seasonspring	-0.9668	0.6223	-15.536	0.12027007
vegfactorGrassland:seasonsummer	-0.2896	0.1356	-21.356	0.03271086
vegfactorOther:seasonsummer	-0.0795	0.0834	-0.9539	0.34013166
vegfactorSaltmarsh:seasonsummer	-0.8819	0.2782	-31.701	0.00152383
vegfactorShrubland:seasonsummer	-0.9194	0.6188	-14.857	0.13736362
vegfactorGrassland:seasonwinter	-0.3385	0.2176	-15.558	0.11974602
vegfactorOther:seasonwinter	-0.0581	0.0876	-0.663	0.50733456
vegfactorSaltmarsh:seasonwinter	0.0824	0.046	17.911	0.07327368
vegfactorShrubland:seasonwinter	-0.7076	0.6272	-11.282	0.25923044
seasonspring:scale(distance)	-0.2752	0.0376	-73.120	< 1e-04
seasonsummer:scale(distance)	0.0721	0.018	40.030	< 1e-04
seasonwinter:scale(distance)	-0.2023	0.0792	-25.548	0.01062541
scale(ndvi):vegfactorGrassland:seasonspring	-0.404	0.0894	-45.202	< 1e-04

scale(ndvi):vegfactorOther:seasonspring	-0.1371	0.0736	-18.636	0.06237648
scale(ndvi):vegfactorSaltmarsh:seasonspring	0.2458	0.0655	37.506	0.00017644
scale(ndvi):vegfactorShrubland:seasonspring	12.509	0.761	16.437	0.10023101
scale(ndvi):vegfactorGrassland:seasonsummer	-0.3203	0.1237	-25.883	0.00964385
scale(ndvi):vegfactorOther:seasonsummer	-0.0237	0.0826	-0.2867	0.7743251
scale(ndvi):vegfactorSaltmarsh:seasonsummer	-0.1175	0.1661	-0.7075	0.47926984
scale(ndvi):vegfactorShrubland:seasonsummer	10.457	0.7626	13.712	0.17030663
scale(ndvi):vegfactorGrassland:seasonwinter	-0.1711	0.1463	-11.695	0.24220873
scale(ndvi):vegfactorOther:seasonwinter	0.1709	0.0756	22.612	0.02374723
scale(ndvi):vegfactorSaltmarsh:seasonwinter	0.1848	0.052	35.529	0.00038108
scale(ndvi):vegfactorShrubland:seasonwinter	13.291	0.762	17.443	0.08110442

Table A4. NDVI trends for the interaction vegfactor*season*ndvi. Model with cattle

Season	vegfactor	ndvi.trend	SE	df	asymp.LCL	asymp.UCL
Fall	Bullrush marsh	0.124	0.325	Inf	-0.5121	0.7603
	Grassland	0.792	0.397	Inf	0.0137	15.701
	Saltmarsh	-0.608	0.262	Inf	-11.208	-0.0956
	Shrubland	-1.548	0.436	Inf	-24.016	-0.694
Winter	**Bullrush marsh**	-1.075	0.228	Inf	-1.523	-0.628
	Grassland	-0.786	0.319	Inf	-1.411	-0.162
	Saltmarsh	-0.104	0.149	Inf	-0.397	0.188
	Shrubland	-1.109	0.464	Inf	-2.018	-0.2
Spring	**Bullrush marsh**	-1.144	0.185	Inf	-1.506	-0.782
	Grassland	0.433	0.293	Inf	-0.142	1.007
	Saltmarsh	0.32	0.523	Inf	-0.706	1.346
	Shrubland	-1.328	0.325	Inf	-1.966	-0.69
Summer	**Bulrush marsh**	-3.996	0.428	Inf	-4.835	-3.156
	Grassland	2.764	0.588	Inf	1.612	3.916
	Saltmarsh	1.395	1.082	Inf	-0.726	3.517
	Shrubland	0.205	0.367	Inf	-0.514	0.925

Table A5. NDVI trends Contrasts for the interaction vegfactor*season*ndvi. Model with cattle

Season	contrast	estimate	SE	df	z.ratio	p.value
Fall	Bullrush marsh - Grassland	-0.668	0.511	Inf	-1.307	0.6867
	Bullrush marsh - Saltmarsh	0.732	0.416	Inf	1.761	0.3967
	Bullrush marsh - Shrubland	1.672	0.54	Inf	3.094	0.0169
	Grassland - Saltmarsh	1.400	0.476	Inf	2.942	0.027
	Grassland - Shrubland	2.340	0.589	Inf	3.973	0.0007
	Saltmarsh - Shrubland	0.94	0.508	Inf	1.851	0.3444
Winter	Bullrush marsh - Grassland	-0.289	0.389	Inf	-0.743	0.9463
	Bullrush marsh - Saltmarsh	-0.971	0.265	Inf	-3.670	0.0023
	Bullrush marsh - Shrubland	0.0338	0.514	Inf	0.066	1.0000

	Grassland - Saltmarsh	-0.682	0.349	Inf	-1.952	0.2897
	Grassland - Shrubland	0.3228	0.561	Inf	0.575	0.9787
	Saltmarsh - Shrubland	10.048	0.485	Inf	2.072	0.2324
Spring	**Bullrush marsh - Grassland**	-1.577	0.341	Inf	-4.623	<.0001
	Bullrush marsh - Saltmarsh	-1.464	0.559	Inf	-2.622	0.0665
	Bullrush marsh - Shrubland	0.184	0.366	Inf	0.503	0.9871
	Grassland - Saltmarsh	0.112	0.6	Inf	0.187	0.9997
	Grassland - Shrubland	1.761	0.431	Inf	4.081	0.0004
	Saltmarsh - Shrubland	1.648	0.617	Inf	2.671	0.0583
Summer	**Bullrush marsh - Grassland**	-6.760	0.727	Inf	-9.302	<.0001
	Bullrush marsh - Saltmarsh	-5.391	1.169	Inf	-4.612	<.0001
	Bullrush marsh - Shrubland	-4.201	0.56	Inf	-7.506	<.0001
	Grassland - Saltmarsh	1.369	1.233	Inf	1.111	0.8011
	Grassland - Shrubland	2.559	0.692	Inf	3.697	0.002
	Saltmarsh - Shrubland	1.190	1.144	Inf	1.040	0.8367

Table A6. NDVI trends for the interaction vegfactor*season*ndvi. Model with horse

Season	vegfactor	ndvi.trend	SE	df	asymp.LCL	asymp.UCL
Fall	**Bullrush marsh**	1.12E-04	2.28E-05	Inf	6.75E-05	1.57E-04
	Grassland	3.37E-04	5.45E-05	Inf	2.30E-04	4.44E-04
	Saltmarsh	-5.52E-05	2.56E-05	Inf	-1.05E-04	-5.02E-06
	Shrubland	-1.10E-03	6.14E-04	Inf	-2.31E-03	1.02E-04
Winter	**Bullrush marsh**	4.80E-05	1.96E-05	Inf	9.45E-06	8.65E-05
	Grassland	1.34E-04	1.01E-04	Inf	-6.38E-05	3.31E-04
	Saltmarsh	3.06E-05	1.59E-05	Inf	-6.89E-07	6.18E-05
	Shrubland	-8.69E-05	6.93E-05	Inf	-2.23E-04	4.88E-05
Spring	**Bullrush marsh**	4.59E-05	1.44E-05	Inf	1.77E-05	7.40E-05
	Grassland	-5.75E-05	4.03E-05	Inf	-1.37E-04	2.15E-05
	Saltmarsh	7.81E-05	3.72E-05	Inf	5.06E-06	1.51E-04
	Shrubland	-1.52E-04	6.26E-05	Inf	-2.75E-04	-2.97E-05
Summer	Bulrush marsh	3.39E-05	2.79E-05	Inf	-2.08E-05	8.86E-05
	Grassland	-1.50E-06	7.67E-05	Inf	-1.52E-04	1.49E-04
	Saltmarsh	-2.29E-04	1.25E-04	Inf	-4.75E-04	1.68E-05
	Shrubland	-3.31E-04	7.03E-05	Inf	-4.69E-04	-1.93E-04

Table A7. NDVI trends contrasts for the interaction vegfactor*season*ndvi, Model with horse

Season	contrast	estimate	SE	df	z.ratio	p.value
Fall	**Bullrush marsh - Grassland**	-2.25E-04	5.89E-05	Inf	-3.815	0.0013
	Bullrush marsh - Saltmarsh	1.67E-04	3.47E-05	Inf	4.828	<.0001
	Bullrush marsh - Shrubland	1.21E-03	6.14E-04	Inf	1.976	0.2779
	Grassland - Saltmarsh	3.92E-04	6.01E-05	Inf	6.519	<.0001
	Grassland - Shrubland	1.44E-03	6.16E-04	Inf	2.334	0.1342

	Saltmarsh - Shrubland	1.05E-03	6.15E-04	Inf	1.703	0.4321
Winter	Bullrush marsh - Grassland	-8.57E-05	1.03E-04	Inf	-0.831	0.9212
	Bullrush marsh - Saltmarsh	1.74E-05	2.42E-05	Inf	0.718	0.9524
	Bullrush marsh - Shrubland	1.35E-04	7.14E-05	Inf	1.889	0.3231
	Grassland - Saltmarsh	1.03E-04	1.02E-04	Inf	1.007	0.8522
	Grassland - Shrubland	2.21E-04	1.23E-04	Inf	1.798	0.3747
	Saltmarsh - Shrubland	1.18E-04	7.07E-05	Inf	1.662	0.4577
Spring	Bullrush marsh - Grassland	1.03E-04	4.24E-05	Inf	2.436	0.1058
	Bullrush marsh - Saltmarsh	-3.22E-05	4.05E-05	Inf	-0.795	0.9322
	Bullrush marsh - Shrubland	1.98E-04	6.44E-05	Inf	3.080	0.0176
	Grassland - Saltmarsh	-1.36E-04	5.48E-05	Inf	-2.472	0.0969
	Grassland - Shrubland	9.50E-05	7.45E-05	Inf	1.274	0.707
	Saltmarsh - Shrubland	2.31E-04	7.27E-05	Inf	3.169	0.0133
Summer	Bullrush marsh - Grassland	3.54E-05	8.14E-05	Inf	0.435	0.9926
	Bullrush marsh - Saltmarsh	2.63E-04	1.30E-04	Inf	2.016	0.258
	Bullrush marsh - Shrubland	3.65E-04	7.58E-05	Inf	4.816	<.0001
	Grassland - Saltmarsh	2.27E-04	1.47E-04	Inf	1.547	0.5319
	Grassland - Shrubland	3.30E-04	1.04E-04	Inf	3.168	0.0133
	Saltmarsh - Shrubland	1.02E-04	1.43E-04	Inf	0.712	0.9538

Table A8. Distance trends for the interaction season*distance. Model with cattle

season	distance.trend	SE	df	asymp.LCL	asymp.UCL
fall	5.02E-05	1.31E-05	Inf	2.45E-05	7.58E-05
spring	-1.42E-04	4.00E-05	Inf	-2.21E-04	-6.40E-05
summer	-2.50E-05	1.11E-05	Inf	-4.68E-05	-3.24E-06
winter	-3.78E-04	7.00E-05	Inf	-5.15E-04	-2.41E-04

Table A9. Distance trends contrasts for the interaction season*distance. Model with cattle

contrast	estimate	SE	df	z.ratio	p.value
fall-spring	1.93E-04	4.22E-05	Inf	4.566	<.0001
fall-summer	7.52E-05	1.70E-05	Inf	4.412	0.0001
fall-winter	4.28E-04	7.13E-05	Inf	6.013	<.0001
spring-summer	-1.17E-04	4.15E-05	Inf	-2.831	0.024
spring-winter	2.36E-04	8.04E-05	Inf	2.935	0.0176
summer-winter	3.53E-04	7.08E-05	Inf	4.991	<.0001

Table A10. Distance trends for the interaction season*distance. Model with horse

season	distance.trend	SE	df	asymp.LCL	asymp.UCL
fall	3.30E-05	1.34E-05	Inf	6.77E-06	5.93E-05
spring	-2.19E-04	3.18E-05	Inf	-2.82E-04	-1.57E-04
summer	9.92E-05	9.69E-06	Inf	8.02E-05	1.18E-04

winter	-1.52E-04	7.14E-05	Inf	-2.92E-04	-1.26E-05

Table A11. Distance trends contrasts for the interaction season*distance. Model with horse

contrast	estimate	SE	df	z.ratio	p.value
fall-spring	2.52E-04	3.45E-05	Inf	7.312	<.0001
fall-summer	-6.62E-05	1.65E-05	Inf	-4.003	0.0004
fall-winter	1.85E-04	7.26E-05	Inf	2.555	0.0519
spring-summer	-3.19E-04	3.34E-05	Inf	-9.549	<.0001
spring-winter	-6.69E-05	7.81E-05	Inf	-0.857	0.827
summer-winter	2.52E-04	7.20E-05	Inf	3.495	0.0027

Table A12. Cross-validated Spearman-rank correlations (rs) between RSF bin ranks and area-adjusted frequencies for individual and average model sets for cattle and horse.

	Cattle		Horse	
Set	r_x	P	r_x	P
1	0.8666667	0.002681	0.8545455	0.003505
2	0.9515152	< 2.2e-16	0.8545455	0.003505
3	0.9393939	< 2.2e-16	0.8909091	0.00138
4	0.9515152	< 2.2e-16	0.9636364	< 2.2e-16
5	0.9151515	0.0004667	0.6484848	0.04904
Average	0.9636364	< 2.2e-16	0.9393939	< 2.2e-16

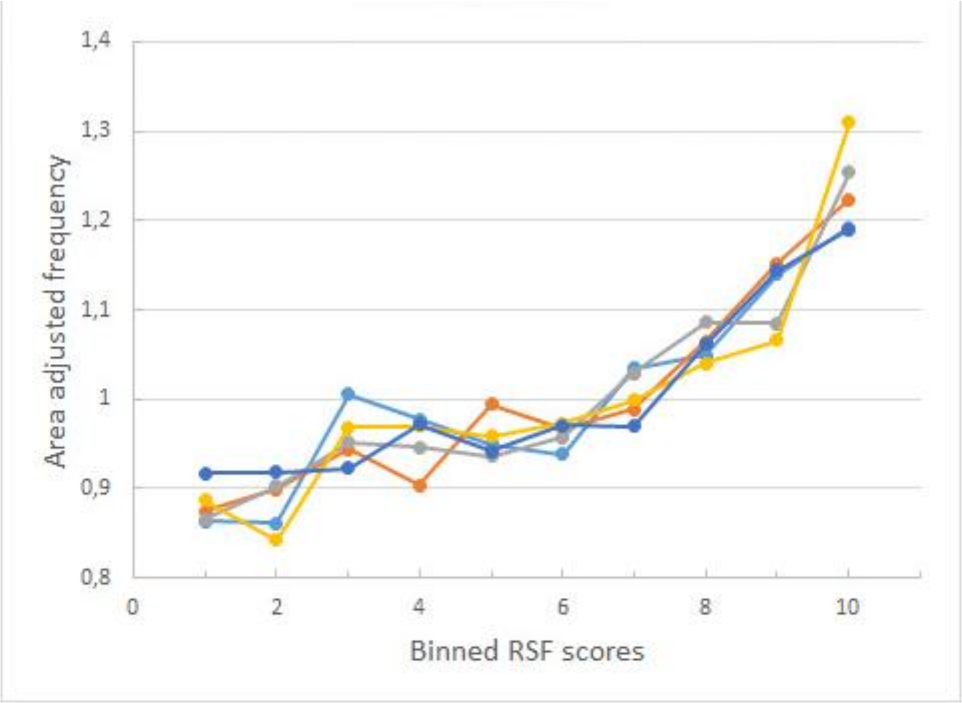

Figure A3. Area-adjusted frequency of categories (bins) of RSF scores for withheld locations of cattle.

Figure A4. Area-adjusted frequency of categories (bins) of RSF scores for withheld locations of horse.

General discussion

Rangelands represent the most extensive land cover type on Earth and they provide multiple ecosystem services. However, due to their variability in rainfall and high evapotranspiration, rangelands in Mediterranean and semiarid areas are extremely vulnerable to human disturbances. To provide effective management strategies that help maintaining their sustainability in the face of climate change, therefore, we urgently need to deepen our knowledge on the complex interactions that regulate their primary and secondary productivity – in particular, those relating plants and large herbivores as well as their interactions with anthropogenic drivers of change. By combining environmental data, information on plant production, phenology and distribution, ungulate population counts and livestock movement data, this thesis investigates ungulate-vegetation interactions in a Mediterranean ecosystem (the Doñana National Park, SW Spain), and the role that habitat heterogeneity plays in regulating the impacts of climate variability.

We investigated: (i) The effects of intra- and inter-annual variation in rainfall, as well as herbivore pressure, on the primary production of four different vegetation types, and the potential impact of different policy strategies under expected climate change scenarios. (ii) The influence of spatiotemporal variability in plant primary production and livestock density on the population dynamics of two wild ungulate species (red and fallow deer). (iii) The resource selection by two free-ranging livestock species (cattle and horse) and the factors regulating its spatiotemporal variation, with particular attention to the effect of vegetation composition and production, water availability and the role of the spatial separation in management units.

The effects of intra- and inter-annual variation in rainfall and herbivore pressure on the primary production of four different vegetation types, and the potential impact of different policy strategies under expected climate change scenarios

Combining remotely sensed data on plant production, phenology and distribution with data on accumulated daily precipitation and population counts of wild and domestic ungulates, we identified differentiated responses of different vegetation types to climate variability and grazing pressure. Although livestock density had a negative effect on primary production, the differences in the phenological and functional responses among vegetation types increased ecosystem resilience to climate variability and grazing pressure. However, high densities of domestic ungulates will probably limit such resilience under the conditions predicted by climate change models, which may lead to long-term land degradation (Chapter 1).

These results highlight the pivotal role of landscape heterogeneity on rangeland stability (Fuhlendorf et al., 2017) and provide valuable information that may aid the development of improved management practices. Such management strategies should take advantage of habitat heterogeneity and phenological alternation, ensuring a balanced access of ungulates to different vegetation types that may supply the diverse forage resources required to cover their dietary needs (Provenza et al., 2003), extending the spatiotemporal availability of forage and preserving biodiversity patterns and processes (Fuhlendorf et al., 2012). In addition, the implementation of more flexible stocking rates and the spatial redistribution of management units should be considered, with the aim of maintaining the resilience of the plant-ungulate system under climate change (Schneider & Kéfi, 2016).

Regarding the effects of ungulates on primary production, we found clear differences between wild and domestic species. Wild species had neutral or positive effects on plant production, while livestock (cattle and horse) showed negative effects even at low densities. This difference may reflect the strong difference in stocking rates between these two groups, especially when expressed in terms of animal biomass; but it may also result from differences in feeding preferences and behavior (Stewart et al., 2009).

Model predictions that incorporate the responses to medium-term changes in rainfall predicted by climate change models indicate that vegetation will suffer an important decrease in primary production, together with displaced phenological peaks. These estimates are likely conservative: the phenological shift of vegetation observed in the Northern Hemisphere in recent decades, which reflects a phenological advance of 0-12 days due to increasing global warming (Menzel et al., 2006; Xu et al., 2019), indicate that accumulated rainfall levels will be even lower for vegetation development. Should current stocking rates be maintained, these effects will probably be exacerbated by the grazing pressure exerted by such (moderately high) livestock densities, especially in marshland vegetation and grasslands. Those effects will limit severely the resilience of vegetation to climate change and may have major consequences on secondary production, limiting population densities of wild ungulate and the productivity of free-ranging livestock ranching. Without the implementation of improved management practices, the ecosystem will likely reach no-return degradation thresholds (Lohmann et al., 2012).

The influence of spatiotemporal variability in plant primary production and livestock density on the population dynamics of the wild ungulate species

Our results showed that the complementary differences in the phenology and production of four different vegetation types to intra- and inter-annual variation in climatic conditions increase the resilience of wild ungulate populations to climate variability (Chapter 2) by increasing the availability and predictability of key forage resources (Chapter 1 and 2). While low to moderate livestock densities had a positive effect on wild ungulate density, high livestock densities had a negative impact on both vegetation production (Chapter1) and wild ungulate populations (Chapter 2). In the absence of compensatory management practices, the later conditions severely restrict the resilience of the plant-herbivore system, threatening ecosystem stability. Fortunately, the analysis of model simulations indicates that a combination of more flexible stocking rates and the implementation of adaptive management strategies (e.g., by increasing wildlife connectivity among management units) might diminish the negative impact on wild ungulate populations.

The differentiated functional and phenological responses of different vegetation types to intra- and inter-annual variation in rainfall resulted in seasonal complementarity, whereby the negative effect of extreme (high or low) rainfall levels on certain vegetation types is compensated by simultaneous positive effects on other types. On the one hand, intra-annual alternation resulted in a phenological gradient from xeric to mesic vegetation, which extended the period of forage availability and buffered the drop in primary production during summer. On the other hand, inter-annual complementarity among vegetation types reinforced such buffering effects. In particular, shrubland vegetation maintained a stable production in both wet and dry years, acting as a “key resource” for herbivores during such unfavorable conditions.

Overall, phenological complementarities may help ungulate populations to cope with intra-annual variation in plant production, while functional complementarities may increase their resilience to inter-annual variation in plant production. The exploration of the effects of plant production and phenology over the years confirmed that access to both marshland and inland vegetation is a key factor to mitigate the impact of climatic variation on wild ungulates. These findings hint to potential management possibilities regarding the distribution and design of management units. In particular, increasing landscape functional heterogeneity by promoting a more balanced and diverse representation of vegetation types within management units is likely to increase the resilience of the plan-ungulate system.

The non-linear responses of wild ungulate populations to the functional and phenological variation of vegetation probably reflects the feeding preferences of both deer species, which select short, more palatable and nutritious vegetation whenever available. This selective foraging behavior, adapted to the functional and phenological complementarity of the various vegetation types, allows ungulates to meet their dietary needs in different periods. In this context, the positive association between livestock densities and deer densities at low livestock stocking rates suggest a facilitation effect of the former, which probably relates to the reduction of tall, unpalatable vegetation. This is consistent with previous research reporting facilitation effects of large herbivores on medium-small ones (Odadi et al., 2011; Fynn et al., 2019). However, medium to high livestock densities resulted in negative effects on wild ungulate populations, which probably reflect resource competition and/or interference by ranching activities (Schieltz & Rubenstein 2016; Gordon 2018).

Increasing connectivity between management units, tailored to allow the access of wild ungulates to a higher diversity of forage resources, and more flexible livestock stocking rates, alone or in combination with additional management interventions (such as limiting supplementary feeding, avoiding restocking immediately after droughts, or adjusting the availability and distribution of artificial water points) will probably help reducing the negative impacts of climatic variation and climate change on wild ungulates and their food plants, therefore increasing ecosystem resilience.

Resource selection by two free-ranging livestock species

The study on the resource selection by livestock (cattle and horse) reinforced the importance of functional heterogeneity on vegetation-ungulate interactions. Results of the resource selection models showed that space use by livestock was clearly influenced by plant production, habitat heterogeneity and water availability and also how these effects varied among vegetation types and seasons. Furthermore, inter-specific differences in feeding preferences revealed contrasting patterns of resource selection between both species.

As we hypothesized, increases in plant production of palatable vegetation had a positive effect on the selection by both species during food-scarcer seasons while had a negative impact on the selection during food-richer seasons. The opposite pattern was found for less palatable vegetation with evident differences between both ungulate species. While cattle avoided more mature bulrush marsh vegetation in summer, horse avoided mature shrubland in fall. These results highlight how ungulates tracked the spatiotemporal gradients of primary production in order to find the best resources at different periods.

Such patterns might respond to different physiological needs, then ungulates select more palatable vegetation with higher nutrient concentration during reproduction and lactation (Grant & Scholes 2006; Fynn et al., 2014) while increase biomass intake for survival and animal growth in others (Selebatso et al., 2018). Thus, some specific vegetation types act as "key resources" which, due to differences in landscape configuration and flooding, revealed contrasting space use among two differentiated groups of management units: management units containing only marshland vegetation (marshland MUs) and management units containing both marshland and inland vegetation types (mixed MUs). In marshland MUs, flooding during rainy months (winter and early spring) limits the foraging area and force both ungulate species to feed on higher (e.g., shallower) areas dominated by saltmarsh and grassland vegetation while during late spring flooding diminish and bulrush marsh emerges and both cattle and horse broadened their ranging areas taking advantage of the more palatable and nutritious bulrush marsh which is recently emerged. However, during summer cattle continued selecting bulrush marsh on areas that become available when flooding receded but horse selected again saltmarsh and grassland vegetation, possibly to avoid competition with cattle. In mixed MUs, in contrast, both species selected the most humid areas of shrubland vegetation during summer, reflecting the relevance of this vegetation type acting as "key resource" when other resources are lacking (sensu Illius & O'Connor, 2000). In other seasons the resource selection by cattle and horse differed in response to the alternation of phenological cycles among vegetation types (Chapter 1) and differences in feeding preferences and digestive strategies which are major drivers of ungulate behavior (Duncan et al., 1990; Illius & Gordon, 1992). These results highlight how resource selection and space use by livestock species is mediated by a complex of factors: flooding, plant phenology and inter-specific differences in feeding preferences and digestive strategies; whose importance varies both spatially and temporally (Fulhendorf et al., 2017).

These patterns of resource use result in spatial shared and complementary resource selection with important implications for management. On the one hand, areas selected by both species simultaneously represent important parts of the landscape providing key resources for them, however, inter-specific competition and grazing pressure is expected to be higher on such areas during resource-limited periods, being subjected to potential impacts from overgrazing. On the other hand, areas with complementary selection will reduce inter-specific competition and the concentration of grazing in space and time which highlights the key role of functional heterogeneity (Fulhendorf et al., 2017) particularly in the presence of multi-species ungulate communities (Schweiger et al., 2015). The analysis of shared and complementary foraging areas at the different management units reinforced these findings and showed contrasting seasonal patterns of inter-specific overlap ((i.e., high selection by both species) between marshland MUs (where overlap is largest during fall and winter) and mixed MUs (where overlap is largest during summer). It is also important to note that the management with the lowest levels of inter-specific overlap (Puntal) hosts the higher levels of habitat heterogeneity with a more balanced representation of different vegetation types. These results suggest that an increased connectivity and/or an improved spatial design of the management units (e.g., by increasing landscape heterogeneity) may allow a higher behavioral flexibility of herbivores in response to the spatiotemporal variation in resource availability, thus reducing grazing impacts on vegetation, increasing the functional heterogeneity for the herbivore guild, and enhancing the plant-herbivore system's capacity to buffering the impact of climatic variation and climate change (Allred et al., 2014) – all of it with potential positive implications for both wildlife conservation (Cromsigt et al., 2009) and livestock production (Fynn, 2012).

Other important findings are related to the effect of water availability on the livestock space use. According to our results, space use increased nearby water sources in high-plant production periods (winter and spring) while decreased in low-plant productive periods (summer and fall). Even considering that high availability of water during rainy seasons may diminish such effect, the patterns observed during dry seasons probably responded to the limited foraging resources available in the surroundings of water sources characteristic of piosphere conditions (Lange, 1969), particularly in marshland MUs due to the low availability of water points. The reduction of water inflows from streams in the marshland and the lowering of the water table due to abstractions for irrigated crops in the mainland are leading to increasing xeric conditions which result in important vegetation changes from mesic to xerophytic vegetation communities (Muñoz-Reinoso, 2001; Serrano & Zunzunegui, 2008). Such conditions will exacerbate the piosphere patterns, reducing the functional heterogeneity for both wild and domestic herbivores and limiting the availability of key resources during droughts, thus intensifying the grazing pressure on sensitive areas with major implications for wildlife conservation and livestock production.

Synthesis and future steps

This thesis provides valuable knowledge on vegetation-ungulate interactions in environments with high climatic variability, as well as on the pivotal role that landscape heterogeneity plays in controlling such relationship. The insight gained through its results may be instrumental to design better management strategies, allowing Mediterranean and semiarid rangelands to face the challenges posed by climate change. We showed that the complementarities among the functional and phenological responses of different vegetation types, resulting from habitat heterogeneity, buffer the impact of rainfall variation on both vegetation and wild ungulates, increasing the resilience of the plant-ungulate system to climate change.

More detailed information, obtained by the use of population models (e.g., state-space population models) for wild ungulates and the incorporation of livestock yield data (weight gain and calf production), in combination with more accurate data on vegetation (e.g., higher spatial resolution for remotely sensed data), could increase further the reliability of these results. Additional research on the space use and resource selection patterns of wild ungulates (including wild boars) and other herbivores (most notably, rabbits and hares) is also needed to fully comprehend the dynamics of the vegetation-herbivore system.

Inadequate management practices such as excessive and/or fixed livestock stocking rates, as well as fencing without due consideration to vegetation functional heterogeneity and the feeding requirements of ungulates, will probably exacerbate the ongoing effects of climate change, reducing the ecosystem resilience and potentially leading to persistent ecosystem degradation. Future experimental research should therefore focus on evaluating, using collaborative adaptive designs, the effects of alternative management practices aimed at maintaining the resilience of the rangeland system. A key element of these designs should be the participation of the full range of experts, managers and stakeholders – making a true effort to overcome decades of distrust and contrasting opinions that severely hamper the design of comprehensive, long-term solutions.

Conclusions

1. Habitat heterogeneity buffers the impact of climatic variation and grazing pressure on vegetation.
2. High livestock stocking rates in combination with climate conditions predicted by climate change models, will result in irreversible ecosystem degradation.
3. Functional and phenological complementarities resulting from vegetation heterogeneity increases the resilience of wild ungulate populations to climate change. The contrasting responses of the two wild ungulate species to variation in primary production reinforce such resilience.
4. Low to medium livestock stocking rates have positive effects on wild ungulate populations, but medium to high stocking rates have a negative impact on them.
5. Scenarios of full ungulate mobility across management units suggest that it may reduce the impact of inter-annual variation in primary production on both deer species under low/moderate livestock densities.
6. Our results indicate that both herbivores show strong seasonal variation in the relationship between vegetation composition, plant production and distance to water and space use.
7. Space use increased with increasing plant production at areas with palatable vegetation types and at food-scarcer seasons, and showed the opposite pattern in food-richer seasons. Space use also decreased with increasing plant production of unpalatable vegetation types, although the type of vegetation involved varied between ungulate species.
8. Resource selection patterns of livestock were also modulated by the proximity to water sources, highlighting piosphere patterns which might be exacerbated under water-limited conditions.
9. Increasing connectivity and/or an improved spatial design of the management units may allow herbivores to deal with spatiotemporal variation in resource availability, reducing grazing impacts on vegetation productivity. By increasing the functional heterogeneity of management units will enhance the resilience of the plant-herbivore system to the impact of climatic variation and climate change.

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