

FROM SPATIAL ECOLOGY TO ECOSYSTEM IMPACT: LARGE GRAZERS IN HEATH AND DUNE LANDSCAPES

LINKING MOVEMENT BEHAVIOUR, HABITAT SELECTION, AND
VEGETATION DYNAMICS IN THE WESTHOEK AND KALMTHOUTSE
HEIDE

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Table of contents

Table of contents.....	2
1. Introduction	5
1.1. Conservation Context of Heath and Dune Ecosystems	5
1.2. Large Herbivores as Ecosystem Engineers.....	7
1.3. Spatial Ecology and Movement Behaviour.....	8
1.4. Study Species	9
1.4.1 The Equid Group: Konik Horses and Shetland Ponies in Coastal Dunes	9
1.4.2. The Bovine Group: Galloway Cattle in Lowland Heathlands.....	10
1.5. Knowledge Gaps and Research Questions	11
2. Research Objectives	13
2.1. Work Package 1: Boundary-Constrained Space Use.....	13
2.2. Work Package 2: Fine-Scale Habitat Selection	13
2.3. Work Package 3: Spatial Ecology and Vegetation Dynamics	14
3. Materials and methods	16
3.1. Study Areas	16
3.1.1. The Westhoek (Coastal Dune Ecosystem)	16
3.1.2. The Kalmthoutse Heide (Lowland Heath Ecosystem)	18
3.2. Study Species & Telemetry Data Collection.....	19
3.2.1. Data Acquisition and Hardware.....	19
3.2.2. Temporal, Attribute and Spatial Cleaning	21
3.2.3. Dynamic Spatial Boundaries: The Westhoek Corridor Intervention	22
3.2.4. Telemetry Performance and Final Dataset	23
3.3. Environmental Data and Spatial Covariates	24
3.3.1. Topographical and Hydrological Variables	24
3.3.2. Distance-based Covariates (Resources and Infrastructure).....	26
3.3.3. Habitat and Vegetation Classification	27
3.3.4. Raster Alignment and Variable Standardization.....	27
3.4. WP1: Movement Models and Home Ranges.....	28
3.4.1. Autocorrelated Kernel Density Estimation (AKDE)	28
3.4.2. Statistical Analysis of Spatial Dynamics	29
3.5. WP2: Population-Level Habitat Selection.....	30
3.5.1. Integrated Resource Selection Functions (iRSF)	30

3.5.2. Population-Level Aggregation and Baseline Alignment	31
3.5.3. Inter-Species Comparison (Westhoek)	32
3.6. WP3: Modelling Vegetation Dynamics	32
3.6.1. Cumulative Equid Space Use Pressure Mapping	32
3.6.2. Vegetation Transition and Abiotic Covariates	33
3.6.3. Multinomial Logistic Regression and Marginal Effects	35
4. Results	36
4.1 WP1: Space Use and Home Range Dynamics	36
4.1.1 Baseline Home Range Estimates (AKDE)	36
4.1.2 Seasonal & Infrastructural Effects (LMM Results)	37
Westhoek Coastal Dune Ecosystem (Equid Group)	37
Kalmthoutse Heide Lowland Heath Ecosystem (Galloway Cattle)	41
4.2 WP2: Environmental Drivers & Spatial Constraints	44
4.2.1. Spatial Strategies in the Westhoek Coastal Dune Ecosystem	45
4.2.2. Spatial Strategies in the Kalmthoutse Heide Lowland Heath Ecosystem	47
4.3 WP2: Fine-Scale Habitat Selection & Species Divergence	49
4.3.1. Westhoek: Equid Habitat Selection	49
4.3.2. Kalmthoutse Heide: Galloway Cattle Selection	53
4.4 WP3: Drivers of Vegetation Height Change.....	56
4.4.1. Model Selection and Predictor Importance.....	56
4.4.2. The Impact of Space Use Intensity (SUI)	56
4.4.3. Abiotic Constraints on Succession	59
5. Discussion	63
5.1 Spatial Constraints and Anthropogenic Landscapes.....	63
5.1.1 Home Range Saturation and the Impact of Corridor Expansion	63
5.1.2. The Influence of Anthropogenic Infrastructure on Spatial Ecology	64
5.2 Seasonal Foraging Strategies and Sub-herd Divergence.....	66
5.2.1. Westhoek Population-Level Dichotomy: Grass vs. Scrub	66
5.2.2. Westhoek Morphological and Social Drivers of Sub-herd Divergence	68
5.2.3. Kalmthoutse Heide Population-Level Selection: Requirement of the Forageable Layer	69
5.2.4. Topographical and Distance to Water Constraints on Spatial Use	70
5.3 Herbivore-Driven Engineering of Vegetation Structure	71
5.4 Methodological Strengths and Limitations.....	75

5.4.1. Analytical Strengths: Autocorrelation and DOF Filtering	75
5.4.2. Telemetry Constraints, Sample Sizes, and Spatial Artifacts	75
5.4.3. Inter-Reserve Discrepancies and Future Directions.....	76
5.5. Implications for Conservation Management	76
5.5.1. <i>Vergrassing</i> and <i>Verstruweling</i> in the Westhoek: A Dual Management Approach	77
5.5.2. Morphological Diversity in the Westhoek: The Case for the Shetland Pony Sub-Herd.....	77
5.5.3. Alignment of Cattle Space Use Preferences with Heathland Conservation Goals	78
5.5.4. Minimum Reserve Size and Strategic Infrastructure	78
6. Conclusions.....	80
6.1. Work Package 1: Boundary-Constrained Space Use.....	80
6.2. Work Package 2: Fine-Scale Habitat Selection	80
6.3. Work Package 3: Spatial Ecology and Vegetation Dynamics	81
6.4. Synthesis	81
7. Summary.....	83
8. Acknowledgements	89
8.1 Statement on the use of Generative AI	89
9. References.....	90
10. Attachments	103

1. Introduction

1.1. Conservation Context of Heath and Dune Ecosystems

Open landscapes in Western Europe, particularly lowland heathlands and coastal dunes, are widely recognized as critical biodiversity hotspots. Lowland heathlands are classic semi-natural ecosystems, shaped by centuries of traditional land-use practices (Piessens & Hermy, 2006; Webb, 1998). While coastal dunes are naturally occurring geomorphological systems (Martínez & Psuty, 2004; Maun, 2009), their open and highly biodiverse successional stages have historically been sustained by a combination of abiotic dynamics and human land use (Provoost et al., 2011). Despite their differing origins, both ecosystems are globally rare and characterized by harsh, nutrient-poor, and highly dynamic environmental conditions. Consequently, they provide essential refuge for a unique assemblage of flora and fauna that cannot survive in closed-canopy woodlands, including rare pioneer plants, specialised invertebrates, reptiles, and ground-nesting birds. Because of their immense ecological value and high vulnerability to environmental change, these open habitats are classified as priority conservation areas and are strictly protected under the European Union's Habitats Directive and Natura 2000 network (European Commission, 1992; Natura 2000, n.d.).

In temperate European regions, maintaining an open landscape inherently requires constant disturbance to arrest the natural process of ecological succession, which would otherwise inevitably drive the system toward a closed-canopy woodland. Historically, lowland heathlands relied entirely on intense human intervention to maintain this arrested state. For centuries, traditional agro-pastoral practices, such as continuous livestock grazing, regular prescribed burning, and periodic sod-cutting, actively stripped accumulated nutrients and organic matter from the soil and continuously suppressed the establishment of tree saplings (Celaya et al., 2012; Smit et al., 2015; Webb, 1998). In contrast, the openness of coastal dunes was primarily maintained by natural abiotic disturbances, specifically wind erosion and the continuous displacement of sand, which prevented vegetation from fully stabilising the soil. However, this abiotic dynamism was supplemented by intense biotic disturbance, most notably through historical livestock grazing and the foraging pressure of large, widespread populations of the European rabbit (*Oryctolagus cuniculus*) (Hagen, 2022; Hoffmann et al., 2005; Provoost et al., 2011). Together, these synergistic forces of wind, fire, nutrient removal, and high-intensity herbivory created a constantly shifting, low-nutrient baseline that prevented dominant grasses and woody shrubs from overtaking these fragile ecosystems.

Today, however, the delicate balance that once sustained these open ecosystems has been fundamentally disrupted by a combination of changing land use (mainly urbanisation in dunes and abandonment in heathlands) and environmental pressures (mainly reduction of wind dynamics in dunes and atmospheric nitrogen deposition in heathlands). Together, these modern threats have led to an acceleration of ecological succession. At the local management scale, the widespread abandonment of traditional farming and grazing practices removed the primary mechanism that historically stripped nutrients from lowland heathlands (Piessens & Hermy, 2006; Webb, 1998). Concurrently, in coastal dunes, the natural and human induced biotic barriers against succession collapsed. During the 20th century, European rabbit populations were severely decimated by viral

diseases, primarily myxomatosis and Rabbit Hemorrhagic Disease (RHD) (Hagen, 2022; Lees & Bell, 2008; Letty et al., 2024; Provoost et al., 2011). Moreover, agricultural use of dunes rapidly ceased during the 20th century. The ecological consequences of losing these physical disturbances are further magnified by a pervasive, landscape-scale threat: atmospheric nitrogen deposition. Airborne nitrogen, originating from modern agricultural and industrial emissions, acts as a continuous fertiliser raining down on these naturally nutrient-poor soils. This rapid eutrophication eliminates the harsh conditions that characteristic pioneer species depend on, providing a competitive advantage to fast-growing, nutrient-demanding plants (Bobbink et al., 1998; De Schrijver et al., 2011; Roem & Berendse, 2000).

The physical manifestation of this altered environmental baseline is a rapid structural transformation of the landscape. Without regular disturbance to reset the successional clock, these ecosystems typically undergo two major, often concurrent trajectories of degradation: grass encroachment and woody encroachment. The expansion of tall, competitive grasses can frequently be triggered by nitrogen enrichment. In lowland heathlands, for example, species such as Purple moor-grass (*Molinia caerulea*) rapidly form thick, impenetrable mats that outcompete and smother characteristic low-growing herbs and dwarf shrubs (Aerts, 1989; Roem & Berendse, 2000; Webb, 1998). Similarly, the rapid expansion of woody species can be triggered by the loss of physical disturbance. In coastal dune systems, for instance, the decimation of European rabbit populations by viral diseases in the mid-20th century led to a successional shift driven by the extensive, clonal spread of Sea buckthorn (*Hippophae rhamnoides*) (Hagen, 2022). Ultimately, whether driven by the dominance of competitive grasses or the rapid spread of woody pioneers, these encroaching species merge to form a continuous cover. If left unchecked, they transition the historically open, dynamic landscape into a closed-canopy woodland, eliminating the structural openness of the original ecosystem.

The transition from a structurally diverse, open landscape to a closed-canopy woodland has devastating consequences for the characteristic biodiversity of these ecosystems. As woody species or dominant grasses form a continuous cover, the amount of solar radiation reaching the soil surface is drastically reduced. This canopy closure fundamentally alters the local microclimate, shifting it from warm and dynamic to consistently cool, humid, and shaded (Webb, 1998). Under these altered conditions, the highly specialised, light-demanding pioneer flora and low-growing herbs simply cannot survive. As the vegetation structure homogenises, the adapted fauna that rely on these specific microhabitats, such as thermophilous invertebrates, reptiles, and ground-nesting birds, are simultaneously driven out (Edgar et al., 2010; Wallisdevries & Van Swaay, 2006). Consequently, the highly specialised and threatened ecological communities of heathlands and coastal dunes undergo a rapid decline, ultimately being replaced by a poorer community of common, shade-tolerant generalist species (Grootjans et al., 2008; M. L. M. Jones et al., 2004; Kooijman & Besse, 2002; Webb, 1998).

To halt this trajectory of biodiversity loss and fulfil the strict conservation mandates of the Natura 2000 network, active management interventions are required to reset the successional clock. For decades, nature conservation agencies have primarily relied on intensive mechanical and manual techniques to maintain these open landscapes, such as large-scale mowing, mechanical sod-cutting, and the manual removal of woody scrub (Provoost et al., 2011; Webb, 1998). While effective on a small, localised scale, these conventional methods are exceptionally labour-

intensive, economically costly, and must be constantly repeated. Furthermore, mechanical interventions often fail to replicate the continuous, highly heterogeneous disturbance patterns that historically sustained these ecosystems. Consequently, there is a critical need for more sustainable, self-regulating, landscape-scale management strategies that can autonomously suppress dominant encroaching species and restore structural diversity. In response to this challenge, the targeted (re)introduction of large mammalian herbivores has emerged as one of the most prominent and ecologically promising solutions in modern European nature conservation (Bakker, 1989; Smit et al., 2015; Vera, 2000).

1.2. Large Herbivores as Ecosystem Engineers

When introduced into these overgrown landscapes, large mammalian herbivores do not merely consume vegetation; they actively function as 'ecosystem engineers'. First conceptualised in the 1990s, ecosystem engineers are defined as organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. Unlike mechanical interventions such as large-scale mowing or sod-cutting, which impose uniform, sudden, and temporary changes across a landscape, free-roaming megafauna introduce continuous, highly heterogeneous disturbance regimes. They actively shape their environment through a complex interplay of top-down consumptive effects, such as the targeted defoliation of dominant plant species, and bottom-up non-consumptive mechanisms, including trampling, soil compaction, and nutrient redistribution. By driving these dynamic ecological processes, large herbivores do not abruptly break the structural uniformity of closed canopies and encroaching grasses. Instead, over extended periods, their presence triggers a complex interplay of grazing pressure, shifting plant facilitation and competition, natural succession, and processes of decay. Through these sustained, long-term interactions, they continuously create and maintain a shifting mosaic of microhabitats, thereby restoring the structural and biological diversity essential for the survival of highly specialised open-landscape flora and fauna (Bakker, 1989; C. G. Jones et al., 1996; Lawton & Jones, 1995; Olff et al., 1999; Smit et al., 2015; Vera, 2000; Wright & Jones, 2006).

The top-down consumptive impact of these ecosystem engineers is highly species-specific, which is why modern conservation strategies frequently rely on mixed-species grazing regimes. Because no single herbivore species consumes all encroaching vegetation, introducing a diverse grazing guild ensures a complementary, landscape-scale impact (Bakker, 1989; Smit et al., 2015; Vera, 2000). These functional differences stem primarily from fundamental variations in their grazing strategies, mouth anatomy, digestive physiology, and spatial use patterns. For instance, equids are hindgut fermenters equipped with both upper and lower incisors and are capable of biting vegetation close to the ground. Conversely, cattle are ruminants whose dental anatomy restricts them to foraging on taller swards, typically requiring a vegetation height above 8 cm (Fleurance et al., 2022; López et al., 2019; Smit et al., 2015; Zielke et al., 2019). Ultimately, through this dietary complementarity, a mixed herd structurally shortens and opens up dominant grasses, alleviating competitive exclusion and providing the essential space and light necessary for a greater variety of subordinate plant species to establish. Additionally, it structurally degrades a wide variety of woody pioneers, collectively preventing canopy closure (Bakker, 1989; Kristensen et al., 2026; Vera, 2000).

Equally critical to their consumptive impact are the bottom-up or non-consumptive mechanisms by which large herbivores physically and chemically alter their environment. The mechanical force of heavy hooves trampling through the landscape breaks apart dense moss layers and thick grass root mats, actively creating patches of exposed bare mineral soil and sand (Henning et al., 2017; Lunt et al., 2021). Behaviours such as wallowing, dustbathing, and the creation of structural pathways introduce a chaotic, small-scale "messiness" that human machinery cannot replicate. This physical disturbance is an essential prerequisite for the germination of light-demanding pioneer seeds and restores the warm microclimates required by thermophilus fauna, such as reptiles and specialised invertebrates (Henning et al., 2017; Lunt et al., 2021; Wallisdevries & Van Swaay, 2006). Furthermore, free-roaming herbivores function as dynamic transport networks across the ecosystem. They consume biomass in one area and excrete it in another, fundamentally redistributing nutrients across the landscape (Bokdam & Gleichman, 2000). Alongside facilitating this nutrient transfer, these animals simultaneously act as critical dispersal vectors, carrying seeds across the landscape both internally via their dung (endozoochory) and externally on their hooves and fur (epizoochory) (Cosyns et al., 2005; Couvreur et al., 2004).

1.3. Spatial Ecology and Movement Behaviour

To fully harness the potential of large herbivores as ecosystem engineers, it is essential to understand not merely how they alter their environment, but exactly where these disturbances occur. Because free-roaming herbivores do not utilise landscapes uniformly, their structural and consumptive impacts are inherently spatially heterogeneous (Bailey et al., 1996; Senft et al., 1987). Spatial ecology provides the critical framework for quantifying these patterns, linking individual animal movements directly to environmental conditions and underlying resource availability (Northrup et al., 2022). Historically, assessing these movement patterns relied on broad, intermittent observational data (Lamoot et al., 2005). Today, however, high-resolution GPS telemetry has revolutionised the field, offering a powerful and precise tool to analyse fine-scale spatial behaviour and habitat use in complex environments such as coastal dunes and heathlands (Cagnacci et al., 2010; Nathan et al., 2008; Silva et al., 2022). By continuously tracking movement trajectories, modern telemetry datasets allow researchers to estimate individual home ranges and habitat preferences, seamlessly connecting behavioural ecology with landscape-level conservation management (Allen & Singh, 2016).

Through the lens of high-resolution tracking, it becomes clear that herbivore movement is rarely random but rather dictated by a complex interplay of natural drivers. At the landscape scale, space use is fundamentally constrained by abiotic factors, such as topography (e.g. slope) and the distribution of surface water (e.g. distance to water) (Bailey et al., 1996; Senft et al., 1987). These natural abiotic pressures are further compounded by seasonality. As weather conditions and resource availability fluctuate throughout the year, herbivores must dynamically adjust their habitat selection to balance nutritional requirements with thermoregulation (Dejeante et al., 2024; Ferreira et al., 2013; López et al., 2019).

While these abiotic and seasonal drivers theoretically dictate optimal space use, the reality for large herbivores in North-Western Europe is profoundly different. Ecosystems such as coastal dunes

and lowland heathlands are typically highly fragmented, anthropogenic landscapes where natural movement is artificially bounded (Tucker et al., 2018). In these settings, spatial ecology is heavily dictated by hard physical boundaries, most notably perimeter fences (Jakes et al., 2018; McInturff et al., 2020). Furthermore, this spatial confinement is compounded by internal human infrastructure. Dense networks of recreational paths and frequent anthropogenic disturbance force herbivores into complex behavioural trade-offs (Frid & Dill, 2002). Consequently, the habitat choices of these ecosystem engineers are rarely driven by natural preferences alone. Instead, they represent a continuous compromise between their biological needs and human spatial constraints.

To quantify this compromise, modern spatial ecology relies on two distinct but complementary metrics: home range estimation and habitat selection analysis. An animal's home range is defined as the area repeatedly used throughout its lifetime for all its normal behaviours and activities, excluding occasional exploratory excursions (Burt, 1943; Silva et al., 2022). Within those boundaries, habitat selection measures a finer-scale behavioural process, defined as the disproportionate use of specific habitat patches compared to their overall availability (Northrup et al., 2022). By disentangling these two metrics, it becomes possible to separate their broad spatial constraints from their fine-scale habitat choices, providing critical insight into their role as ecosystem engineers.

1.4. Study Species

1.4.1 The Equid Group: Konik Horses and Shetland Ponies in Coastal Dunes

The equid group in this study consists of two distinct breeds: Konik horses and Shetland ponies. The Konik is a hardy Eastern European breed that is often claimed to trace its lineage back to the extinct Tarpan (*Equus ferus ferus*) (Pasicka, 2013). However, recent research has definitively disproved this direct ancestral connection (Laidlaw, 2023; Lovász et al., 2021; Tjitze van Vuure, 2014). The Shetland pony is an ancient breed uniquely adapted to the harsh, nutrient-poor conditions of the Scottish islands (Porter et al., 2016). Historically restricted to their respective native ranges in Eastern Europe and northern Scotland, both breeds currently have a widespread European distribution. Because their evolutionary habitats required physiological hardiness and the ability to survive winter conditions without supplemental feeding, they have been broadly repurposed from domestic or feral populations into ecological management tools within fenced, semi-natural European nature reserves (Pasicka, 2013; Porter et al., 2016). Despite their hardiness in semi-wild conditions, neither breed can be managed entirely without human intervention. Legal and ethical welfare standards require managers to actively monitor the herds for food scarcity, heat stress, and parasite infections (Brinkmann et al., 2013; Górecka-Bruzda et al., 2020).

As hindgut fermenters, equids possess a digestive physiology that is relatively less efficient at extracting nutrients compared to ruminants. To compensate for this lower extraction rate, they must spend significantly more time feeding (Bergin et al., 2026; Ferreira et al., 2013; Lamoot et al., 2005; López et al., 2019). This grazing activity typically peaks in the morning and evening, with resting occurring mainly in the middle of the day (Ferreira et al., 2013). A defining anatomical feature of equids is the presence of two sets of incisors, which enable them to crop vegetation close to the ground, often accessing forage that is too short for bovids to consume. They preferentially select

short (≤ 4 cm) to intermediate regrowths, which allows them to actively create and maintain short-grass patches within a taller vegetation matrix (Fleurance et al., 2022).

Equids are grazers that occupy various open habitat types but show a marked preference for grass-dominated pastures (López et al., 2019; Popp & Scheibe, 2014; Zielke et al., 2019). This preference is also reflected in dynamic coastal dune ecosystems, where equids consistently select for grasslands over shrub or sandy areas (Cromsigt et al., 2018; Henning et al., 2017; Lamoot et al., 2005). Koniks, in particular, are well-documented as large, graminoid-focused grazers whose targeted grazing pressure is effective at suppressing tall, competitive pioneer grasses like *Calamagrostis epigejos* (Henning et al., 2017). However, while they can successfully shift dune systems away from tall grass dominance, their browsing pressure alone is often insufficient to reduce established woody scrub without additional intervention. Furthermore, the overarching ecological outcomes of equid grazing are heavily site- and intensity-dependent. As a management tool, the specific equid breed selection exerts less influence on the landscape than fundamental variables such as stocking rate, the existing habitat mosaic, and soil conditions (Hoffmann et al., 2005; Plassmann et al., 2010; Tahmasebi Kohyani et al., 2008).

Beyond foraging, equid spatial ecology is heavily dictated by complex behavioural and social dynamics. In multi-breed settings, they form tight, socially stratified herds, where dominant individuals can exert competitive exclusion, displacing subordinate individuals into peripheral or sub-optimal habitats (Ingólfssdóttir & Sigurjónsdóttir, 2008; Linnartz & Linnartz-Nieuwdorp, 2017; Lisa Nash et al., 1987).

While sharing these general equid traits, Konik horses and Shetland ponies differ significantly in morphology. Due to their distinct body sizes, with Koniks being considerably larger and heavier than Shetlands, their biomechanical capabilities and movement patterns across complex terrain likely diverge. However, there is currently a lack of empirical research directly comparing how the specific morphological differences between Koniks and Shetlands translate into divergent spatial behaviours within coastal dune ecosystems.

1.4.2. The Bovine Group: Galloway Cattle in Lowland Heathlands

The bovine group is represented by Galloway cattle, an ancient, naturally hornless (polled) breed originating from the province of Galloway in southwestern Scotland. The historical landscape of this region, characterized by high upland pastures, rich moorlands, and a damp, frequently cold climate, played a defining role in shaping the breed's physical hardiness (Mullen, 1902). Because this evolutionary adaptation makes them perfectly suited for year-round survival without supplemental feeding, they have been broadly repurposed from traditional agricultural populations into vital ecological management tools within fenced, semi-natural European nature reserves (Schaich et al., 2010). However, much like equids, they are not a completely maintenance-free management tool. Because year-round grazing on low-fertility heathlands can expose free-ranging cattle to severe mineral deficiencies and subsequent malnutrition, ethical management still requires active welfare monitoring or ensuring herd access to heterogeneous, higher-quality habitat patches (Wallisdevries, 1996).

As ruminants, cattle possess a specialized digestive system capable of efficiently breaking down fibre-rich diets, including coarse and woody plant material (Cromsigt et al., 2018; López et al., 2019). In general, cattle are classified as grazers that select habitats based on high nutritional value and high biomass production, preferring habitats that offer higher crude protein and lower fibre content (Cromsigt et al., 2018; Ferreira et al., 2013; López et al., 2019; Rivero et al., 2021). However, their foraging strategy is highly constrained by their mouth and dental anatomy. Because they lack upper incisors, they are unable to graze efficiently on the shortest patches, typically requiring an optimal sward height above 8 cm (Fleurance et al., 2022; López et al., 2019). In lowland heath ecosystems, cattle dynamically adjust their habitat use; they primarily graze on improved pastures and increase their use of the heathland matrix only when grass availability on those productive pastures declines (Ferreira et al., 2013; López et al., 2019). Even in heathlands without improved pastures (like the Kalmthoutse Heide) cattle actively increase their direct consumption of heather (*Calluna vulgaris*) as the grazing season progresses (Celaya et al., 2011; Grant et al., 1987). This dietary shift is facilitated by their ruminant physiology, which allows them to effectively detoxify the high concentrations of secondary plant compounds, such as tannins, inherently present in heather (López et al., 2019). Alongside their dietary habits, they exhibit periods of high activity during the early morning and late afternoon, separated by periods of low activity during which they typically select open areas to lie down, ruminate and rest (Ferreira et al., 2013; Popp & Scheibe, 2014). Ultimately, their continuous grazing and physical disturbance play a critical role in enhancing structural diversity within the heathland ecosystem (Bokdam & Gleichman, 2000).

In addition to their role as ecosystem engineers, cattle are highly social animals that rely on dominant-subordinate hierarchies to maintain herd stability. An individual's rank, primarily determined by age, breed, and longevity, allows dominant cattle to regulate immediate access to localized resources. However, recent evidence indicates that social dominance rank in cattle does not significantly dictate synchronized herd movements or overall spatial distribution. Their collective, landscape-scale movements are driven by environmental constraints rather than strict social hierarchies (Hubbard et al., 2021).

1.5. Knowledge Gaps and Research Questions

While the baseline benefits of conservation grazing are well established, conventional grazing regimes are often insufficient to fully arrest successional processes in heath and dune landscapes (Bokdam & Gleichman, 2000; Hagen, 2022; Lunt et al., 2021; Provoost et al., 2011; Webb, 1998). To optimize management, it is crucial to understand the site-specific spatial ecology of different grazer groups, such as hindgut-fermenting equids (e.g., Konik horses and Shetland ponies) and ruminant bovines (e.g., Galloway cattle). However, accurately quantifying these movement mechanisms remains methodologically challenging. Historically, studies have relied heavily on brief, intermittent observational windows, leaving a critical knowledge gap regarding long-term space use (Lamoot et al., 2005). Even when modern, continuous year-round GPS telemetry is employed, researchers often fail to account for the inherent temporal autocorrelation of the tracking data, severely compromising statistical inference (Fleming et al., 2015; Northrup et al., 2022; Silva et al., 2022). Furthermore, in the heavily fenced reserves typical of north-western Europe, conventional spatial estimators frequently suffer from 'spillover bias' by mathematically projecting animal space use across impassable physical barriers. Consequently, there is a critical need to

apply advanced, continuous-time movement models equipped with local boundary corrections to accurately map constrained space use (Hollins et al., 2024; Knight et al., 2009; Noonan et al., 2019). Ultimately, without statistically robust, boundary- and autocorrelation-corrected data that explicitly links the animals' spatial behaviour with ecosystem impact, our capacity to design evidence-based, site-specific grazing regimes is fundamentally restricted.

To address these critical knowledge gaps, this master's dissertation asks the following overarching research question: How do physical boundaries and abiotic factors shape the movement behaviour and habitat selection of large grazers in the Westhoek and the Kalmthoutse Heide, and to what extent does this spatial ecology drive vegetation dynamics within the Westhoek? To answer this, the study aims to quantify the boundary-constrained space use of equids (Konik horses and Shetland ponies) in the Westhoek and bovines (Galloway cattle) in the Kalmthoutse Heide. This research is conducted at Ghent University in close collaboration with the Research Institute for Nature and Forest (INBO), under the supervision of Prof. Dr. Jan Van Uytvanck, Marijke Thoonen MSc., and Sam Provoost MSc.. Furthermore, this dissertation is embedded within INBO's multi-year project (2020–2026) evaluating extensively grazed Flemish nature reserves (INBO, 2020). Regional policy is currently shifting from traditional pattern-based conservation toward climate-robust, process-driven management. Consequently, this work aims to directly inform and optimize the long-term management of these important ecosystems. By integrating continuous-time movement modelling with fine-scale vegetation, environmental and habitat data, this thesis sets out to achieve the specific research objectives and evaluate the working hypotheses detailed in the following chapter.

2. Research Objectives

Building upon the critical knowledge gaps identified in the previous chapter, the overarching aim of this master's dissertation is to unravel the complex spatial ecology of large grazer groups within two heavily fragmented north-western European ecosystems: a coastal dune reserve, the Westhoek, and a lowland heath reserve, the Kalmthoutse Heide. Specifically, this study seeks to quantify how physical boundaries and abiotic factors shape the movement behaviour and fine-scale habitat selection of equids (Konik horses and Shetland ponies) in the Westhoek and bovines (Galloway cattle) in the Kalmthoutse Heide, and to explicitly determine how these spatial patterns drive local vegetation dynamics within the Westhoek. To systematically address these goals, the research objectives and specific working hypotheses are operationalised into three interconnected Work Packages (WPs), transitioning from broad-scale space use (WP1) to fine-scale resource selection (WP2), and to ecosystem-level impacts (WP3).

2.1. Work Package 1: Boundary-Constrained Space Use

The primary objective of Work Package 1 (WP1) is to quantify the baseline spatial ecology of the targeted grazers by determining the biological saturation of their home ranges, mapping seasonal variations, and evaluating the impact of altered landscape connectivity. To achieve this, continuous-time movement modelling, specifically Autocorrelated Kernel Density Estimation (AKDE) with boundary correction, will be applied to the telemetry data. This approach explicitly corrects for inherent temporal autocorrelation, allowing for a statistically robust estimation of the boundary-constrained space use of equids in the Westhoek and bovines in the Kalmthoutse Heide. To address this objective, WP1 evaluates the following working hypotheses:

- **Hypothesis 1.1. Spatial Saturation:** Based on the calculated saturation index, the grazing species are predicted to utilize < 75% of the available landscape, thereby not exhibiting biological saturation within their respective fenced reserves.
- **Hypothesis 1.2. Seasonal Dynamics:** The seasonal AKDE home ranges of the grazers differ significantly in overall size, spatial location, and core-area centre. It is expected that these spatial shifts occur as the herbivores dynamically adjust their ranging behaviour in response to temporal fluctuations in resource availability, microclimate, and thermoregulatory requirements.
- **Hypothesis 1.3. Landscape Connectivity:** The restoration of landscape connectivity, specifically the opening of a corridor connecting the northern and southern sectors of the Westhoek in the winter of 2022-2023, caused a significant shift in the spatial ecology of the resident equids. This physical intervention is expected to have measurably altered the size, spatial location, or saturation index of the horse and pony home ranges.

2.2. Work Package 2: Fine-Scale Habitat Selection

The objective of Work Package 2 (WP2) is to determine the fine-scale habitat preferences of the different grazer groups across seasons, and to evaluate how underlying continuous constraints

modulate these behavioural choices. To accurately model resource selection within enclosed reserves, WP2 employs integrated Resource Selection Functions (iRSF). This advanced statistical framework explicitly resolves the challenge of defining habitat availability by using each individual's boundary-corrected home range (AKDE) as the availability baseline, ensuring that selection is evaluated strictly within the context of the habitats the animal actively had access to. By incorporating both categorical habitat maps and a set of continuous environmental and anthropic variables, this work package evaluates the following working hypotheses:

- **Hypothesis 2.1. Baseline-Relative Selection:** The targeted grazers exhibit distinct, non-random habitat preferences. It is expected that herbivores will disproportionately select for resource-rich, structurally open vegetation matrices (e.g., grasslands) relative to a pre-defined baseline habitat category.
- **Hypothesis 2.2. Abiotic Constraints:** Fine-scale selection is significantly constrained by natural landscape features. Based on physiological and biomechanical requirements, it is hypothesised that herbivores will actively select for areas in closer proximity to surface water and they are expected to prefer flatter terrain (avoiding steep slopes).
- **Hypothesis 2.3. Anthropogenic Avoidance:** In addition to natural landscape gradients, animal space use is modulated by human infrastructure. It is expected that grazers will exhibit spatial avoidance of anthropogenic features, disproportionately selecting for areas further away from path networks (which encompass both recreational trails and service roads) and further from the reserve perimeters/fences.

2.3. Work Package 3: Spatial Ecology and Vegetation Dynamics

The final objective, addressed in Work Package 3 (WP3), is to explicitly link the quantified herbivore movement behaviour to landscape-level ecological impacts, while simultaneously accounting for underlying environmental drivers. Specifically, this package aims to determine the extent to which the terrain use of the equids, relative to abiotic factors, drives local vegetation dynamics within the Westhoek. To achieve this, high-resolution vegetation height data recorded in 2020 and 2025 will be used to quantify structural landscape alterations, categorising every spatial pixel into distinct vegetational transition states (Regression, Stable, or Encroachment). By integrating the cumulative spatial use of the grazers with fine-scale environmental gradients, WP3 evaluates the following working hypotheses:

- **Hypothesis 3.1. Terrain Use Impact:** Terrain use intensity will function as a significant driver of structural vegetation change. It is expected that high cumulative space use by equids will actively suppress and reverse successional advancement, correlating negatively with Encroachment and positively with Regression of rough vegetation and scrub.
- **Hypothesis 3.2. Abiotic Drivers:** In addition to herbivore pressure, fine-scale abiotic gradients will independently dictate successional trajectories. It is hypothesised that hydrological constraints (groundwater depth) will function as a primary limiting factor for deeper-rooted woody species (modulating scrub growth and encroachment via

desiccation), while the expansion and regression dynamics of shallower-rooted grasses and herbs will be driven by high environmental stress, such as erosion on steep terrain slopes and drought from high solar exposure and deep groundwater tables.

3. Materials and methods

3.1. Study Areas

This research was conducted within two distinct, fenced nature reserves situated in the Flanders region of Belgium: the coastal dune ecosystem of the Westhoek and the lowland heathland ecosystem of the Kalmthoutse Heide. These specific sites represent two contrasting, historically open habitats that currently rely on the extensive grazing of large herbivores to mitigate structural encroachment. Both study areas fall under a temperate maritime climate (Köppen climate classification Cfb), characterised by mild winters, relatively cool summers, and fairly evenly distributed precipitation throughout the year (Beck et al., 2018). While they share this overarching macroclimate, the two reserves diverge significantly in their underlying geomorphology, local hydrology, and successional vegetation dynamics, providing a robust comparative framework for evaluating grazer spatial ecology.

3.1.1. The Westhoek (Coastal Dune Ecosystem)

The Westhoek is a coastal dune reserve located in the municipality of De Panne, in the extreme west of Flanders, along the French border. Protected in 1957 as the very first public nature reserve in the Flemish region, it currently preserves 340 hectares of an originally 550-hectare coastal dune complex and is managed by the Flemish Agency for Nature and Forests (ANB) (Leten et al., 2022).

Geomorphologically, the reserve encompasses a complete coastal gradient, ranging from upper beach pioneer habitats and stabilized front dunes to a complex spatial matrix of parabolic dune slacks, steep dune ridges, and coppice dunes. The landscape was historically defined by open, shifting sands, which included a massive central (formerly) mobile dune locally known as the 'Sahara' (spanning 60 to 100 hectares) (Leten et al., 2022). However, this dynamic system has undergone significant successional stabilisation over the past several decades. The process of widespread woody encroachment has been underway since the mid-twentieth century, driven largely by the historical release of grazing pressure around World War II (Provoost & Declerck, 2021). Today, the vegetation comprises a diverse mosaic of calcareous dune grasslands, moss dunes, and extensive scrub patches. Crucially, this encroachment occurs in distinct structural phases. The initial pioneer scrub phase is characterized by the expansion of low-growing scrub species such as Sea buckthorn (*Hippophae rhamnoides*), Creeping willow (*Salix repens* subsp. *dunensis*), and Wild privet (*Ligustrum vulgare*). Over time, these pioneer patches facilitate secondary scrub formation, developing into a taller, more complex structural layer comprising species like Hawthorn (*Crataegus monogyna*) and Blackthorn (*Prunus spinosa*) (Provoost & Declerck, 2021). Distinguishing between these low pioneer stages and taller, secondary scrub is relevant to ecosystem management, as large grazers exert fundamentally different top-down foraging pressures and structural impacts on these two phases. Without intervention, this successional trajectory can change open pioneer stages into closed, person-high scrub in less than a decade (Leten et al., 2022; Provoost & Declerck, 2021).

To mitigate this rapid structural encroachment and maintain the biodiversity of the open dune matrix, the reserve is managed via a combination of targeted mechanical interventions and year-

round extensive grazing. Notably, the active clearance of multiple hectares of established woodland and scrub has fundamentally reshaped the spatial distribution of available habitats across the reserve. Because these large-scale removals create new patches of open pioneer vegetation, they directly influence the spatial movement and subsequent foraging patterns of the resident herbivores. The grazing group consists of equids, specifically Konik horses (*Equus caballus*) and Shetland ponies (*Equus caballus*), which share the landscape with a herd of Scottish Highland cattle (*Bos taurus*) (though these were not tracked) (Table 1).

Spatially, the movement of these herbivores is constrained by management infrastructure, including hard perimeter fencing. The total available grazing area analysed in this study encompasses approximately 170 hectares. Crucially for the spatial ecology of the resident grazers, this fenced block was historically fragmented into a distinct northern (98.6 ha) and southern (67.4 ha) sector. In the winter of 2022-23, a management intervention restored year-round landscape connectivity by opening a physical corridor between these zones, allowing the grazers to range across the fully integrated reserve (Figure 1).

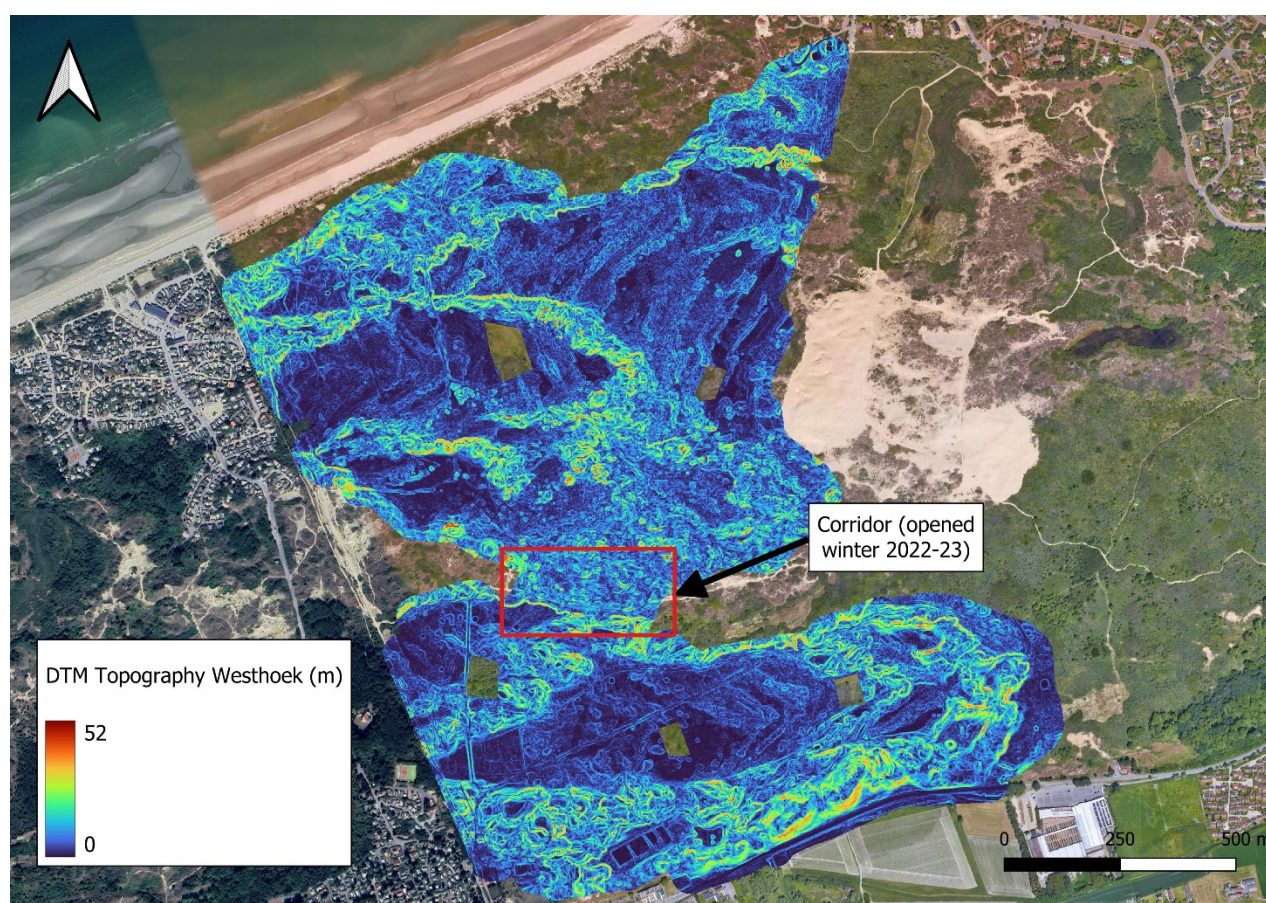


Figure 1. Topography of the Westhoek grazing reserve (170 hectares). The map illustrates the geomorphology of the coastal dune ecosystem based on a Digital Terrain Model (DTM, 1 m resolution) (Digitaal Vlaanderen, 2015). The displayed boundary represents the management outer perimeter expanded by a 40-meter buffer. Note the location of the management corridor (opened in the winter of 2022-23) connecting the historically separated northern and southern sectors.

3.1.2. The Kalmthoutse Heide (Lowland Heath Ecosystem)

The Kalmthoutse Heide is a prominent cross-border nature park, with the Belgian portion situated in the province of Antwerp, directly adjacent to the Dutch border, preserving a total area of approximately 6,000 hectares (Grenspark Kalmthoutse Heide, n.d.). The specific study area encompasses a fenced grazing block spanning approximately 565 hectares (Figure 2). The Kalmthoutse Heide is an inland sand dune ecosystem featuring prominent drift dune complexes, with some dune tops (such as the Kambuusduinen and Hazenduinen) reaching up to 30 meters above sea level. Crucially, in contrast to the calcareous coastal dunes of the Westhoek, the inland sands of the Kalmthoutse Heide are decalcified. This acidic, nutrient-poor soil chemistry establishes a fundamentally different botanical baseline. Within this ecosystem, spatial heterogeneity is driven by the complex interaction between the topography, the soil, and fine-scale variations in hydrology. A critical sub-surface feature is the 'Kempen clay' layer (*Klei van de Kempen*), which acts as a semi-impermeable barrier separating deep and shallow groundwater systems. These underlying abiotic gradients and the resulting groundwater fluctuations create a complex, moisture-dependent mosaic, differentiating the landscape into dry heathlands on the elevated sandy ridges and wet heathlands or oligotrophic fens in the waterlogged depressions (De Blust, 2018).

The historical and characteristic vegetation of the reserve is dominated by dwarf shrubs, specifically Common heather (*Calluna vulgaris*) in the dry zones and Cross-leaved heath (*Erica tetralix*) in the wetter, low-lying depressions. However, the open structural character of this ecosystem is currently undergoing rapid successional shifts. While woody encroachment is an inherently natural process that contributes to the overall biodiversity and structural complexity of the landscape, anthropogenic drivers heavily amplify its current trajectory. Specifically, historical drainage via ditch networks (desiccation) and atmospheric nitrogen deposition have artificially accelerated these spontaneous transitions (De Blust, 2018). Consequently, the heathland is experiencing widespread grass encroachment, overwhelmingly dominated by Purple moor-grass (*Molinia caerulea*), alongside the rapid pioneer establishment of woody species such as pine (*Pinus* spp.) and birch (*Betula* spp.). Furthermore, elevated nitrogen levels have facilitated the expansion of the invasive Heath star moss (*Campylopus introflexus*) across the open sandy patches (De Blust, 2018).

To mitigate severe grass encroachment and maintain the structural diversity of the heathland matrix, the reserve is managed via targeted grazing. Historically, this management objective was pursued using a traditional seasonal flock of approximately 350 sheep, supplemented by a small seasonal herd of Icelandic horses (*Equus caballus*) and Galloway cattle (INBO, 2025). However, the focal management group in the Kalmthoutse Heide has shifted in the period of 2021-2024 to bovines, specifically to a herd of 36 Galloway cattle (INBO, 2025) (Table 1).

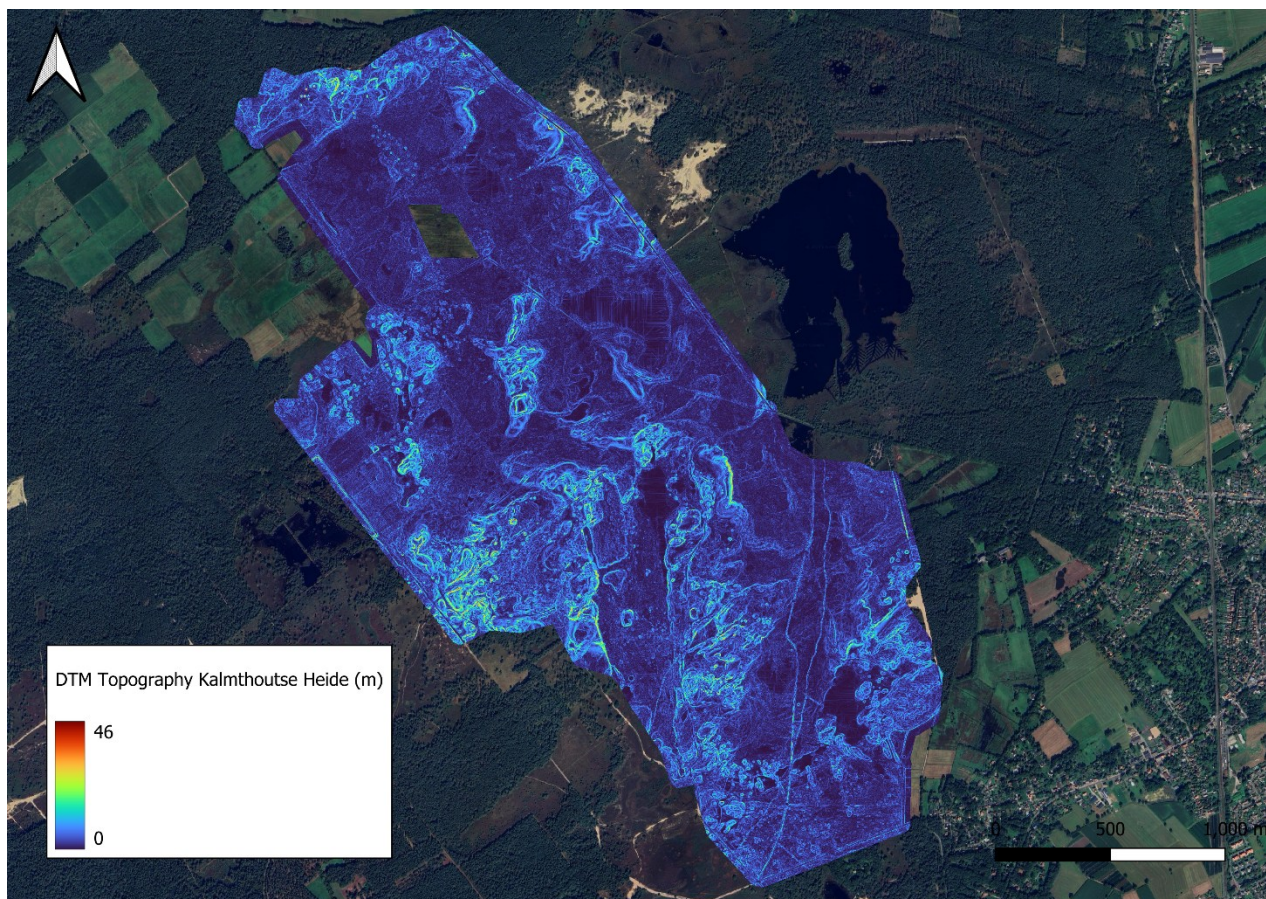


Figure 2. Topography of the Kalmthoutse Heide grazing reserve (565 hectares). The map illustrates the geomorphology (albeit heavily influenced by human sand extraction in the 20th century) of the heath ecosystem based on a Digital Terrain Model (DTM, 1 m resolution) (Digitaal Vlaanderen, 2015). The displayed boundary represents the management perimeter expanded by a 40-meter buffer.

3.2. Study Species & Telemetry Data Collection

3.2.1. Data Acquisition and Hardware

To continuously monitor the spatial ecology and habitat selection of the focal herbivore groups, representative individuals were equipped with commercial GPS telemetry tracking collars (Digit Animal / Sensolus). To ensure a high-resolution spatial trajectory while balancing the battery life of the devices, all collars across both study areas were programmed with a standardized temporal fix rate, recording a geographic location once every 30 minutes (Table 1).

Table 1. Overview of the large herbivore herds present within the study areas, detailing the total population size, the specific subset of individuals equipped with GPS telemetry collars and the grazing regime during the 2021–2024 tracking period.

Study area	Grazer species	Total population size	Collared individuals	Grazing regime
Westhoek	Konik horse	17, 3 sub-herds of 4, 6, and 7	3 (1 per sub-herd)	year-round

	Shetland pony	5 (2021-22), 4 (2023-24)	1	year-round
	Scottish Highland cattle	6 (2022-23), 10 (2024)	0 (untracked)	year-round
Kalmthoutse Heide	Galloway cattle	36	3 (4 in 2021)	autumn, spring, summer

Within the Westhoek coastal dune reserve, a total of four collars were continuously deployed between 2021 and 2024 (Figure 3). To capture a representative spatial and demographic sample of the resident population, these devices were deliberately distributed across distinct social groups and spatial zones. One tracking device (ID: AN785) was fitted to a Shetland pony representing a mixed demographic herd. The remaining three collars (IDs: AN788, AN789, and AP513) were fitted to Konik horses representing three distinct social sub-herds, which consisted of one bachelor group of stallions (AN788) and two mixed demographic herds comprising mares, a stallion, yearlings, and foals (AN789 and AP513). During the initial separated phase of the reserve, so prior to the opening of the central corridor, these tracked animals were physically divided by infrastructure. The Shetland pony (AN785) and the AN789 Konik sub-herd were confined to the southern compartment, while the AN788 and AP513 Konik sub-herds were restricted to the northern compartment.

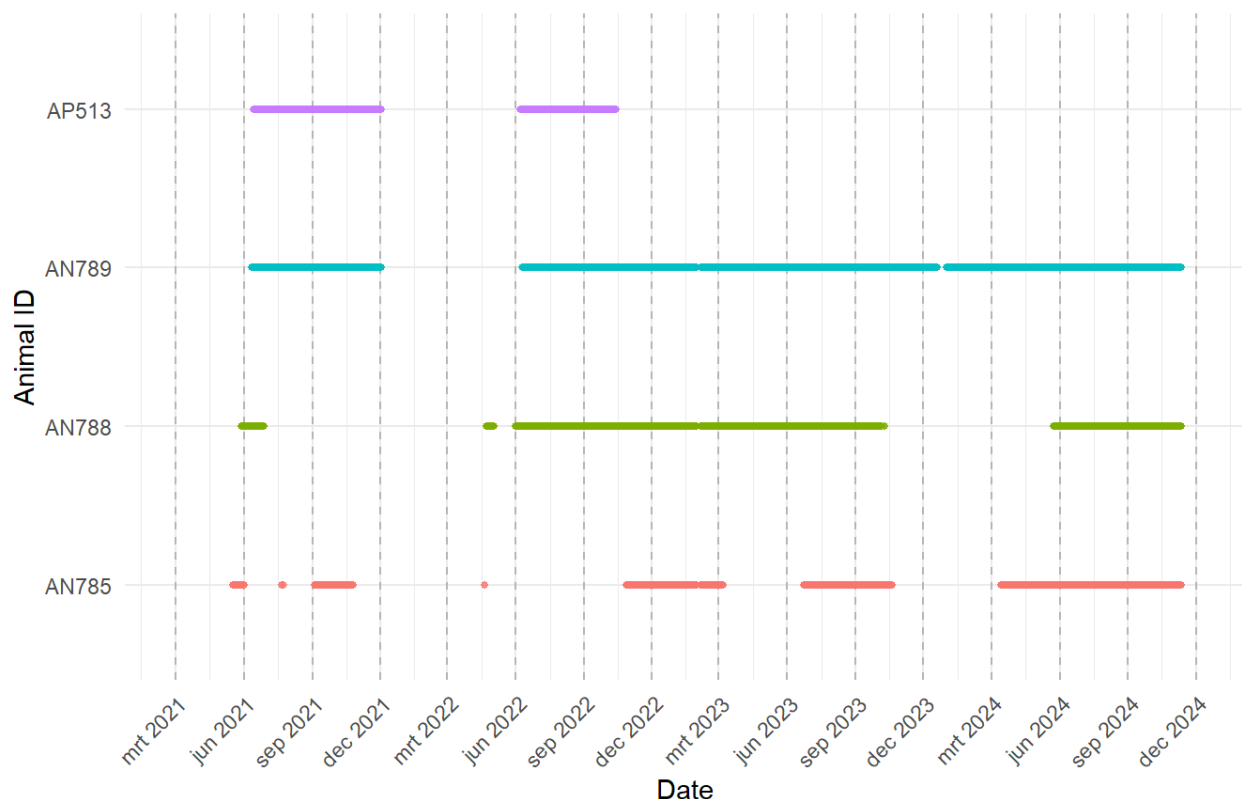


Figure 3. Temporal coverage of the GPS telemetry data collected in the Westhoek during the 2021-2024 study period. The timeline illustrates the active tracking periods for each individual collar deployed on the grazers, highlighting both the continuous tracking phases and the intermittent gaps where data collection failed.

Within the Kalmthoutse Heide lowland heath ecosystem, tracking focused on a herd of Galloway cattle. A total of four GPS collars (IDs: AP518, AP519, AP521, and AP522) were deployed on adult individuals within this herd to track their spatial behaviour during the targeted seasonal grazing windows spanning the 2021-2024 period (Figure 4).

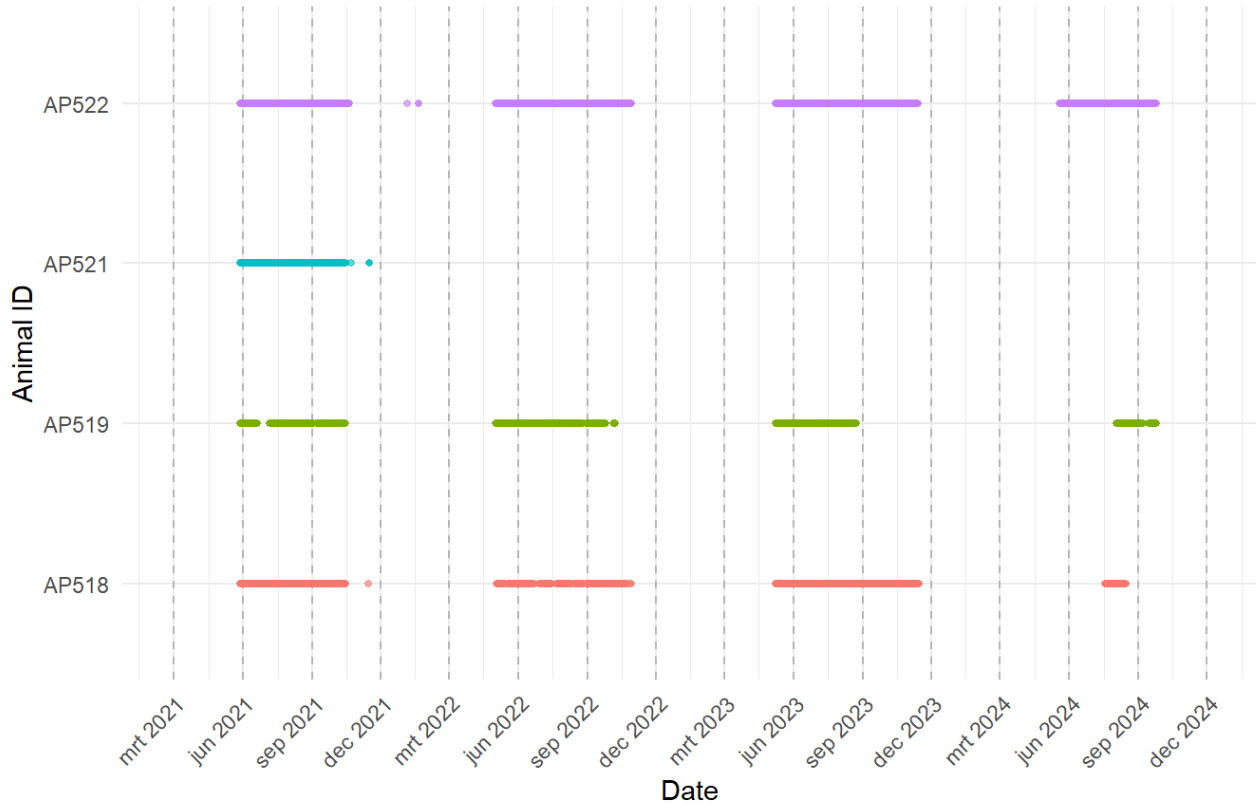


Figure 4. Temporal coverage of the GPS telemetry data collected in the Kalmthoutse Heide during the 2021-2024 study period. The timeline illustrates the active tracking durations for each individual collar deployed on the grazers, highlighting both the successful seasonal grazing windows and the periods where spatial data was unavailable.

3.2.2. Temporal, Attribute and Spatial Cleaning

All spatial data pre-processing and quality control procedures were primarily conducted in the R programming environment, using various data manipulation and spatial analysis packages, predominantly *tidyverse*, *dplyr*, *sf*, and *lubridate*. To ensure full methodological transparency and reproducibility, all custom R scripts and spatial workflows utilized throughout this study are permanently accessible in a digital repository (see Section 10. Attachments). The raw telemetry datasets generated by the collars were first subjected to attribute cleaning, which included the identification and removal of exact duplicate tracking records. To ensure accurate distance and area calculations in subsequent spatial analyses, all geographic coordinates were transformed from the global WGS84 reference system (EPSG:4326) to the local Belgian Lambert 72 coordinate reference system (EPSG:31370).

After initial formatting, the dataset was screened for temporal consistency. By calculating the time between consecutive GPS fixes, the data was checked for recording gaps to verify whether the collars successfully maintained their programmed 30-minute recording interval. Furthermore,

biological filtering was applied to exclude tracking periods that did not represent true animal movement. This was achieved through a visual assessment of the spatial trajectories and spatial distributions using Geographic Information System (GIS) software (QGIS). Specific seasonal tracking periods for individual collars were systematically excluded from the dataset if their home range sizes were unrealistically small, strongly indicating that the collar had detached from the animal.

Finally, to ensure that the analysed tracking data exclusively represented habitat selection within the designated management zones, the point data was spatially filtered. Using the *st_within* function in R, the coordinate data was intersected with the defined management perimeter polygons. Crucially, a 40-meter spatial buffer was applied to the outer reserve perimeters to account for inherent GPS location error. This buffer ensured that valid spatial fixes representing 'fence-hugging' behaviour, where animals navigate or forage immediately adjacent to the physical fence line, were not erroneously excluded from the dataset due to telemetry noise. Without this buffer, strictly filtering coordinates based on the exact physical boundary would risk systematically underestimating the animals' true presence along the reserve margins.

3.2.3. Dynamic Spatial Boundaries: The Westhoek Corridor Intervention

A critical methodological consideration in the spatial pre-processing of the Westhoek telemetry data was the management intervention executed during the winter of 2022–2023, which opened a physical connecting corridor between the historically separated northern and southern grazing sectors (Figure 1). To ensure that habitat availability and structural covariates accurately reflected the true landscape accessible to the herbivores at any given time, the physical environment was modelled dynamically using two distinct environmental raster scenarios: a 'CLOSED' landscape matrix and an 'OPEN' landscape matrix. Spatial covariates sensitive to reserve geometry, such as the 'distance to fence' raster, were calculated independently for both scenarios.

However, because an exact administrative management record detailing the precise date of the fence removal was unavailable, the transition timeline between these two spatial states had to be estimated. To resolve this undocumented timeline, a retrospective spatial telemetry analysis was conducted to identify the precise temporal point at which the first collared equids crossed the internal boundary into the previously inaccessible sector. This initial data-driven animal crossing was subsequently established as the operational proxy for the corridor opening date. During the subsequent movement modelling and Resource Selection Function (RSF) phases, the telemetry datasets were temporally stratified based on this estimated threshold. Tracking data recorded prior to this calculated crossing point (2021–2022) was exclusively paired with the CLOSED environmental stack, which maintained the internal partition as a hard barrier. Conversely, telemetry data recorded after the estimated intervention date (late 2022–2024) was paired with the OPEN environmental stack, representing the fully integrated reserve. While this movement-based proxy provided a robust and functional timeline for data stratification, the inherent reliance on initial animal displacement rather than an official physical management log warrants careful interpretation when assessing immediate pre- and post-corridor spatial expansions.

3.2.4. Telemetry Performance and Final Dataset

Westhoek Coastal Dune Ecosystem (Equid Group)

Between May 2021 and November 2024, GPS telemetry data were recorded for a total of 4 individuals, comprising 3 Konik horses and 1 Shetland pony. Following the initial data filtering and quality control procedures (as detailed in Section 3.2.2), a final dataset of 116,958 GPS locations was retained for subsequent spatial analysis.

Overall device performance was reliable, though variable between individuals. While the collars successfully maintained the programmed sampling interval, the fix success rate averaged 57.6% across the sampled population. This fix success rate is defined as the proportion of successfully recorded locations relative to the theoretical maximum expected under the programmed schedule. These missed fixes were adequately resolved by the continuous-time movement modelling framework, which mathematically accounts for irregular sampling frequencies. A summary of individual tracking durations, data volumes, and specific fix success rates is provided in Table 2.

To facilitate the macro-level spatial modelling in WP1, these continuous tracking durations were segmented into distinct biological seasons. Employing a minimum spatial data threshold of $\text{DOF} \geq 4$ (see Section 3.4.1 for methodology), this segmentation yielded a total of 38 successfully estimated individual-season home ranges for the Westhoek equids (spring: $n = 8$; summer: $n = 11$; autumn: $n = 12$; winter: $n = 7$). These equid totals include 8 successfully estimated individual-season home ranges for the single Shetland pony (spring: $n = 2$; summer: $n = 1$; autumn: $n = 3$; winter: $n = 2$).

Table 2. Summary of GPS telemetry performance for tracked Konik horses and Shetland ponies, detailing individual tracking durations, total retained spatial fixes, and the success rate of the programmed 30-minute sampling interval.

Animal ID	Species	Tracking Duration (Days)	Interval (min)	Total Retained Fixes	Fix Success Rate (%)
AN785	Shetland pony	1,275	30	24,442	39.9%
AN788	Konik horse	1,264	30	31,196	51.4%
AN789	Konik horse	1,250	30	47,237	78.8%
AP513	Konik horse	486	30	14,083	60.3%
Overall	Average	1,069	30	116,958 (total)	57.6%

Kalmthoutse Heide Lowland Heath Ecosystem (Galloway Cattle)

Between May 2021 and September 2024, GPS telemetry data were recorded for a total of 4 Galloway cattle in the Kalmthoutse Heide reserve. Following identical initial data filtering and quality control procedures as applied to the Westhoek population, a final dataset of 27,060 GPS locations was retained for spatial analysis.

Device performance across the Kalmthoutse Heide deployment remained reliable. Crucially, because all grazers were physically removed from the reserve during the winter months, expected recording schedules were mathematically adjusted to calculate success rates based strictly on active tracking days. During these active deployment periods, the collars successfully maintained

their programmed sampling intervals (30 minutes for three individuals, and 60 minutes for one individual), achieving an overall fix success rate of 42.6%. As with the previous dataset, the continuous-time movement modelling framework successfully resolved these irregular sampling frequencies to prevent artificial spatial inflation. A summary of individual active tracking durations, data volumes, and specific fix success rates is provided in Table 3.

Segmenting these active tracking periods yielded a total of 33 successfully estimated individual-season home ranges for the Galloway cattle (spring: $n = 9$; summer: $n = 13$; autumn: $n = 11$). Consistent with management practices, no winter tracking models were generated as the herd is removed from the reserve during this season.

Table 3. Summary of GPS telemetry performance for tracked Galloway cattle in the Kalmthoutse Heide, detailing active tracking durations, total retained spatial fixes, and the success rate of the programmed sampling interval.

Animal ID	Species	Active Tracking Duration (Days)	Interval (min)	Total Fixes	Retained	Fix Success Rate (%)
AP518	Galloway cattle	490	30	7,411		31.5%
AP519	Galloway cattle	407	60	4,238		43.4%
AP521	Galloway cattle	143	30	4,003		58.3%
AP522	Galloway cattle	643	30	11,408		37.0%
Overall	Average	421	38	27,060 (total)		42.6%

3.3. Environmental Data and Spatial Covariates

3.3.1. Topographical and Hydrological Variables

To evaluate the influence of terrain on both herbivore movement and vegetation dynamics, high-resolution topographical data was acquired for both study areas. A Digital Terrain Model (DTM) with a 1-meter spatial resolution was sourced from the *Digitaal Hoogtemodel Vlaanderen II* (DHMV II), provided by Digitaal Vlaanderen (Digitaal Vlaanderen, 2015). Using this elevation data, a continuous slope raster (measured in degrees) was calculated for both the Westhoek and the Kalmthoutse Heide. Capturing these topographical gradients is critical for the spatial models, as it allows for the explicit testing of selective or biomechanical constraints when animals navigate complex terrain, such as the steep coastal dune ridges.

In addition to slope, specific abiotic rasters were generated exclusively for the vegetation dynamics modelling (WP3) in the coastal dune ecosystem to account for hydrology and microclimate. First, to quantify local hydrological constraints, a continuous groundwater depth raster was incorporated. Derived from the 'Beheersevaluatie Kust' report, this layer specifically represents the average spring groundwater level, calculated over the 2014-2018 period, and is expressed in meters below ground level (Provoost et al., 2020) (Figure 5). Second, a custom solar index raster at a 5-meter resolution was generated to quantify fine-scale microclimatic variations (Figure 5). Using the *terra* package in R, this index was generated by simulating the sun's trajectory across the landscape during the summer solstice (June 21st) at the local latitude (51°N). By integrating the terrain's underlying slope and aspect, the model calculated hourly surface illumination based on the Cosine Law and averaged these values into a normalized scale ranging from 0 to 1. Higher relative values (e.g., > 0.50) represent topographical features, such as flat dune tops or south-facing slopes, which

receive maximum direct sunlight, thereby fostering a hotter and drier microclimate. Conversely, lower relative values represent shaded topography, such as steep north-facing slopes or deep hollows, which are shielded from direct solar radiation and subsequently maintain a cooler, wetter microclimate.

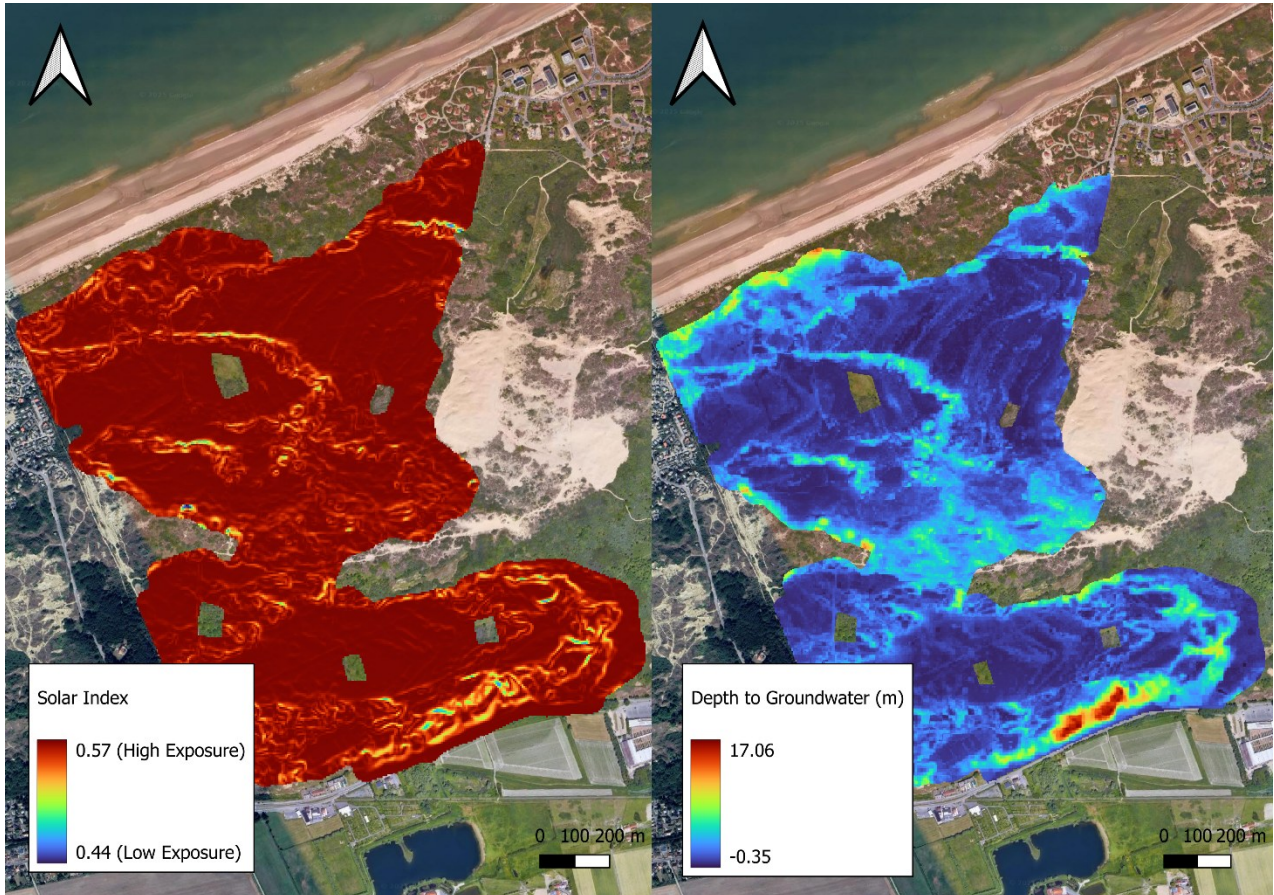


Figure 5. Abiotic covariates generated for the Westhoek coastal dune ecosystem to model vegetation dynamics. (Left) A custom 5-meter resolution, normalized Solar Index that reflects localized solar exposure, ranging from shaded, cooler microclimates (0.44) to more exposed, hot topography (0.57). (Right) Average Spring Groundwater Depth calculated over the 2014–2018 period, expressed in meters below ground level (Provoost et al., 2020).

Crucially, the decision to exclude the groundwater depth raster as a covariate from the equid movement models (WP2) was a deliberate ecological choice. Large herbivores actively navigate the landscape based on perceptible environmental cues, such as visual topography and the immediate energetic cost of traversing a slope. Unlike terrain steepness, sub-surface groundwater depth cannot be directly perceived or intentionally targeted by an animal. While shallow groundwater can breach the surface to form permanent perceptible pools, this specific dynamic is already explicitly captured within the movement models by the 'distance to open water' covariate (Section 3.3.2). Therefore, including groundwater depth as a predictor in WP2 would misrepresent actual behavioural selection. Conversely, because hydrology is a fundamental, physiological driver of plant succession regardless of sensory perception, the groundwater depth raster was strictly retained alongside slope as an independent predictor for the vegetation dynamics models (WP3). This distinction was supported by a Variance Inflation Factor (VIF) check prior to modelling. The

VIF confirmed that terrain slope and groundwater depth did not exhibit detrimental multicollinearity, reinforcing that the variables are statistically uncorrelated.

3.3.2. Distance-based Covariates (Resources and Infrastructure)

To evaluate the influence of critical resources, path infrastructure, and physical barriers on herbivore space use, three continuous distance-based covariates were generated: Distance to Water, Distance to Path, and Distance to Fence. For all three variables, Euclidean distance rasters (measured in meters) were calculated from the source vector layers using the R programming environment.

Distance to Water

Proximity to fresh water is an important driver of large herbivore distribution (Kristensen et al., 2026; Rech et al., 2025). Because the available habitat data differed between the two regions, water bodies were extracted using different maps. For the Westhoek, standing water bodies were extracted from a vegetation map provided by the Research Institute for Nature and Forest (INBO) (Provoost et al., 2010). For the Kalmthoutse Heide, water bodies were identified and extracted using specific habitat codes from the 'Biologische Waarderingskaart' (BWK) (Vriens et al., 2011). Once extracted, a continuous Euclidean distance raster was generated, calculating the distance from every pixel within the reserve to the nearest available water source.

Distance to Path

Recreational and service paths serve a dual ecological function: they can function as a source of anthropogenic disturbance (e.g., hikers and free-roaming dogs) or as corridors of least resistance for animal movement. Similar to the water variable, the path networks were sourced distinctly for each reserve. In the Westhoek, the path network was derived from the site-specific vegetation map. Crucially, the majority of the paths within the Westhoek grazing blocks function as service roads that are inaccessible to the general public, presenting low human disturbance. The primary exception is a heavily trafficked east-west sandy footpath running through the corridor that connects the northern and southern grazing blocks. In the Kalmthoutse Heide, an up-to-date path network was extracted from OpenStreetMap (OSM) vector data using the QuickOSM plugin within QGIS. Continuous distance rasters were subsequently calculated from these line features.

Distance to Fence and Dynamic Boundaries

Because both study areas are fenced nature reserves, the management perimeter can function as a hard physical constraint on animal movement. The edges of the reserve polygons for both study areas were converted into line features to calculate the continuous distance to the nearest physical barrier. Crucially, to mathematically account for the Westhoek corridor intervention (as detailed in Section 3.2.3), two distinct 'Distance to Fence' rasters were generated: a 'Closed' scenario and an 'Open' scenario. These rasters were then paired with the temporally stratified telemetry data to ensure all spatial calculations matched the physical reality of the reserve.

3.3.3. Habitat and Vegetation Classification

To evaluate the selective foraging strategies and habitat preferences of the different herbivore groups, categorical vegetation maps were acquired for both study areas.

For the Westhoek, habitat classification was based on a vegetation map provided by the Research Institute for Nature and Forest (INBO) (Provoost et al., 2010). For the Kalmthoutse Heide, spatial habitat data was sourced from the 'Biologische Waarderingskaart' (BWK) (Vriens et al., 2011). Because the raw BWK contains a high diversity of specific classifications, the Kalmthoutse Heide data was aggregated into distinct groups. This aggregation was performed specifically to reduce analytical complexity and facilitate a clearer, more robust ecological interpretation of herbivore behaviour. Based on expert opinion, the highly detailed BWK polygons were grouped into broader habitat categories (e.g., combining various degraded grass states into a single 'grass-encroached dry heath' class). These broader categories better reflect the actual scale at which large herbivores make their foraging decisions.

During spatial processing, open water habitat classes were systematically removed from the categorical map to prevent confounding effects, as the behavioural response to water was explicitly evaluated via the continuous 'Distance to Water' covariate. The decision to employ a spatial gap-filling procedure rather than traditional NA masking was driven by strict computational constraints. The Resource Selection Function (RSF) modelling framework required a continuous, unbroken spatial matrix and failed to process missing (NA) values within the availability grid. Furthermore, assigning a dummy categorical value to these pixels was not a viable alternative, as it would mathematically reintroduce the exact confounding effect the exclusion sought to prevent. Therefore, to satisfy these algorithmic requirements, a nearest-neighbour focal modal filter was applied in R, replacing the excluded water pixels with the surrounding terrestrial habitat. While this computationally necessary step marginally alters the fine-scale availability of terrestrial habitats, it was the most robust methodological compromise to ensure model stability without introducing confounding variables or causing computational failure. This procedure successfully produced a continuous, unbroken categorical raster for both reserves.

3.3.4. Raster Alignment and Variable Standardization

To ensure analytical precision and mathematical consistency across the spatial models, all environmental data layers were strictly aligned prior to extraction. First, continuous distance rasters, topographical variables, and categorical habitat maps were cropped and masked to the respective reserve boundaries, inclusive of the previously established 40-meter spatial buffer. Subsequently, all layers were resampled to match a perfectly aligned master grid based on the topographical data, standardized to the Belgian Lambert 72 coordinate reference system (EPSG: 31370) at a fine-scale spatial resolution of 1 meter. During resampling, continuous covariates were aligned utilising bilinear interpolation, whereas categorical habitat boundaries were strictly preserved using nearest-neighbour assignment. Finally, to allow for the direct comparison of effect sizes (coefficients) within the Resource Selection Function (RSF) models, all continuous spatial covariates were standardized using Z-score scaling. Prior to final model fitting, multicollinearity among these

standardized continuous variables was formally assessed using Pearson correlation matrices to ensure spatial independence.

3.4. WP1: Movement Models and Home Ranges

3.4.1. Autocorrelated Kernel Density Estimation (AKDE)

To accurately quantify herbivore space use, home ranges were estimated using the *ctmm* (Continuous-Time Movement Modelling) package in R (Calabrese et al., 2016). In high-frequency GPS telemetry, consecutive tracking points are inherently non-independent; an animal's current location is fundamentally constrained by its previous position and movement velocity. Prior to spatial estimation, empirical variograms were generated for each individual to explicitly model this autocorrelation structure and to conduct a spatial saturation check. Visually, a home range is considered 'saturated' when the semi-variance of movement flattens out over time and reaches a clear asymptote. In the context of these enclosed reserves, this step verified that the tracking duration was sufficient for the animals to fully explore their available space and establish stable spatial patterns. Subsequently, continuous-time movement models (e.g., Ornstein-Uhlenbeck Foraging [OUF]) were fitted to the telemetry data using the *ctmm.select* function. This function utilizes perturbative maximum likelihood estimation and selects the optimal movement model for each individual track based on the lowest Akaike Information Criterion (AIC). By explicitly accounting for this autocorrelation, the selected movement model prevents the high-frequency GPS data from artificially underestimating the resulting home range estimates (Fleming et al., 2015).

Using the selected movement models, Autocorrelated Kernel Density Estimation (AKDE) was applied to calculate the 95% home range and the 50% core area for each animal. Due to the highly regular sampling interval of the telemetry devices (approximately one fix every 30 minutes), optimal spatial weighting (weights = FALSE) was intentionally excluded from the AKDE algorithm. In datasets with strict temporal regularity, unweighted estimation provides mathematically identical spatial boundaries while avoiding the significant computational instability and excessive processing times associated with weighted optimization.

Crucially, because both study areas are strictly enclosed nature reserves, standard AKDE methods are prone to "spillover bias," wherein the probability density cloud mathematically leaks outside the physical fence line, leading to an overestimation of available space. To mathematically respect these hard physical barriers, a locally corrected AKDE method was applied (Hollins et al., 2024). By integrating the reserve boundary polygons directly into the AKDE calculation as a spatial constraint, the probability density was redistributed inside the enclosures. This yielded the true realized home range area.

Finally, to evaluate seasonal dynamics and spatial stability, the telemetry data was temporally stratified into biological seasons: spring (March–May), summer (June–August), autumn (September–November), and in the Westhoek reserve also winter (December–February). Crucially, because the spatial connectivity of the Westhoek reserve was altered midway through the study by the opening of the central corridor fence (December 2022), this temporal stratification

was further subdivided. The baseline home ranges for the equids were explicitly calculated for both the structurally “Separated” (pre-intervention) and “Connected” (post-intervention) periods. Seasonal AKDEs were generated for each time-stratified track. To ensure statistical reliability, spatial estimates were strictly filtered based on their effective sample size, denoted as the Degrees of Freedom (DOF) within the ctmm framework. Unlike raw GPS fix counts, DOF represents the number of statistically independent times an individual traversed its estimated home range. Because home range area is fundamentally a two-dimensional spatial variance metric, estimating its boundary requires a strict mathematical minimum of independent range crossings to produce finite, bounded confidence intervals. Therefore, any seasonal estimate with a DOF of less than 4 was systematically excluded from the final analysis, as these subsets represented individuals that had not traversed their environment enough times to yield mathematically stable or biologically meaningful area estimates (Calabrese et al., 2016; Fleming et al., 2015).

For the remaining robust models, a set of spatial metrics was derived. To evaluate the intensity of spatial confinement, a Saturation Index was calculated as the ratio of the realized 95% home range area to the total accessible fenced compartment. Because no validated ecological cutoff exists in the literature to determine if an individual's home range is saturated or not, we set 0.75 as an a priori operational threshold. This value was chosen as a balance between a lower threshold (such as 0.6), which would classify animals as saturated despite substantial unused space remaining, and a higher threshold (such as 0.9) that would demand near-complete reserve utilization. Such near-complete utilization is an ecological improbability, as herbivores will rarely occupy 90 to 100% of a fenced area. Within any given reserve, a baseline proportion of the landscape inherently consists of naturally avoided or physically inaccessible features, such as deep water bodies, human infrastructure, or impenetrable patches of mature scrub. Consequently, relying on a 0.9 threshold fails to account for this natural spatial heterogeneity and would likely overlook biologically meaningful fence constraints. Therefore, values below 0.75 were classified as 'not saturated', and values above 0.75 were classified as 'saturated'. Furthermore, transitional spatial dynamics were quantified by calculating the absolute Size Change (km²), the Euclidean Centre Shift (km), and the geometric Site Fidelity (Jaccard overlap index) for both the 95% home ranges and 50% core areas between consecutive seasons.

3.4.2. Statistical Analysis of Spatial Dynamics

To formally test for seasonal patterns across all spatial and behavioural metrics, Linear Mixed-Effects Models (LMM) were fitted for each metric using the *lme4* package in R. To account for both individual idiosyncrasies and inter-annual environmental stochasticity, 'Animal_ID' and 'Year' were incorporated as random intercepts. 'Season' was modelled as the primary fixed categorical effect. Crucially, for the Westhoek population, the winter 2022-2023 infrastructure corridor-fence opening represented a significant spatial confound. To control for this shifting landscape, 'Fence Status' (Closed vs. Open) was explicitly included as a secondary fixed effect in the Westhoek models.

Overall significance of the fixed effects was evaluated using Type III Analysis of Variance (ANOVA). When metrics exhibited a significant seasonal effect, post-hoc pairwise comparisons were conducted. These were calculated using Estimated Marginal Means (EMMs) via the *emmeans* package, with Tukey adjustments applied to correct for multiple comparisons. Finally, residual normality was tested for all models using Shapiro-Wilk tests.

Additionally, due to the limited sample size of the monitored species in the Westhoek reserve (three Konik horses and one Shetland pony), Species could not be included as a fixed effect in the mixed models to avoid singularity and overfitting. Instead, potential species-specific differences in spatial behaviour were evaluated descriptively. This was achieved by extracting the individual random effect estimates (Best Linear Unbiased Predictors, or BLUPs) for the *Animal_ID* intercept from the population-level LMMs. This approach allowed for an exploratory comparison of the pony's individual spatial deviations relative to the variance exhibited by the Konik horses, without violating statistical assumptions regarding sample size.

3.5. WP2: Population-Level Habitat Selection

To evaluate fine-scale resource selection, the herbivore telemetry data was integrated with the environmental covariates developed in Section 3.3. The standardized spatial rasters represented continuous variables: topography (Slope), Distance to Water, and anthropogenic infrastructure (Distance to Paths and Fences), as well as categorical vegetation classes. Prior to modelling, all environmental rasters were aggregated from a 1-meter to a 20-meter resolution. This spatial upscaling was performed to balance computational efficiency with the ecologically relevant scale of large herbivore foraging behaviour and inherent GPS telemetry error.

3.5.1. Integrated Resource Selection Functions (iRSF)

Standard Resource Selection Functions (RSFs) evaluate habitat preference by comparing an animal's actual locations against randomly generated 'available points' drawn from the broader study area. This classical method is flawed for two primary reasons:

- First, it assumes spatial uniform accessibility, often misrepresenting the true biological constraints of the landscape.
- Second, it treats high-frequency telemetry fixes as statistically independent events, which heavily biases selection toward resting habitats due to temporal autocorrelation.

To overcome these limitations, habitat selection was modelled using the continuous-space RSF framework (*rsf.fit*) within the *ctmm* package. To correct for spatial constraints, an individual's 'available' habitat is strictly defined by its own mathematically derived Autocorrelated Kernel Density Estimate (AKDE). By using the boundary-corrected utilization distribution as the underlying availability baseline, the model evaluates resource selection strictly within the context of the specific habitats the animal actively had access to. Simultaneously, to correct for temporal autocorrelation, the continuous-time framework down-weights densely clustered location fixes. This ensures that prolonged resting behaviour is treated as a continuous spatial decision rather than artificially dominating the selection model through high data density.

Because habitat selection can vary based on individual idiosyncrasies and seasonal variations, RSF models were fitted independently for each individual animal per season. To ensure the spatial boundaries and temporal weightings of the available habitat were mathematically reliable, individual movement models were dynamically selected (prioritizing the continuous-velocity OUF model, with the position-only OU model as a fallback) and strictly filtered. While a minimal effective

sample size (e.g., $\text{DOF} \geq 4$) is sufficient to estimate a broad home range boundary in WP1, the iRSF models in WP2 evaluate fine-scale selection across a highly multidimensional environmental space comprising up to 15 continuous and categorical covariates. Statistically, fitting a selection model with this many parameters requires a proportionally high number of independent spatial events to prevent severe overfitting, false correlations, and mathematical non-convergence. Therefore, a strict threshold of Degrees of Freedom (DOF) ≥ 20 was enforced for the iRSF analysis. Any seasonal track falling below this threshold was excluded. Following the model fitting, a secondary strict exclusion boundary was applied: any resulting RSF model that failed to achieve a final RSF $\text{DOF} > 1$ was also rejected. This filter served as a mathematical safeguard, ensuring that models which technically converged, but lacked the statistical stability to resolve a finite availability domain, were removed from the analysis. Successful models that passed both the AKDE and RSF exclusion boundaries yielded a unique set of selection coefficients (β) for each environmental covariate per individual, representing log-odds ratios of selection relative to availability.

Following this strict spatial filtering, the final iRSF analysis comprised 30 successful individual-season models for the Westhoek equids (spring: $n = 4$; summer: $n = 10$; autumn: $n = 12$; winter: $n = 4$). Because several individuals were tracked across multiple years, these successful models resulted in a final population-level sample size of unique animals per season: spring ($N = 3$), summer ($N = 4$), autumn ($N = 4$), and winter ($N = 3$). These equid totals include the continuous year-round tracking of the single Shetland pony (spring: $n = 1$; summer: $n = 1$; autumn: $n = 3$; winter: $n = 1$). In the Kalmthoutse Heide, a total of 22 individual-season models were successfully retained for the Galloway cattle (spring: $n = 4$; summer: $n = 11$; autumn: $n = 7$), resulting in a population-level sample size of unique animals per season: spring ($N = 3$), summer ($N = 4$), and autumn ($N = 4$). Consistent with management practices, no winter models were generated for the bovine population.

3.5.2. Population-Level Aggregation and Baseline Alignment

To scale these individual behaviours up to a biologically robust, population-level inference, a custom aggregation protocol was applied. For categorical habitat variables, selection coefficients must be evaluated against a reference category. To accurately reflect the ecological contexts of the two distinct reserves, specific reference baselines were established for each study area:

- **Westhoek:** *Open duindoornstruweel* (Open Sea buckthorn scrub) was selected as the baseline due to its mathematical robustness and ecological relevance. Mathematically, as the third most abundant habitat in the reserve (13.8% of the total area), it was spatially available to every tracked individual across every modelled season. Ecologically, it represents a critical state of coastal dune succession, where scrub encroachment is actively occurring but has not yet formed an unnavigable, closed scrubland.
- **Kalmthoutse Heide:** *Vergraste, gedegradeerde droge heide* (Grass-encroached degraded dry heath) was designated as the reference category. Like the Westhoek baseline, it provided mathematical stability; as the second most abundant habitat (24.8% of the total area), it was spatially available to all tracked individuals across every modelled season. Furthermore, reversing this specific degraded state back into open heathland represents a primary conservation objective of the grazing regime.

To execute this baseline alignment, a custom data-processing protocol was developed to standardize the outputs of the individual movement models. Because the original models inherently utilized varying habitats as their internal reference categories (which are mathematically treated as a coefficient of 0.0), these internal baselines first had to be reconstructed within the dataset before they could be realigned. This was achieved by taking the coefficient of the designated reference habitat for that specific individual and season, and subtracting it from all other categorical habitat estimates. This mathematical shift successfully zeroed the new reference baseline without altering the relative selection magnitudes between the habitats. Notably, any habitat that originally served as an internal reference will naturally present a reconstructed point estimate lacking accompanying confidence intervals after this realignment. Continuous variables (e.g., slope, distance to water) were inherently independent of this categorical realignment and remained unchanged.

Following alignment, both the continuous and realigned categorical coefficients were averaged per individual animal for each respective season across all available tracking years. This crucial step condensed the data into a single, independent seasonal estimate per individual, preventing temporal pseudoreplication. Finally, these individual metrics were aggregated to calculate population-level means and standard errors. To assess whether the population's selection for a specific environmental feature significantly deviated from zero (indicating active selection or avoidance), one-sample, two-tailed Student's t-tests were conducted, yielding population-level 95% Confidence Intervals (CIs) and respective p-values.

3.5.3. Inter-Species Comparison (Westhoek)

Finally, to investigate potential niche partitioning within the mixed-species Westhoek population, the spatial preferences of the Konik horses were explicitly compared against those of the Shetland pony. Because only a single Shetland pony was collared, it is important to establish that all comparative spatial estimates for this species inherently represent the specific behaviour of the resident Westhoek pony sub-herd, rather than a generalized species-level extrapolation. Due to the sample size of the Shetland pony ($N = 1$), standard population-level t-tests could not be applied. Instead, inter-specific differences were evaluated by comparing the multi-year 95% Confidence Intervals of the individual Shetland pony against the population-level 95% Confidence Intervals of the Konik herd. Selection for a specific resource was considered significantly divergent between the species if their respective confidence intervals did not mathematically overlap. Furthermore, to capture ecologically meaningful shifts in behaviour, differences in selection state (preference, avoidance or neutral) were also explicitly evaluated. Instances where one species demonstrated active selection or avoidance (a CI strictly bounding away from zero) while the other exhibited neutral use (a CI crossing zero) were identified as functionally divergent foraging strategies, even in cases of partial interval overlap.

3.6. WP3: Modelling Vegetation Dynamics

To evaluate the ecological impact of the herbivore populations on the landscape, the spatial behaviour of the animals was linked to multi-year (5-year) transitional changes in the vegetation structure.

3.6.1. Cumulative Equid Space Use Pressure Mapping

Traditional ecological impact models often rely on generalized stocking rates (e.g., animals per hectare), which falsely assume uniform grazing and trampling across an entire reserve (Senft, 1989). To overcome this limitation and accurately quantify true landscape utilization, individual movement models from WP1 were translated into a spatially explicit metric of cumulative space use pressure. This was achieved by mathematically stacking and summing the individual, boundary-corrected Autocorrelated Kernel Density Estimates (AKDEs) for all tracked animals. To ensure strict biological accuracy, this summation was metabolically weighted; Konik horse spatial distributions were weighted at 1.0, while the Shetland pony distribution was weighted at 0.67 to account for the difference in body mass and corresponding ecological impact. By aggregating these weighted utilization distributions, a continuous spatial raster was generated. The resulting map provides an accurate proxy for the true spatial intensity of cumulative equid grazer pressure across the reserve.

3.6.2. Vegetation Transition and Abiotic Covariates

The longitudinal structural changes in vegetation were quantified using high-resolution drone photogrammetry collected and processed by the Research Institute for Nature and Forest (INBO). Aerial imagery was captured across the study blocks using drone-mounted visual cameras, with spatial accuracy ensured through the placement of fixed Ground Control Points (GCPs) and ground-truth validation data. The highly overlapping aerial photographs were processed using the Structure-from-Motion (SfM) technique (Fonstad et al., 2013; Westoby et al., 2012) via Agisoft software. This photogrammetric computer vision approach identifies corresponding spatial coordinates across multiple stereoscopic images to generate dense 3D point clouds and photorealistic orthomosaics with a spatial resolution of 2.5 cm.

From these 3D point clouds, a 'top of canopy' Digital Surface Model (DSM) was derived, mapping the absolute elevation of the landscape (in m TAW). To determine the true, relative vegetation height, a Canopy Height Model (CHM) was calculated by subtracting the baseline bare-earth Digital Terrain Model (DHM-Vlaanderen II) from the DSM.

By comparing the CHMs generated from the respective drone flights in 2020 and 2025, absolute vertical height differences were calculated for every spatial pixel across the study area. To evaluate how cumulative grazer pressure influenced landscape-level ecological succession, these temporal height changes were categorized into a 9-class classification framework (Table 4). These classes fall into three strict, mutually exclusive ecological transition states:

- **Regression:**
 - Scrub regression (*Struweelregressie*)
 - Rough vegetation regression (*Ruigte-regressie*)
 - Grass/herb regression (*Kruid-regressie*)
- **Stable:** Areas exhibiting no or negligible structural change in vegetation class.
- **Growth and encroachment:**

- Grass/herb growth (*groei van lage gras/kruid vegetatie*)
- Rough vegetation encroachment (*Verruiging*)
- Scrub encroachment (*Verstruweling*)
- Low scrub growth (*Struweelgroei laag*)
- High scrub growth (*Struweelgroei hoog*)

Table 4. Classification matrix detailing the 9 mutually exclusive vegetation transition processes. Transition states are derived by cross tabulating the baseline vegetation structural class (columns) with the absolute vertical height difference recorded between the surveys in 2020 and 2025 (rows). N/A indicates mathematically impossible transitions (e.g., short herbs cannot experience a negative height difference exceeding their maximum canopy height).

Absolute Height Difference	Short herbs (< 25 cm)	Tall herbs (25–50 cm)	Rough vegetation (50–100 cm)	Low scrub (1–2 m)	High scrub (> 2 m)
< -1 m	N/A	N/A	N/A	Scrub regression	Scrub regression
-75 to -100 cm	N/A	N/A	Rough vegetation regression	Scrub regression	Scrub regression
-50 to -75 cm	N/A	N/A	Rough vegetation regression	Scrub regression	Scrub regression
-25 to -50 cm	N/A	Rough vegetation regression	Rough vegetation regression	Scrub regression	Stable
-5 to -25 cm	Grass/herb regression	Grass/herb regression	Rough vegetation regression	Stable	Stable
-5 to +5 cm	Stable	Stable	Stable	Stable	Stable
+5 to +25 cm	Grass/herb growth	Rough vegetation encroachment	Rough vegetation encroachment	Stable	Stable
+25 to +50 cm	Grass/herb growth	Rough vegetation encroachment	Scrub encroachment	Low scrub growth	High scrub growth

+50 to +75 cm	Rough vegetation encroachment	Scrub encroachment	Scrub encroachment	High scrub growth	High scrub growth
+75 to +100 cm	Rough vegetation encroachment	Scrub encroachment	Low scrub growth	High scrub growth	High scrub growth
> +1 m	Scrub encroachment	Scrub encroachment	High scrub growth	High scrub growth	High scrub growth

To isolate the specific impact of herbivory, the model explicitly controlled for underlying abiotic landscape drivers. The continuous covariates previously discussed in Section 3.3.1 (Terrain Slope, Spring Groundwater Depth, and the custom microclimatic Solar Index) were incorporated into the models to account for the inherent topographical and hydrological drivers of coastal dune succession.

3.6.3. Multinomial Logistic Regression and Marginal Effects

The statistical relationship between cumulative space use pressure, abiotic constraints, and vegetation transition was modelled using a Multinomial Logistic Regression framework via the *nnet* package in R. Prior to modelling, all continuous predictors were z-standardized to facilitate the direct comparison of coefficient effect sizes and ensure mathematical stability. This approach simultaneously evaluates the probability of a specific spatial pixel undergoing a specific Regression or Encroachment process, using the Stable state as the mathematical reference baseline. To ensure model parsimony and avoid overfitting, a stepwise Akaike Information Criterion (AIC) selection procedure was utilized to determine the optimal combination of predictors, explicitly testing for both additive effects and complex environmental interactions. During this process, if complex landscape interactions only marginally improved the model fit, they were intentionally excluded in favour of a strictly additive base model utilizing the four primary covariates: Space Use Intensity (SUI), Spring Groundwater Depth, Terrain Slope, and Solar Exposure. This approach ensures mathematical parsimony and maximizes the direct interpretability of the absolute marginal effects for applied conservation management. Furthermore, a Variance Inflation Factor (VIF) check was conducted across these final predictors to guarantee the absence of problematic multicollinearity.

Because raw multinomial logit coefficients represent abstract log-odds ratios, they are difficult to interpret directly within an applied ecological context. To resolve this and provide actionable conservation metrics, Average Marginal Effects (AMEs) were calculated post-hoc using the *emmeans* package. AMEs mathematically translate the complex log-odds back into intuitive, real-world percentage probabilities. This advanced approach allows the final model to explicitly quantify the absolute effect size (e.g., demonstrating that a 1-Standard Deviation increase in cumulative space use pressure alters the absolute probability of scrub growth by a specific percentage), thereby directly evaluating the effectiveness of the grazing intervention as a landscape restoration tool.

4. Results

4.1 WP1: Space Use and Home Range Dynamics

4.1.1 Baseline Home Range Estimates (AKDE)

Westhoek Coastal Dune Ecosystem (Equid Group)

During the initial separated phase, the Konik horses maintained an average corrected 95% baseline home range of 48.3 hectares (varying individually from 25.5 ha to 69.0 ha). The Shetland pony, confined to the southern compartment, exhibited a comparable baseline 95% home range of 52.9 hectares (Table 5).

Following the removal of the corridor barrier, the average 95% baseline home range of the Konik horses expanded to 84.1 hectares, while the Shetland pony's baseline home range nearly doubled to 97.7 hectares (Table 5; for visual spatial representation of this expansion, see Figure 6 in Section 4.1.2).

Table 5. Comparison of the unconstrained and boundary-corrected 95% AKDE baseline home ranges for the Westhoek equids, categorized by species and herd demographic type. Estimates are provided for both the initial separated phase (closed fence) and the subsequent connected phase (open fence). The reduction percentage highlights the spatial area removed by the geometric boundary constraints.

Animal ID	Species	Herd type	Reserve phase	Unconstrained AKDE (ha)	Corrected AKDE (ha)	Reduction (%)
AN785	Shetland pony	Mixed herd	Separated south (closed)	83.2	52.9	36.4%
			Connected (open)	139.8	97.7	30.1%
AN788	Konik horse	Bachelor group	Separated north (closed)	81.8	69.0	15.7%
			Connected (open)	154.0	112.1	27.2%
AN789	Konik horse	Mixed herd	Separated south (closed)	59.8	50.5	15.6%
			Connected (open)	64.0	56.0	12.5%
AP513	Konik horse	Mixed herd	Separated north (closed)	25.7	25.5	0.8%

Kalmthoutse Heide Lowland Heath Ecosystem (Galloway Cattle)

Unlike the Westhoek reserve, the Kalmthoutse Heide did not undergo structural connectivity changes during the study period. Over their respective active tracking periods, the Galloway cattle maintained an average corrected 95% baseline home range of 305.1 hectares, with individual home ranges varying between 133.9 ha and 422.7 ha (Table 6).

Table 6. Comparison of the unconstrained and boundary-corrected 95% AKDE baseline home ranges for the tracked Galloway cattle in the Kalmthoutse Heide. The reduction percentage highlights the spatial area removed by the geometric boundary constraints.

Animal ID	Species	Unconstrained AKDE (ha)	Corrected AKDE (ha)	Reduction (%)
AP518	Galloway cattle	567.7	350.4	38.3%
AP519	Galloway cattle	465.4	313.5	32.6%
AP521	Galloway cattle	180.0	133.9	25.6%
AP522	Galloway cattle	613.2	422.7	31.1%

4.1.2 Seasonal & Infrastructural Effects (LMM Results)

Westhoek Coastal Dune Ecosystem (Equid Group)

The Role of the Corridor Opening (Fence Status)

As summarized in Table 7, the most significant driver of home range size was not seasonality, but physical infrastructure (Figure 6 and 7). As visualized in Figure 6, the removal of the central corridor fence triggered a highly significant spatial expansion across the population ($F = 19.71$, $p < 0.001$). Controlling for season, opening the fence expanded the average individual home range by 23.2 hectares (Estimate = $+0.232 \text{ km}^2$). Concurrently, this expansion caused a significant drop in the reserve Saturation Index ($F = 34.59$, $p < 0.001$). Controlling for the high inter-individual variance, the estimated marginal mean for population saturation dropped from 55.1% before the corridor opening to 33.7% afterwards, reflecting a total reduction of 21.4%. While the pre-intervention population mean of 55.1% was mathematically skewed downward by the highly restricted spatial footprint of a single outlier (Konik AP513), the remaining monitored sub-herds consistently operated near or above the 75% saturation mark during the closed phase (Figure 8). Consequently, relative to the a priori 75% threshold, the intervention transitioned the herds from a higher state of artificial physical confinement to a freer-ranging spatial distribution. This indicates that while the equids explored the newly available landscape, they did not immediately utilize the expanded area at the same intense density as their previously restricted compartments (Figure 8). It is important to note that the polygons in Figure 6 represent the cumulative merged spatial footprint across all respective seasons, which visually inflates apparent reserve saturation. True individual seasonal saturation within these borders remains significantly lower (Figure 8).

The mixed models revealed high inter-individual variance regarding this spatial response (Figure 6). The variance attributed to individual identity (Animal_ID variance = 0.045) was more than four times greater than the unexplained stochastic noise (Residual variance = 0.010) and vastly exceeded inter-annual environmental fluctuations (Year variance = 0.000). For example, while most individuals experienced a sharp drop in saturation upon the fence's removal, the Konik horse AN788 exhibited an inverse trajectory. As visualized in the saturation timeline (Figure 8), AN788 even showed an increase in saturation, indicating that this individual (and its sub-herd) exploited

the newly connected landscape more than his conspecifics. Furthermore, longitudinal tracking revealed that this spatial expansion was not a singular, immediate stabilization. As visualized in the chronological and saturation timeline (Figure 7 and 8), both the AN788 Konik sub-herd and the Shetland pony (AN785) exhibited a secondary spatial expansion during the final monitored season (Autumn 2024).

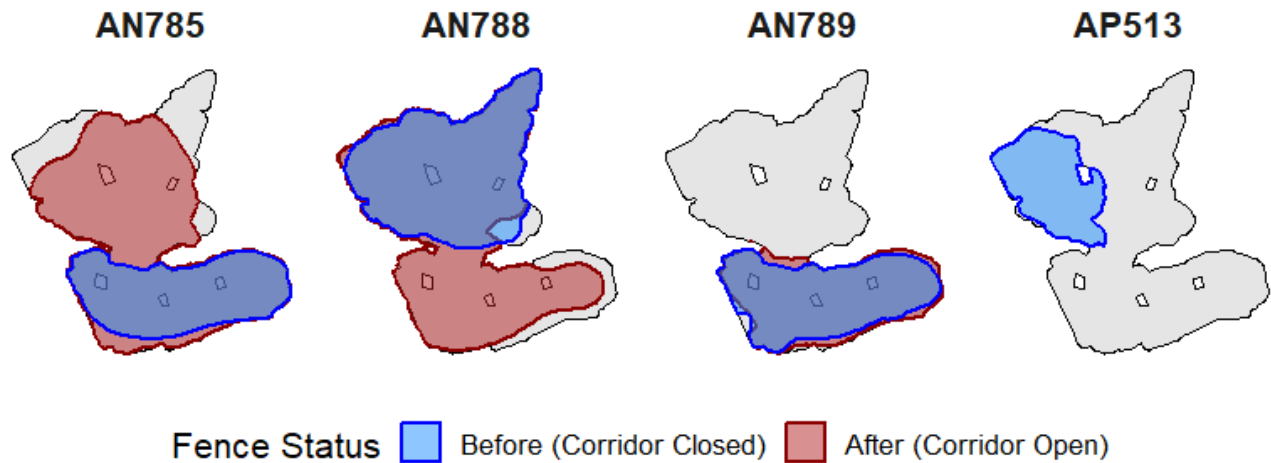


Figure 6. Spatial response of the Westhoek equid group to the removal of the central corridor fence. The map visualizes the total boundary-corrected baseline home ranges (95% AKDE) for tracked individuals before (blue) and after (red) the corridor was opened. The visualization highlights high inter-individual variance regarding the newly available space, contrasting the spatial expansions of the Shetland pony (AN785) and the AN788 Konik sub-herd with the high site fidelity of the AN789 Konik sub-herd. Post-intervention spatial data is absent for AP513 due to the discontinuation of tracking prior to the corridor's removal. Note that these polygons represent the cumulative merged spatial footprint across all respective seasons, which visually inflates apparent reserve saturation. True individual seasonal saturation within these borders remains significantly lower (see Figure 8).

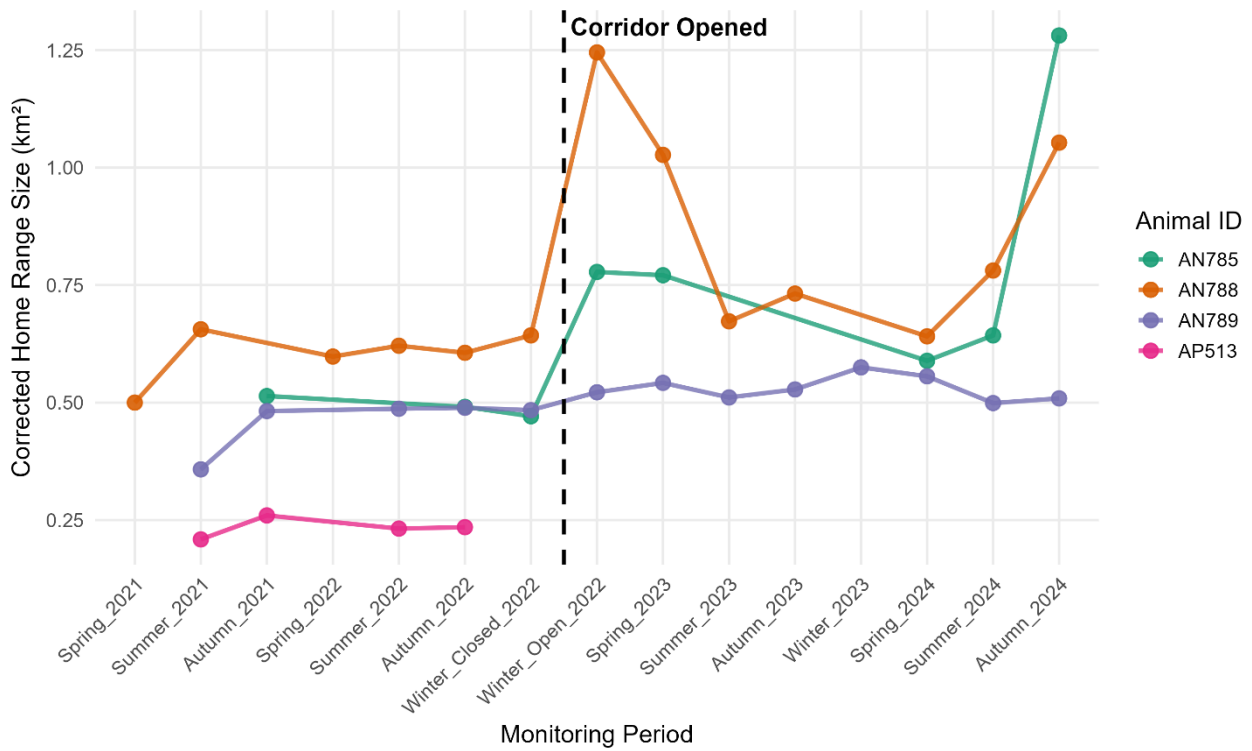


Figure 7. Chronological timeline of individual boundary-corrected baseline home range sizes (95% AKDE) for the tracked equids within the Westhoek reserve. Coloured trajectories represent the seasonal spatial footprint of each individual animal in square kilometres. The vertical black dashed line marks the removal of the central corridor fence.

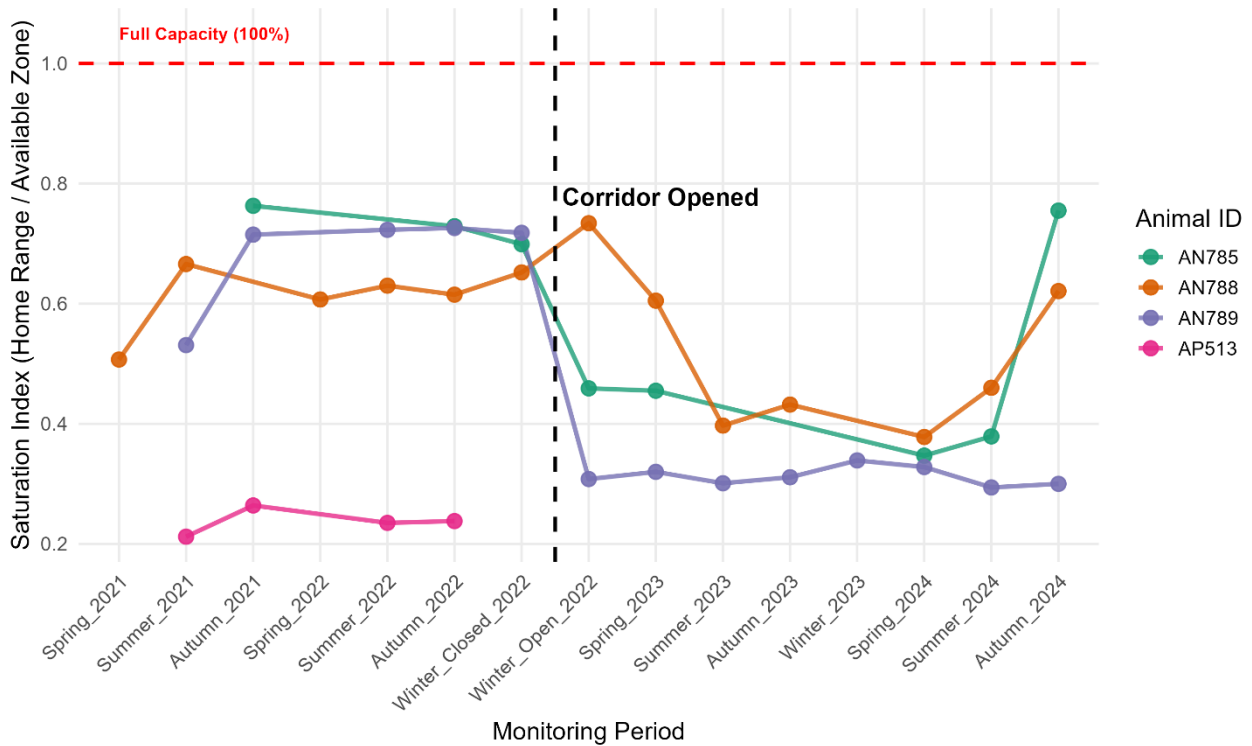


Figure 8. Chronological timeline of the reserve Saturation Index for tracked equids in the Westhoek. The graph illustrates

individual seasonal trajectories and the theoretical maximum available capacity threshold (horizontal red dashed line). The vertical black dashed line marks the removal of the central corridor fence.

Seasonal Dynamics in Space Use

Macro-level space use remained stable in the Westhoek reserve. Neither absolute baseline home range sizes ($F = 1.45$, $p = 0.248$) nor the geometric Site Fidelity of their total 95% home range boundaries showed any significant response to the seasonal cycle ($F = 0.73$, $p = 0.546$).

Instead, the only significant effect of seasonality was observed in the geometric Core Fidelity (50% Overlap) ($F = 3.35$, $p = 0.034$), indicating that their affinity for specific core foraging patches fluctuates throughout the year. Pairwise comparisons revealed that the 50% core area overlap was significantly lower when transitioning from winter into spring (mean overlap = 0.200, or 20.0%) compared to the transition from summer into autumn (mean overlap = 0.456, or 45.6%; $p = 0.039$). This drop in fidelity confirms a core area relocation during spring, with equids retaining only a fifth of their previous core area. In contrast, the transition into autumn is characterized by significantly higher spatial stability, as the animals maintain nearly half of their core area.

While the location of these core patches shifted significantly, the overall area of their 95% home range exhibited only a marginally significant seasonal trend regarding expansion and contraction ($F = 2.59$, $p = 0.075$). Model estimates revealed that spring acts as the primary period of spatial contraction (mean change = -0.08 km^2 relative to winter), whereas autumn triggers spatial expansion of the total home range boundary (mean change = $+0.11 \text{ km}^2$ relative to summer; Tukey $p = 0.076$). Furthermore, while the removal of the corridor fence fundamentally increased the baseline size of the home ranges, it had no effect on the rate of this seasonal expansion and contraction ($p = 0.792$).

Crucially, while the decision to relocate core patches is partly governed by the seasonal cycle, the physical distance the herd travels to relocate the centre of the total 95% home range (Centre Shift) proved to be entirely stochastic. Neither the seasonal cycle ($F = 1.56$, $p = 0.222$) nor the removal of the corridor fence ($p = 0.788$) significantly influenced how far the animals shifted their home range centres. Notably, random effects analysis revealed that both individual (Animal_ID) and inter-annual (Year) variances for these shifts were mathematically zero. This absence of seasonal, infrastructural, individual, or inter-annual predictors implies that the centre shift distances are purely random.

Table 7. Summary of Linear Mixed-Effects Model (LMM) Type III ANOVA results testing the influence of Season and infrastructural Fence Status on the spatial metrics of the Westhoek equids. Significant p-values are bolded.

Spatial Metric	Driver: Season (F-value)	Season (p-value)	Driver: Fence Status (F-value)	Status (p-value)
Home Range Size	1.45	0.248	19.71	< 0.001
Seasonal Size Change	2.59	0.075	0.09	0.792
Centre Shift Distance	1.56	0.222	0.07	0.788

Site Fidelity (95% Overlap)	0.73	0.546	0.50	0.554
Core Fidelity (50% Overlap)	3.35	0.034	1.01	0.420
Reserve Saturation Index	2.29	0.099	34.59	< 0.001

Individual Trajectories: The Shetland Pony

Analysis of these individual deviations revealed that the smaller body size of the Shetland pony (AN785) did not translate into a consistently smaller spatial footprint. The pony's individual deviation for home range size (+0.046) was nested comfortably within the spectrum of the larger Konik horses (ranging from -0.156 to +0.191). However, the pony exhibited the lowest spatial stability of the monitored group regarding both its total home range (Site Fidelity deviation = -0.070), and its core foraging patches (Core Fidelity deviation = -0.041). Together, these extracted effects indicate that while the pony utilized a similar volume of space as the larger equids, it operated with a more nomadic spatial strategy, shifting its foraging locations more frequently than the horses.

Kalmthoutse Heide Lowland Heath Ecosystem (Galloway Cattle)

In contrast to the structurally dynamic Westhoek reserve, the Kalmthoutse Heide study area remained infrastructurally static throughout the monitoring period. Consequently, the Linear Mixed-Effects Models (LMMs) for the Galloway cattle focused purely on isolating the effects of seasonal ecology (Table 8).

Home Range Size and Reserve Saturation

Unlike the stochastic macro-level boundaries observed in the equids, the overall home range of the cattle was significantly influenced by the seasonal cycle. Seasonality exerted a strong influence on absolute home range size ($F = 6.03$, $p = 0.007$). Model estimates revealed that spring is characterized by the most restricted home range size, with baseline home ranges (mean = 2.17 km²) significantly smaller than those established in summer ($p = 0.014$) and autumn ($p = 0.013$). Summer (2.86 km²) and autumn (2.89 km²) ranges were statistically indistinguishable ($p = 0.991$). Note that the spatial distribution visualized in Figure 9 represents the raw, unadjusted data and thus differs slightly from the estimated means above, as the raw visualization does not mathematically account for the inter-annual and individual variability controlled for by the mixed models.

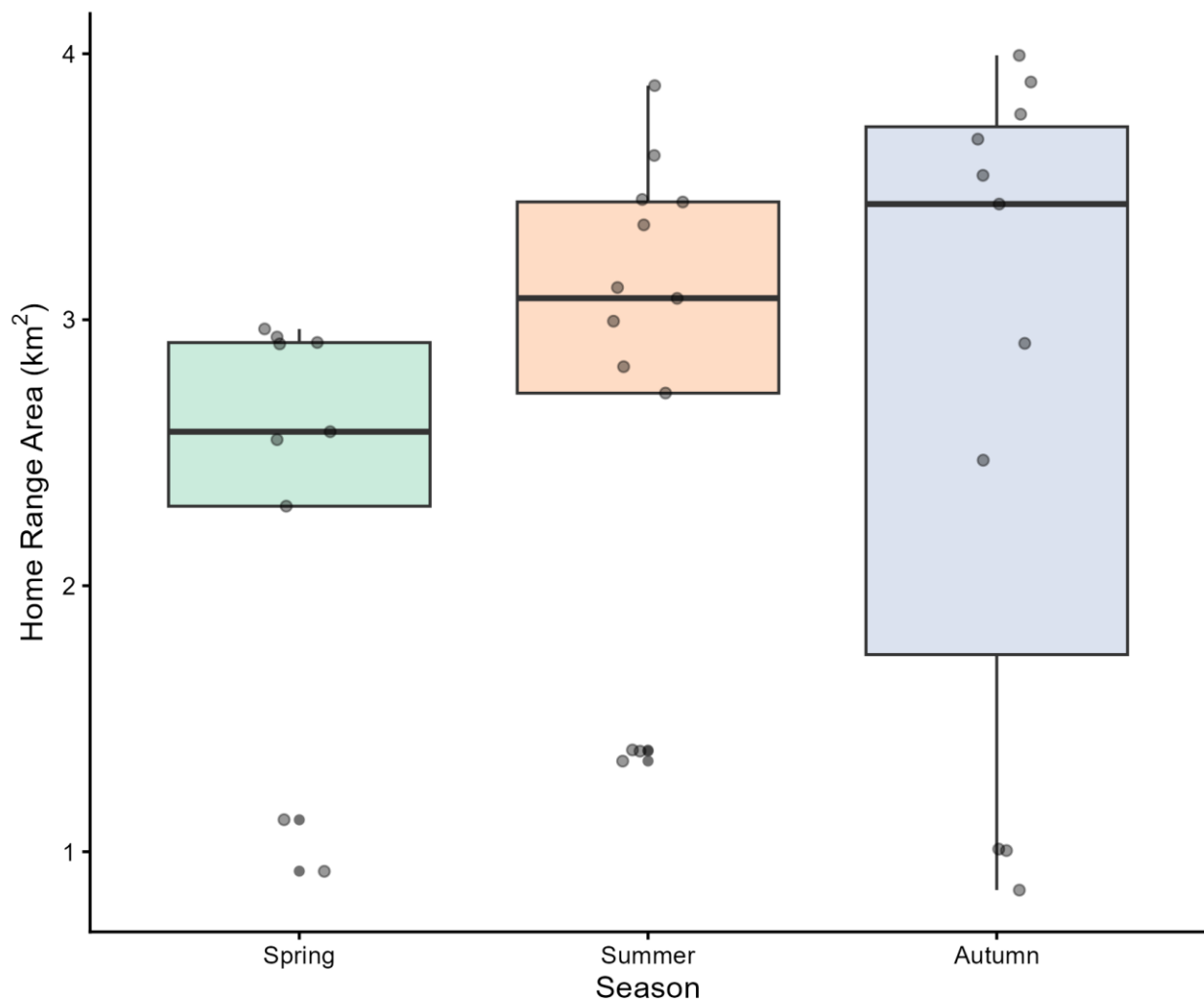


Figure 9. Seasonal distribution of the boundary-corrected baseline home range sizes (95% AKDE) for Galloway cattle within the Kalmthoutse Heide reserve. Boxplots represent the median and interquartile ranges of the home range area (in square kilometres) across the three tracked biological seasons, with individual seasonal estimates overlaid as raw data points.

This seasonal dichotomy was mirrored in the intensity of landscape use. The Reserve Saturation Index was significantly driven by the season ($F = 6.02$, $p = 0.007$), with the cattle using a significantly lower proportion of the total reserve during spring (38.4%) compared to the more saturated summer (50.6%) and autumn (51.1%) phases (Figure 10). Crucially, even during their peak spatial expansion in autumn, the average saturation index of 51.1% remained well below the predefined 75% threshold. This confirms that the Galloway cattle were never spatially saturated by the reserve boundaries. It is important to note that the polygons in Figure 10 represent the cumulative merged spatial footprint across multiple years, which visually inflates apparent reserve saturation. True individual seasonal saturation within these borders remains lower.

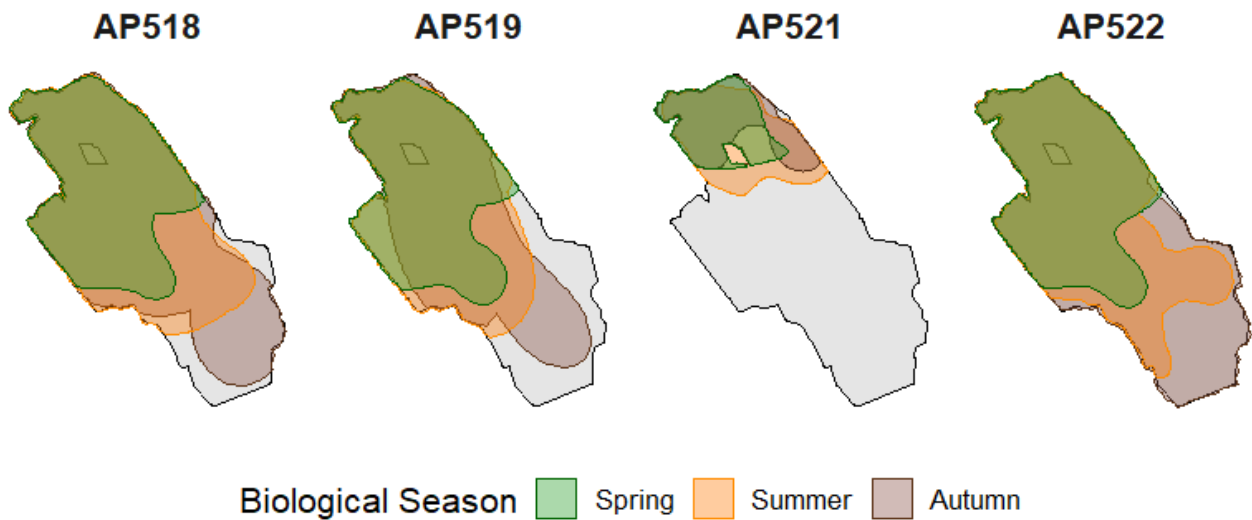


Figure 10. Cumulative seasonal spatial dynamics of the Kalmthoutse Heide Galloway cattle. The map visualizes the 95% AKDE baseline home ranges for tracked individuals, stratified and layered by biological season. This visualization highlights seasonal spatial variance, demonstrating the marked difference in spatial footprint size between the restricted spring range (green) and the significantly larger summer (orange) and autumn (brown) ranges. Note that each polygon represents the cumulative merged spatial footprint for that specific biological season across the entire multi-year tracking period, which visually inflates apparent reserve saturation. True individual seasonal saturation within these borders remains lower.

Size Change, Centre Shift and the Fidelity Paradox

Given the restricted home range sizes and lower reserve saturation observed in spring, we logically expected to see a subsequent spatial expansion reflected in the Seasonal Size Change metric. While linear mixed models evaluating this rate of spatial change revealed a borderline non-significant overall seasonal trend ($F = 2.50$, $p = 0.103$), the underlying biological pattern perfectly aligns with these expectations. Specifically, spring operates as a period of mild spatial contraction or stasis (mean change = -0.17 km^2), which is followed by a period of spatial expansion during the transition into summer. Fixed effect estimates indicate that the expansion rate in summer is $+0.73 \text{ km}^2$ greater than in spring, reflecting a marginally significant unadjusted behavioural shift ($p = 0.061$). The lack of strict statistical significance for this expansion phase after multiple-comparison adjustments (Tukey $p = 0.156$) is primarily driven by a high degree of unexplained stochasticity (Residual SD = 0.76).

The physical distance between the centre of consecutive seasons (Centre Shift) proved to be stochastic. The seasonal cycle had no significant effect on the distance the home range centre moved ($F = 1.25$, $p = 0.303$). Furthermore, the random effects for both Animal_ID and Year were negligible or zero, indicating that these physical distances are random.

This stochastic centre shift distance creates a paradox when evaluated alongside their macro-level geometric Site Fidelity (95% Overlap), which was driven by the seasonal cycle ($F = 8.33$, $p = 0.002$). In spring, the animals exhibit their lowest spatial stability, retaining only 38.6% of their previous total home range, which is significantly lower than their stability in summer ($p = 0.002$) and autumn ($p = 0.019$). This apparent paradox, that their boundaries shift significantly in spring, yet the centre

distance does not, is a mathematical consequence of their restricted home range size. Because spring home ranges are significantly smaller (2.17 km²), even a moderate shift in the range centre is sufficient to cause a reduction in spatial overlap. In contrast, the larger home ranges of summer and autumn buffer against these random central shifts, allowing the herd to maintain high macro-level stability (approximately 61–67% overlap).

Finally, while these macro-level 95% boundaries stabilize during summer and autumn, their internal micro-level movements do not. The geometric Core Fidelity (50% Overlap) showed no significant seasonal effect ($F = 1.38$, $p = 0.267$). Overlap values for core patches remained low across all seasons (ranging between 24.0% and 38.8%). Furthermore, the random effects for both individual identity (Animal_ID) and inter-annual environmental conditions (Year) were mathematically zero. This indicates that while the outer boundaries of the herd's territory stabilize, the core foraging patches within that territory shift continuously and opportunistically throughout the year.

Population Dynamics: Herd Cohesion vs. Inter-annual Variance

Crucially, the random effects components of these mixed models revealed a different population structure compared to the Westhoek equids. For macro-spatial metrics like home range size and reserve saturation, the variance attributed to individual identity (Animal_ID) was lower than the variance attributed to inter-annual environmental conditions (Year) (e.g., Year variance for Saturation = 208.3, compared to Animal_ID variance = 33.4). Because the tracked cattle all belonged to a single herd, this low individual variance confirms that they operate as a rather cohesive unit. Consequently, the spatial footprint of the herd is dictated by broad environmental conditions specific to a given year, rather than by individual deviation. This stands in stark contrast to the Westhoek equids, where spatial dynamics were heavily driven by sub-herd divergence.

Table 8. Summary of Linear Mixed-Effects Model (LMM) Type III ANOVA results testing the influence of Season on the spatial metrics of the Kalmthoutse Heide Galloway cattle. Significant p-values are bolded.

Spatial Metric	Driver: Season (F-value)	Season (p-value)
Home Range Size	6.03	0.007
Seasonal Size Change	2.50	0.103
Centre Shift Distance	1.25	0.303
Site Fidelity (95% Overlap)	8.33	0.002
Core Fidelity (50% Overlap)	1.38	0.267
Reserve Saturation Index	6.02	0.007

4.2 WP2: Environmental Drivers & Spatial Constraints

While the spatial models in WP1 quantified the macro-level territorial boundaries of the tracked herbivores, home range estimations inherently treat the landscape within those borders as a functionally uniform space. However, grazing herbivores do not utilize their available territories homogeneously. To disentangle the mechanisms driving their internal movements, WP2 transitions from macro-level spatial geometry to fine-scale habitat selection.

By employing integrated continuous models, this analysis simultaneously assesses the role of the natural landscape, specifically topography (slope) and distance to water, alongside the complex influence of anthropogenic infrastructure. This includes modelling the seasonal attraction of paths and the reserve boundaries.

4.2.1. Spatial Strategies in the Westhoek Coastal Dune Ecosystem

Continuous environmental variables proved to be significant drivers of space use within the Westhoek, though the specific spatial strategies frequently diverged between the Konik horses and the Shetland pony.

Regarding the natural landscape, the equid population displayed an aversion to steep terrain during the latter half of the year, while treating topography as a neutral spatial feature during winter and spring. As detailed in Figure 11, the models revealed a statistical trend for slope avoidance during summer (mean $\beta = -0.234$, $p = 0.080$) and a significant negative selection during autumn (mean $\beta = -0.288$, $p = 0.006$). Crucially, stratifying the models by species (Figure 12) revealed that this topographic avoidance diverged: during the summer, Konik horses avoided steeper terrain, while the Shetland pony displayed a neutral selection for slope. Distance to water selection was characterized by high inter-individual variability. Consequently, it yielded no significant population-level trends across any season (all $p > 0.48$). The only notable deviation occurred in the Shetland pony, which actively selected for greater distances from open water sources during the spring.

Beyond the constraints of the natural environment, anthropogenic infrastructure exerted a distinct influence. The network of paths did not function as a spatial deterrent. Instead, the population displayed a seasonal path attraction effect. As seen in Figure 11, the population exhibited a statistical trend for path attraction during winter (mean $\beta = -0.357$, $p = 0.073$) and spring (mean $\beta = -0.227$, $p = 0.094$). However, disaggregating this data (Figure 12) revealed that this attraction was heavily driven by the Shetland pony, which exhibited a consistent, year-round preference for the path network, whereas the Konik horses remained generally indifferent.

Finally, regarding the reserve perimeter, during the first half of the year, the population demonstrated a significant spatial aversion to the reserve boundaries (Figure 11), selecting for greater distances away from the fence during both spring (mean $\beta = 0.340$, $p = 0.002$) and winter (mean $\beta = 0.403$, $p = 0.007$). Again, this fence avoidance effect was not uniform across the group (Figure 12). The Shetland pony demonstrated a consistent, year-round avoidance of the perimeter, while the Konik horses only showed this tendency in spring and winter.

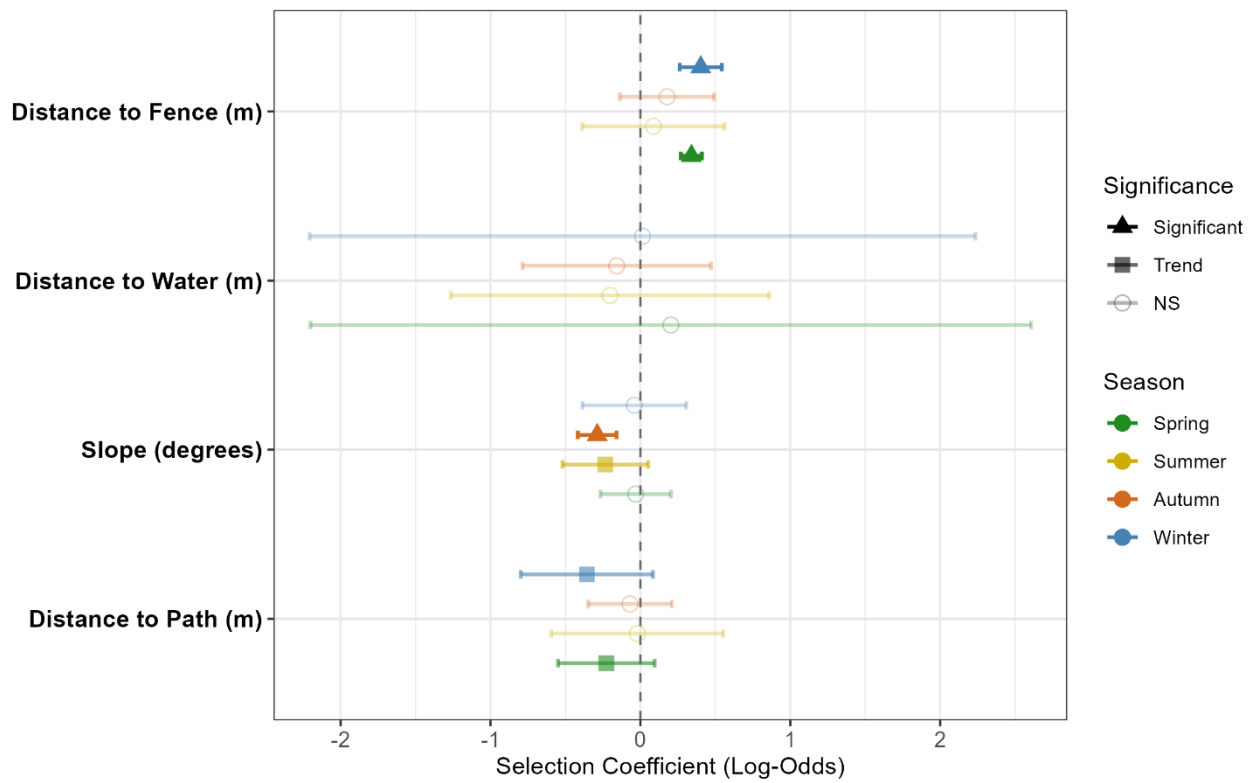


Figure 11. Forest plot of the integrated Resource Selection Function (iRSF) models detailing the population-level selection for continuous environmental and structural covariates among the Westhoek (Equid Group) across four biological seasons. Plotted values represent the estimated mean β -coefficients, with horizontal bars indicating the 95% confidence intervals. Crucially, for the Distance to... covariates, a positive value ($\beta > 0$) indicates selection for greater distances (i.e., spatial avoidance of the feature), whereas a negative value ($\beta < 0$) indicates selection for shorter distances (i.e., spatial attraction to the feature). For the topographical Slope covariate, a positive value indicates a preference for steeper terrain, while a negative value indicates a preference for flatter terrain.

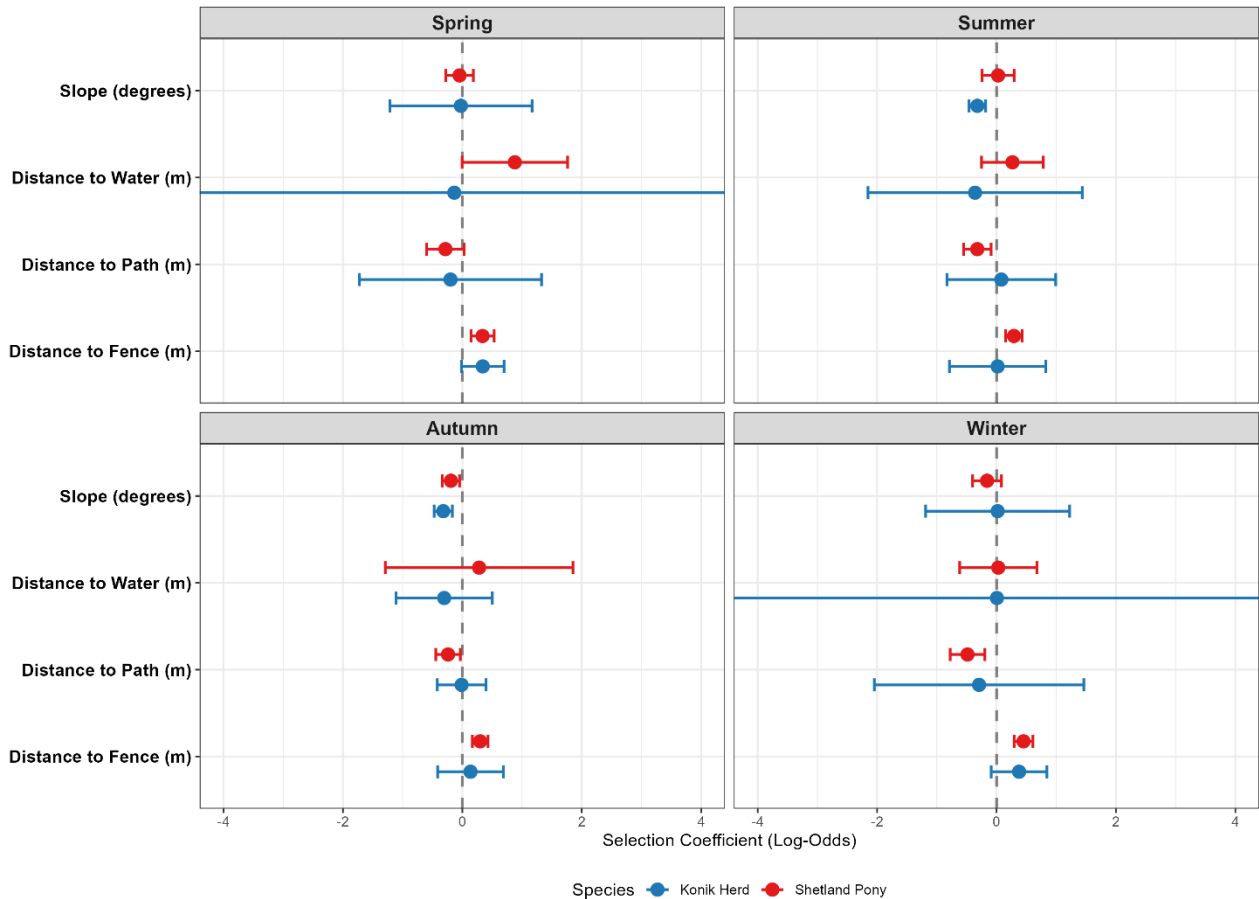


Figure 12. Species-specific comparison of continuous environmental and structural covariate selection within the Westhoek reserve. The integrated Resource Selection Function (iRSF) models are disaggregated to contrast the spatial strategies of the Konik horses with the Shetland pony across four biological seasons. Markers represent the estimated mean β -coefficients. The 95% confidence intervals (horizontal bars) represent different variance structures depending on the sample size and identity: (1) For the Konik horses ($n > 1$), bars represent inter-individual variance across the sub-herd; (2) For the Shetland pony in autumn ($n = 3$), bars represent inter-annual variance of the single individual across multiple years; (3) For the Shetland pony in spring, summer, and winter ($n = 1$), bars represent the internal mathematical uncertainty (model confidence intervals) derived from the spatial variance of the single continuous-time track. Crucially, for the Distance to... covariates, a positive value ($\beta > 0$) indicates selection for greater distances (i.e., spatial avoidance of the feature), whereas a negative value ($\beta < 0$) indicates selection for shorter distances (i.e., spatial attraction to the feature). For the topographical Slope covariate, a positive value indicates a preference for steeper terrain, while a negative value indicates a preference for flatter terrain.

4.2.2. Spatial Strategies in the Kalmthoutse Heide Lowland Heath Ecosystem

In the Kalmthoutse Heide, the Galloway cattle demonstrated distinct, seasonal spatial strategies regarding both natural and anthropogenic features (Figure 13).

Regarding the natural landscape, the herd demonstrated a significant aversion to steep terrain, similar to the Westhoek equids, though this behaviour emerged under a different seasonal context. Models indicated a statistically significant avoidance of steep slopes exclusively during the spring (mean $\beta = -0.284$, $p = 0.005$), before transitioning into neutral selection during summer and autumn (all $p > 0.41$). Despite their fundamental physiological need for water, the herd actively selected for

greater distances away from open water bodies during both spring (mean $\beta = 0.357$, $p = 0.010$) and summer (mean $\beta = 0.455$, $p = 0.025$), before returning to a neutral spatial relationship in autumn ($p = 0.46$).

Beyond natural landscape features, anthropogenic infrastructure exerted a distinct influence on spatial selection. While path attraction in the Westhoek was strictly seasonal, the trail network in the Kalmthoutse Heide functioned as a persistent spatial covariate. This attraction reached strict statistical significance during the summer (mean $\beta = -0.216$, $p = 0.039$) and formed a strong statistical trend during both spring (mean $\beta = -0.118$, $p = 0.059$) and autumn (mean $\beta = -0.534$, $p = 0.058$).

Conversely, the herd exhibited a seasonally shifting relationship with the reserve perimeter fence. During spring, the cattle demonstrated a statistically significant attraction to the reserve boundary (mean $\beta = -0.145$, $p = 0.025$). This spatial strategy inverted during summer, revealing a statistical trend toward edge avoidance (mean $\beta = 0.273$, $p = 0.093$), before transitioning into a statistically non-significant relationship by autumn ($p = 0.58$).

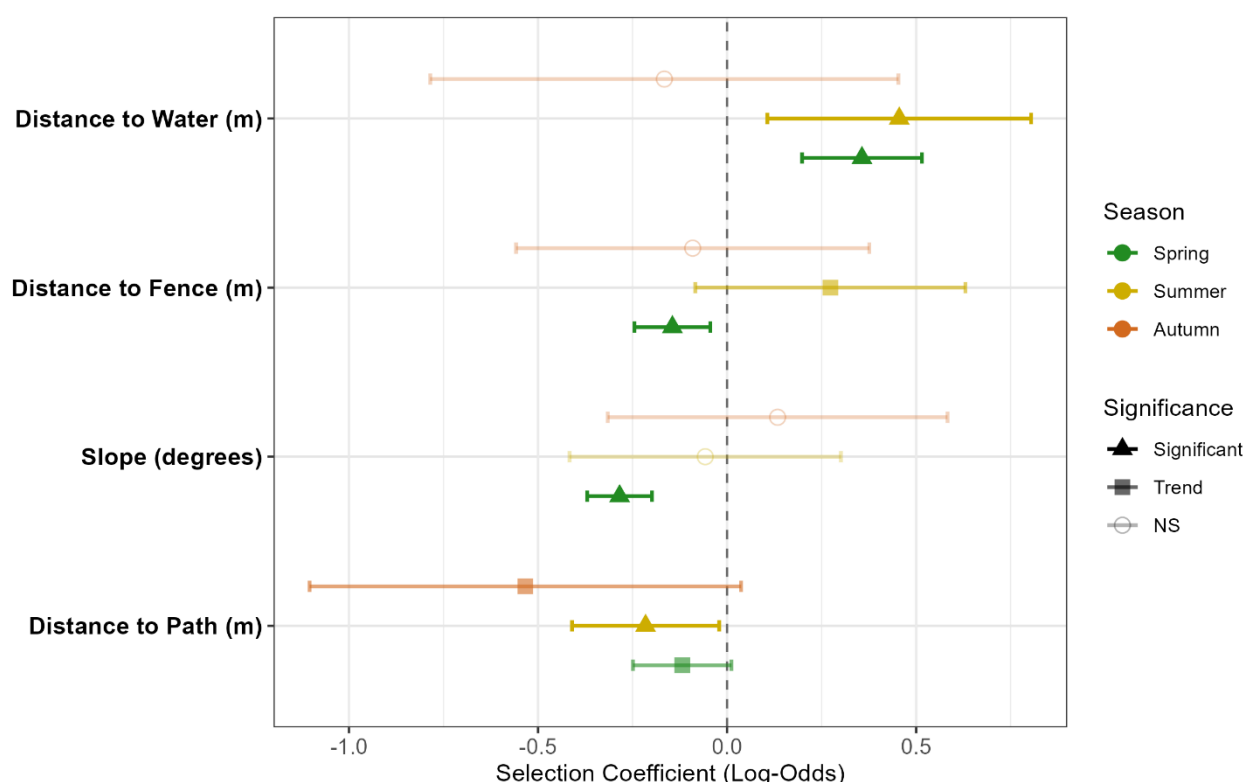


Figure 13. Forest plot of the integrated Resource Selection Function (iRSF) models detailing the population-level selection for continuous environmental and structural covariates among the Kalmthoutse Heide (Galloway Cattle) across three biological seasons. Plotted values represent the estimated mean β -coefficients, with horizontal bars indicating the 95% confidence intervals. Crucially, for the Distance to... covariates, a positive value ($\beta > 0$) indicates selection for greater distances (i.e., spatial avoidance of the feature), whereas a negative value ($\beta < 0$) indicates selection for shorter distances (i.e., spatial attraction to the feature). For the topographical Slope covariate, a positive value indicates a preference for steeper terrain, while a negative value indicates a preference for flatter terrain.

4.3 WP2: Fine-Scale Habitat Selection & Species Divergence

While continuous environmental features like topography and human infrastructure dictate the physical constraints of herbivore movement, the primary biological driver of their spatial distribution is the search for forage and shelter.

4.3.1. Westhoek: Equid Habitat Selection

Relative to the open scrub baseline, the equid population exhibited distinct and statistically robust habitat preferences largely in favour of open and low-vegetation types (Figure 14).

Population-Level Open Habitat Preference

At the population level, the equid group demonstrated a statistically significant preference for *Duingrasland* (Dune grassland) across all four biological seasons (spring: mean $\beta = 1.31$, $p = 0.036$; summer: mean $\beta = 1.14$, $p = 0.007$; autumn: mean $\beta = 1.02$, $p = 0.012$; winter: mean $\beta = 1.02$, $p < 0.001$). This consistent positive selection confirms that the equids prioritize open grass patches year-round, actively selecting them over the *Open duindoornstruweel* scrub baseline. Furthermore, this population-level preference for open and low-vegetation states extended beyond the short grasses:

- The equids displayed significant positive selection for *Grasruigte* (Tall grass/herbaceous vegetation) during three seasons (spring: mean $\beta = 0.82$, $p = 0.023$; summer: mean $\beta = 0.59$, $p = 0.028$; winter: mean $\beta = 0.58$, $p = 0.017$).
- They displayed significant positive selection for *Duinvallei* (Dune slack) during summer (Mean $\beta = 0.88$, $p = 0.044$) and a strong positive trend during autumn (mean $\beta = 0.67$, $p = 0.057$).
- They displayed significant positive selection for Schaarsbegroeid (Sparse vegetation) during summer (mean $\beta = 1.93$, $p = 0.009$) and a strong positive trend during autumn (mean $\beta = 0.81$, $p = 0.055$).
- They displayed a positive trend for *Mosduin* (Moss dune) during summer (mean $\beta = 0.26$, $p = 0.067$).

Relative to the reference baseline of *Open duindoornstruweel* (Open Sea buckthorn), the equids showed no preference or avoidance for similar high scrub vegetation, like *Duindoornstruweel* (Sea buckthorn) and *Opgaand struweel* (Tall scrub). Low scrub vegetation like *Kruipwilg_LaagStruweel* (Creeping willow low scrub), on the other hand, were positively selected in winter (mean $\beta = 0.56$, $p = 0.041$), but neutrally in other seasons. Only *Bos* (Forest) in spring showed a trend of avoidance (mean $\beta = -0.40$, $p = 0.076$) relative to *Open duindoornstruweel* (Open Sea buckthorn). The other seasons of *Bos* (Forest) showed a neutral selection.

Sub-herd Divergence (Konik vs. Shetland)

Crucially, disaggregating the models revealed that the sub-herd spatial strategies diverged substantially across the successional vegetation classes (Figure 15). It is important to note that whenever spatial preference, neutrality, or avoidance is discussed within this section, it is strictly relative to the reference baseline habitat, *Open duindoornstruweel* (Open Sea buckthorn scrub). Furthermore, because the sub-herd coefficients were mathematically aligned to this reference baseline post-hoc, in specific seasons where a habitat was utilized as the internal reference category by the original RSF model, this alignment yields a point estimate without an accompanying confidence interval (as previously detailed in Section 3.5.2). This is, for instance, visualised in the Konik estimate of *Duingrasland* in winter (Figure 15).

- ***Duingrasland* (Dune Grassland):** This habitat represents a shared preference for both species since they both exhibited pronounced positive effect sizes. The Shetland pony demonstrated strictly positive selection across all four seasons (CIs strictly > 0), while the Konik herd only achieved strict positive selection during summer (mean β = 1.113, CI: [0.098, 2.127]) and winter (mean β = 1.003). During spring and autumn, the horses did maintain strong positive directional tendencies (e.g., autumn mean β = 0.929, CI: [-0.071, 1.929]).
- ***Schaarsbegroeid* (Sparse Vegetation):** This vegetation type marks a divergence in foraging intensity between the species. The Konik sub-herds only positively selected for this habitat during the summer (mean β = 1.787, CI: [0.047, 3.526]), treating it as neutral during the rest of the year although showing a positive trend in spring and autumn. In contrast, the Shetland pony demonstrated a strict preference across all four biological seasons, peaking in summer (mean β = 2.350, CI: [1.584, 3.116]) and spring (mean β = 1.986, CI: [1.072, 2.899]), alongside continued strict positive selection in autumn (mean β = 1.504, CI: [0.797, 2.211]) and winter (mean β = 1.292, CI: [0.112, 2.472]).
- ***Kruipwilg_LaagStruweel* (Creeping Willow Low Scrub):** The Shetland pony displayed strict positive selection for this low scrub habitat during both spring (mean β = 1.310, CI: [0.286, 2.334]) and summer (mean β = 1.004, CI: [0.031, 1.977]), reverting to neutrality in autumn and winter. In contrast, the Konik horses treated the willow scrub as strictly neutral (with all CIs crossing zero) throughout the entire year.
- ***Duinvallei* (Dune Slack):** A similar divergence occurred in the dune slacks. The Shetland pony demonstrated strict positive selection for this habitat year-round, utilising the slacks most heavily during the summer (mean β = 1.397, CI: [0.651, 2.143]) and autumn (mean β = 1.216, CI: [0.217, 2.215]), alongside continued positive selection in winter (mean β = 1.012, CI: [0.139, 1.885]) and spring (mean β = 0.955, CI: [0.005, 1.906]). In contrast, the Konik sub-herds treated the Duinvallei as mathematically neutral throughout the entire year (with all CIs crossing zero).
- ***Duindoornstruweel* (Sea Buckthorn Scrub):** While the Konik sub-herds maintained strict mathematical neutrality toward this standard scrub habitat across all four seasons (with all CIs crossing zero), the Shetland pony displayed a strict positive selection for it specifically

during the summer (mean β = 0.903, CI: [0.183, 1.622]). During the rest of the year, the pony's spatial relationship reverted back to baseline equivalence.

- **Opgaand struweel (Tall Scrub):** The Konik sub-herds demonstrated avoidance of this dense habitat exclusively during autumn (mean β = -0.469, CI: [-0.636, -0.301]), treating it as mathematically neutral relative to the baseline during the rest of the year. Meanwhile, the Shetland pony treated it as mathematically neutral throughout the entire year (with all CIs crossing zero).
- **Mosduin (Moss Dune):** The Konik herd demonstrated strict spatial avoidance of Moss dunes during the winter (mean β = -0.390, CI: [-0.720, -0.060]), while treating them as neutral relative to the baseline during the rest of the year. The Shetland pony maintained mathematical neutrality toward this habitat year-round (with all CIs crossing zero). Both species also displayed a shared positive spatial inclination toward moss dunes during summer (Konik mean β = 0.206; Shetland mean β = 0.428), which resulted in a positive trend on the equid level (Figure 14).
- **Bos (Forest):** Both species largely converged on mathematical neutrality regarding the forest environment. Neither the Konik horses nor the Shetland pony exhibited strict spatial selection or avoidance of closed-canopy areas compared to the open scrub baseline across any of the modelled seasons (with all CIs consistently crossing zero). However, despite this baseline equivalence, both taxa displayed a shared negative spatial inclination toward the forest during spring (Konik mean β = -0.291; Shetland mean β = -0.629), which resulted in a negative trend on the equid level (Figure 14).
- **Grasruigte (Tall Grass/Herbaceous):** For the tall herbaceous vegetation, both the Konik herd and the Shetland pony converged on mathematical neutrality during autumn (both CIs crossing zero). The Konik herd maintained this neutrality throughout the entire year, despite displaying moderate positive spatial tendencies. Conversely, the Shetland pony exhibited strict positive selection point estimates for Grasruigte during the spring (mean β = 1.007), summer (mean β = 0.805), and winter (mean β = 0.627). As established in section 3.5.2, because this specific habitat functioned as the internal reference category in the original RSF models for these seasons, its internal variance was fixed at zero, resulting in these realigned point estimates lacking accompanying confidence intervals (Figure 15).

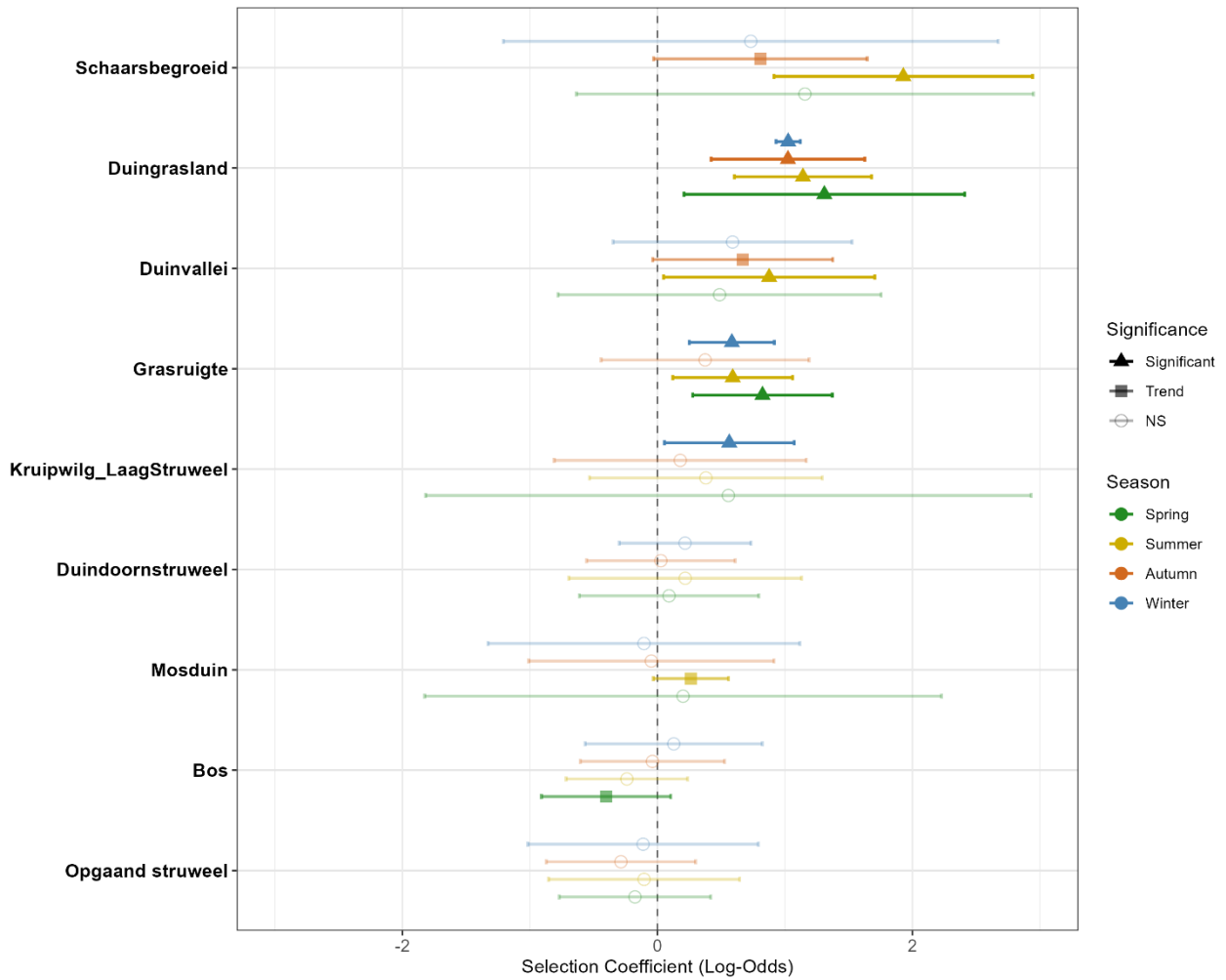


Figure 14. Forest plot of the integrated Resource Selection Function (iRSF) models detailing the population-level categorical habitat selection among the Westhoek equids across four biological seasons. Plotted values represent the estimated mean β -coefficients, with horizontal bars indicating 95% confidence intervals based on inter-individual variance. Selection is evaluated relative to the transitional *Open duindoornstruweel* (Open Sea buckthorn scrub) baseline, mathematically fixed at zero (dashed vertical line). Values greater than zero ($\beta > 0$) indicate positive selection (preference) relative to the baseline, while values less than zero ($\beta < 0$) indicate negative selection (avoidance).

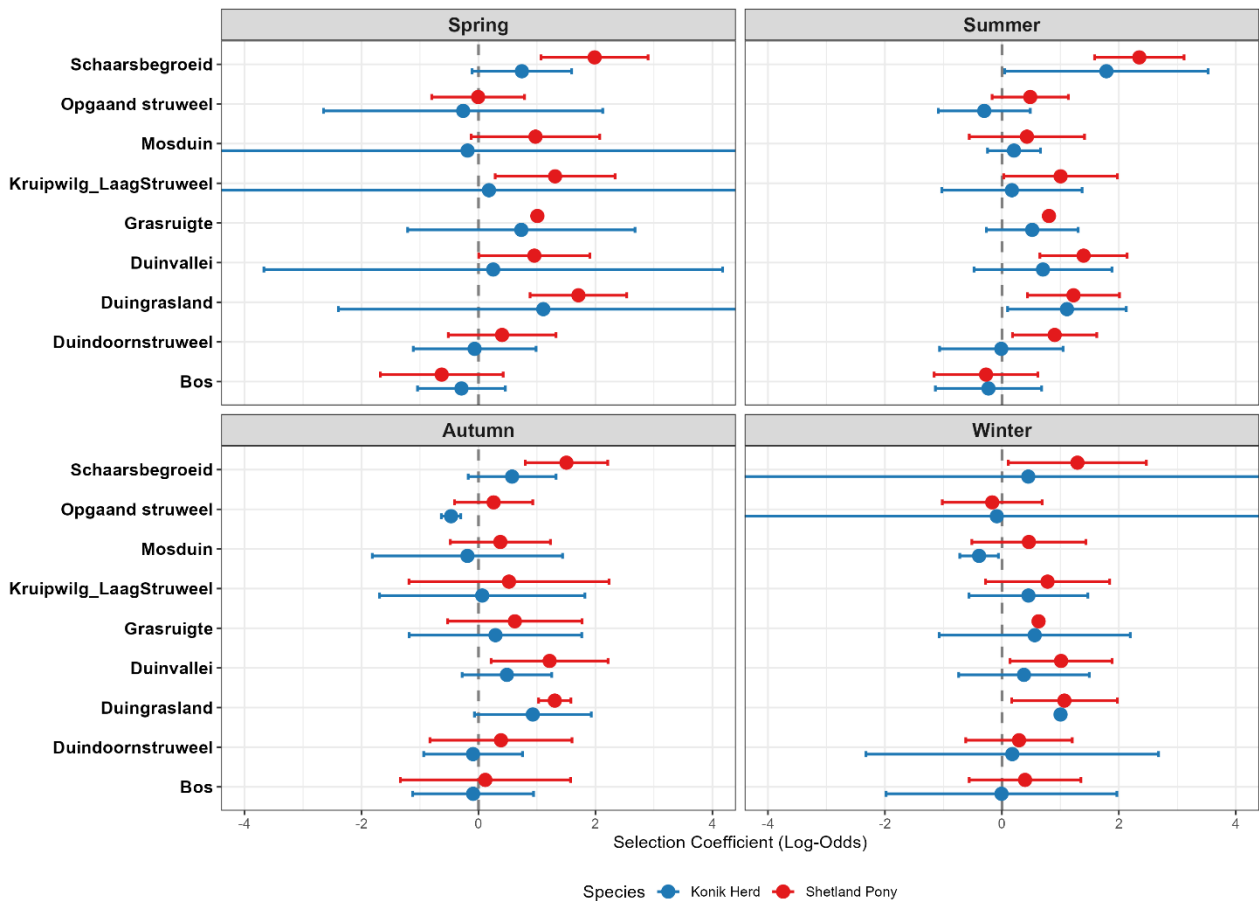


Figure 15. Species-specific comparison of categorical habitat selection within the Westhoek reserve. The models are disaggregated to contrast the spatial strategies of the Konik horses with the Shetland pony across four biological seasons relative to the *Open duindoornstruweel* baseline (dashed vertical line). The 95% confidence intervals (horizontal bars) represent different variance structures: (1) For the Konik horses ($n > 1$), bars represent inter-individual variance; (2) For the Shetland pony in autumn ($n = 3$), bars represent inter-annual variance of the single individual; (3) For the Shetland pony in spring, summer, and winter ($n = 1$), bars represent internal model confidence intervals derived from the spatial variance of the continuous-time track. Values greater than zero ($\beta > 0$) indicate positive selection (preference) relative to the baseline, while values less than zero ($\beta < 0$) indicate negative selection (avoidance).

4.3.2. Kalmthoutse Heide: Galloway Cattle Selection

In the Kalmthoutse Heide, the Galloway cattle exhibited a highly seasonal, shifting relationship with the vegetation when evaluated against the *Vergraste, gedegradeerde droge heide* (Grass-encroached degraded heath) baseline (Figure 16).

Positive Selection (Targeted Habitats)

At the population level, the cattle demonstrated a preference for transitional habitats characterized by structural variety, specifically areas experiencing tree encroachment.

- ***Droog schraalland met boomopslag* (Dry poor grassland with tree encroachment):**
The cattle displayed strict positive selection for this habitat during spring (Mean $\beta = 1.06$, p

= 0.025) and autumn (Mean β = 0.94, p = 0.031). During summer, this spatial relationship reverted back to baseline equivalence.

- **Droge heide met boomopslag (Dry heath with tree encroachment):** Similarly, the herd demonstrated a significant positive selection for tree-encroached dry heath during summer (Mean β = 0.29, p < 0.001), which persisted as a statistical trend into autumn (Mean β = 0.76, p = 0.063). During spring, this spatial relationship reverted back to baseline equivalence. It should be noted that the statistical significance of this preference during summer is partly mathematically amplified; the Confidence Intervals were highly constrained due to the fact that it was often used as the baseline habitat in the original iRSF models, see section 3.5.2.

Neutral Selection (Baseline Equivalence)

Habitats that did not achieve statistical significance indicate a neutral spatial relationship, meaning the herd utilized them proportionally equivalent to the *Vergraste, gedegradeerde droge heide* (Grass-encroached degraded heath) baseline.

- **Forested Habitats:** The cattle maintained strict baseline equivalence year-round across all three seasons for *Naaldbos met ondergroei van grassen* (Coniferous forest with grass understory) and *Loofbos* (Deciduous forest). Both of these habitats consistently yielded positive directional estimates, but inter-individual variance prevented strict statistical selection.
- **Open & Bare Habitats:** The cattle similarly treated *Droog schraalland* (Dry poor grassland) as mathematically neutral year-round. Conversely, they displayed a persistent negative spatial inclination toward *Open duin/vegetatieloos* (Bare dunes) across all three seasons (e.g., summer Mean β = -1.41), but because this habitat comprises only 0.38% of the total reserve area, the exceptionally wide confidence intervals restrict the model's statistical power, rendering it functionally neutral relative to the baseline.

Negative Selection (Avoided Habitats)

- **Vochtige, natte en venige heide (Moist, wet, and peaty heath):** The herd demonstrated spatial avoidance of the wetter heathlands during spring (Mean β = -0.79, p = 0.005) and summer (Mean β = -0.35, p = 0.010), before reverting to baseline neutrality in autumn.
- **Droge heide (Dry heath):** A nearly identical avoidance pattern occurred in the standard dry heath, where the cattle significantly avoided the habitat relative to the encroached baseline during spring (Mean β = -0.87, p = 0.017) and summer (Mean β = -0.43, p = 0.007), before reverting to baseline neutrality in autumn.
- **Struweel (Scrub):** The scrub matrix also functioned as a strong spatial deterrent. The cattle exhibited a significant spatial avoidance of this habitat during summer (Mean β = -1.93, p = 0.004), alongside a strong statistical trend for avoidance during spring (Mean β = -1.24, p = 0.075), before reverting to baseline neutrality in autumn.

- **Naaldbos (Coniferous forest):** While the cattle were neutral toward coniferous forests with grass understories, they demonstrated spatial avoidance of pure *Naaldbos* during summer (Mean $\beta = -0.81$, $p = 0.003$), before reverting to baseline neutrality in autumn and spring.

Seasonal Trend: Reduction in Selectivity

Viewed collectively, these selection categories reveal a temporal trajectory. During the spring and summer months, the cattle exhibited strict spatial strategies, characterized by positive preferences and multiple significant avoidances. However, by autumn, the vast majority of previously avoided habitats, including pure heathlands, scrub, and coniferous forest, reverted to statistical neutrality. This widespread shift toward baseline equivalence indicates a significant reduction in overall habitat selectivity during the autumn.

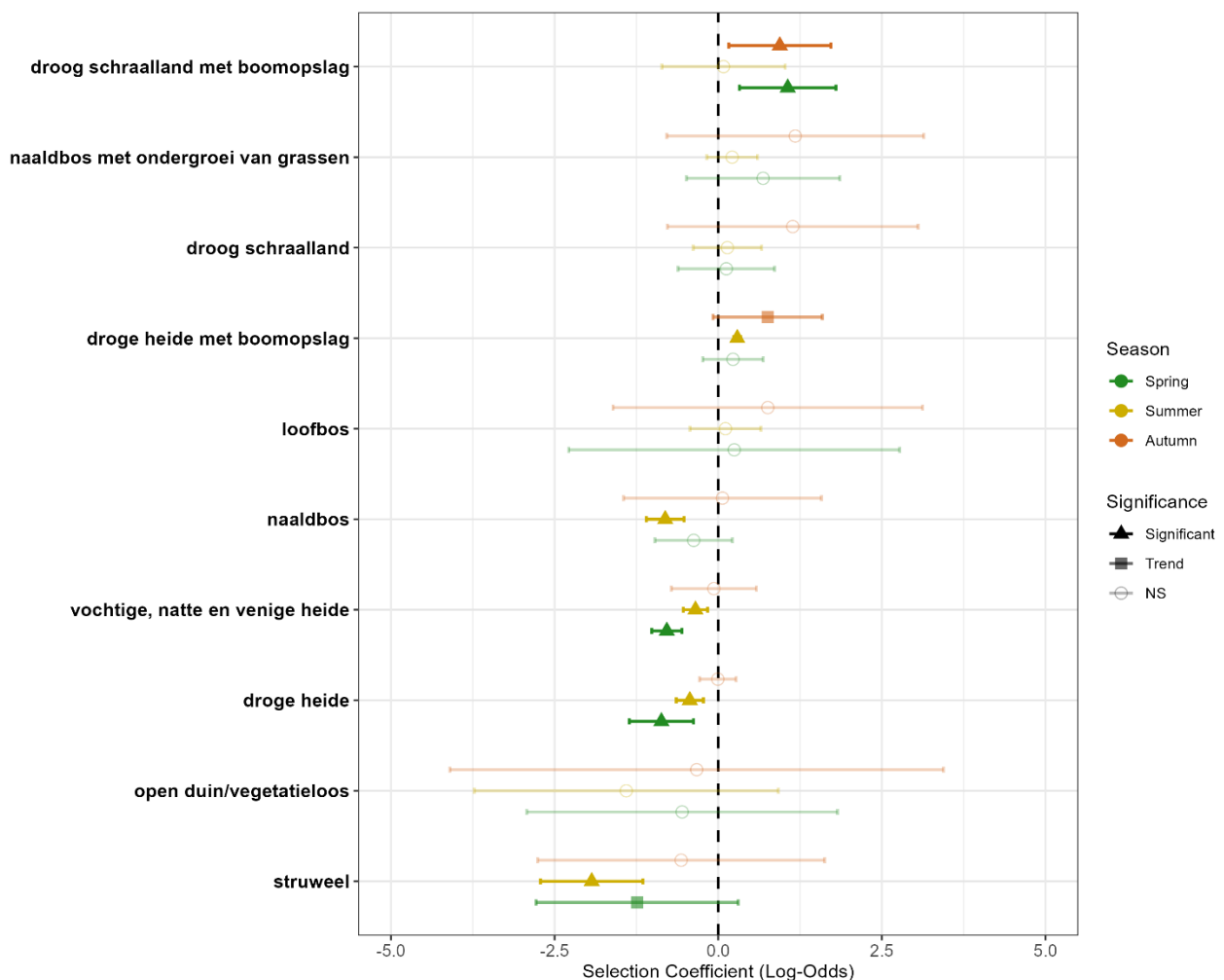


Figure 16. Forest plot of the integrated Resource Selection Function (iRSF) models detailing the population-level categorical habitat selection among the Galloway cattle in the Kalmthoutse Heide. Plotted values represent the estimated mean β -coefficients, with horizontal bars indicating 95% confidence intervals based on inter-individual variance. Selection is evaluated relative to the *Vergraste, gedegreerde droge heide* (Grass-encroached degraded dry heath) baseline,

mathematically fixed at zero (dashed vertical line). Values greater than zero ($\beta > 0$) indicate positive selection (preference) relative to the baseline, while values less than zero ($\beta < 0$) indicate negative selection (avoidance).

4.4 WP3: Drivers of Vegetation Height Change

4.4.1. Model Selection and Predictor Importance

The stepwise Akaike Information Criterion (AIC) selection procedure confirmed that all four evaluated predictors, Space Use Intensity (SUI), Spring Groundwater Depth, Terrain Slope, and Solar Exposure, were significant drivers of vegetation transition and essential to the final additive model. Multicollinearity among these final predictors was confirmed to be negligible (all VIFs < 5). Analysis of the model's internal metrics revealed that Spring Groundwater Depth functioned as the most influential landscape predictor, causing a severe AIC penalty of +226.7 upon its removal. Crucially, cumulative Space Use Intensity (SUI) emerged as the second most powerful driver of successional change, yielding an AIC penalty of +82.0 upon removal.

4.4.2. The Impact of Space Use Intensity (SUI)

By converting the raw multinomial log-odds into Average Marginal Effects (AME), the absolute impact of the equid group on the landscape was isolated while holding all abiotic covariates constant (Figure 17). The findings statistically confirm that SUI functions as a significant driver of structural vegetation dynamics in the Westhoek (Figure 18 and 19).

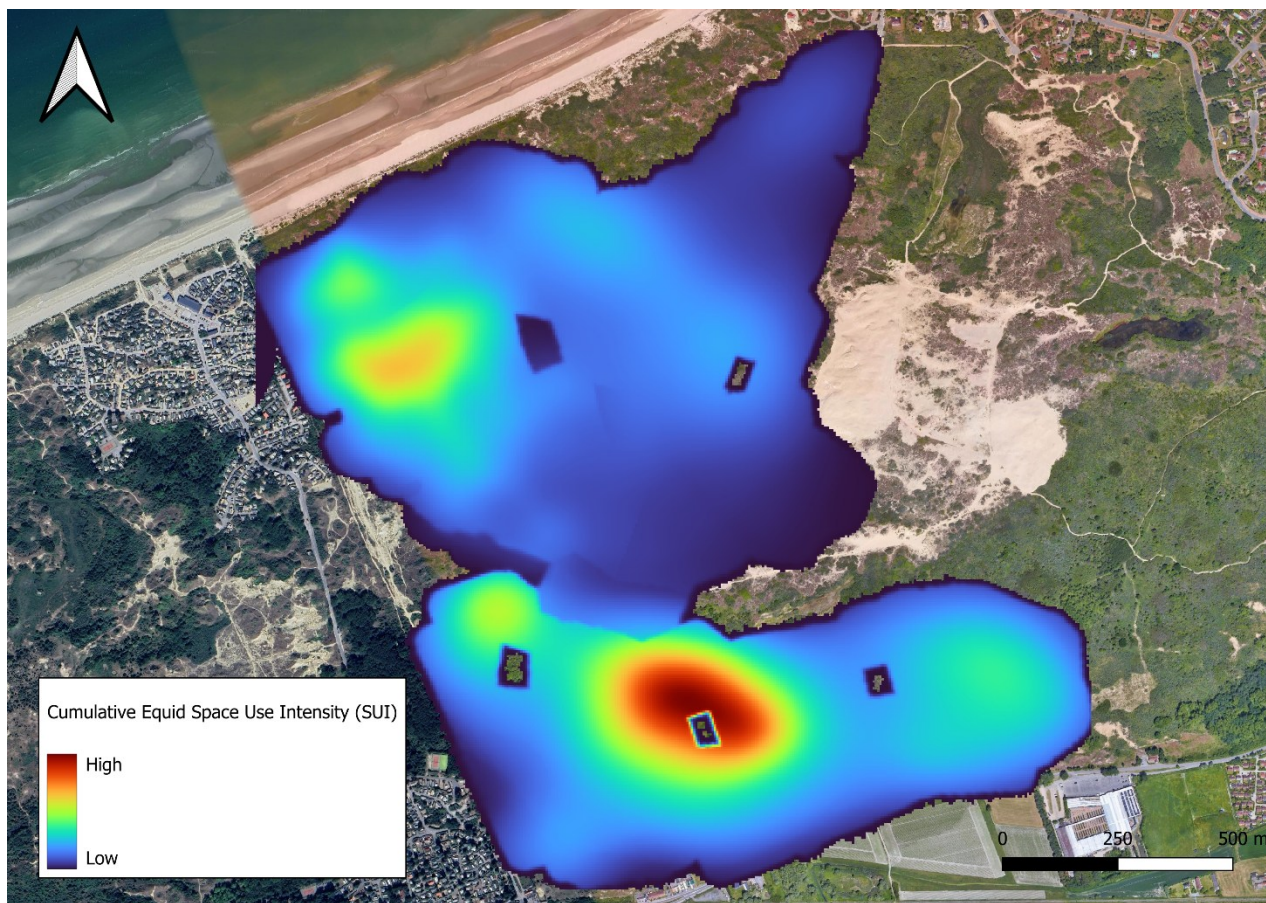


Figure 17. Cumulative Equid Space Use Intensity (SUI) of the Westhoek equid group. The map visualizes the aggregated spatial utilization distribution of the tracked population across the multi-year study period. To accurately reflect true ecological impact, individual continuous-time home ranges (AKDE) were mathematically stacked and metabolically weighted (Konik horses = 1.0; Shetland pony = 0.67) to create a continuous spatial raster. The resulting gradient highlights high-intensity space use areas, contrasting with areas of low landscape utilization.

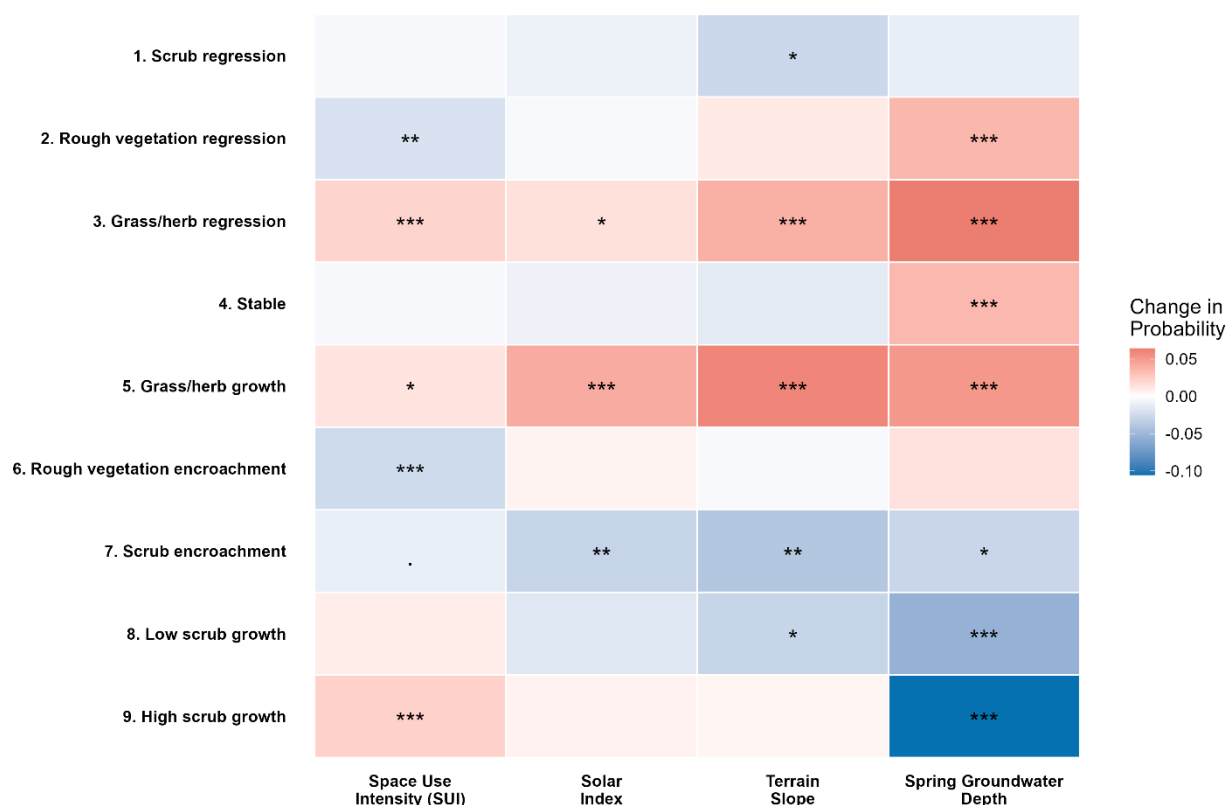


Figure 18. Heatmap of the Average Marginal Effects (AME) detailing the absolute probability of vegetation structural transition in the Westhoek. Values represent the percentage shift in probability of occurrence per 1-Standard Deviation increase in the predictor variable. Blue indicates a lower probability of occurrence, while red indicates a higher probability of occurrence. The significance codes are: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; . $p < 0.10$.

Significant Increases in Probability (Promoted Processes): A one-standard-deviation (1-SD) increase in SUI significantly increased the absolute probability of Grass/herb regression (Slope = +0.0212, $p < 0.001$) and Grass/herb growth (Slope = +0.0134, $p = 0.033$). Additionally, this same 1-SD increase significantly accelerated High scrub growth (Slope = +0.0229, $p < 0.001$).

Significant Decreases in Probability (Suppressed Processes): Conversely, the herd actively suppressed rougher successional stages. Increased SUI severely decreased the probability of rough vegetation encroachment (Slope = -0.0256, $p < 0.001$) and rough vegetation regression (Slope = -0.0202, $p = 0.005$). It also demonstrated a marginal statistical trend toward suppressing Scrub encroachment (Slope = -0.0114, $p = 0.096$).

Neutral Baseline Equivalence: SUI did not significantly alter the probability of Scrub regression, Low scrub growth, or Stable.

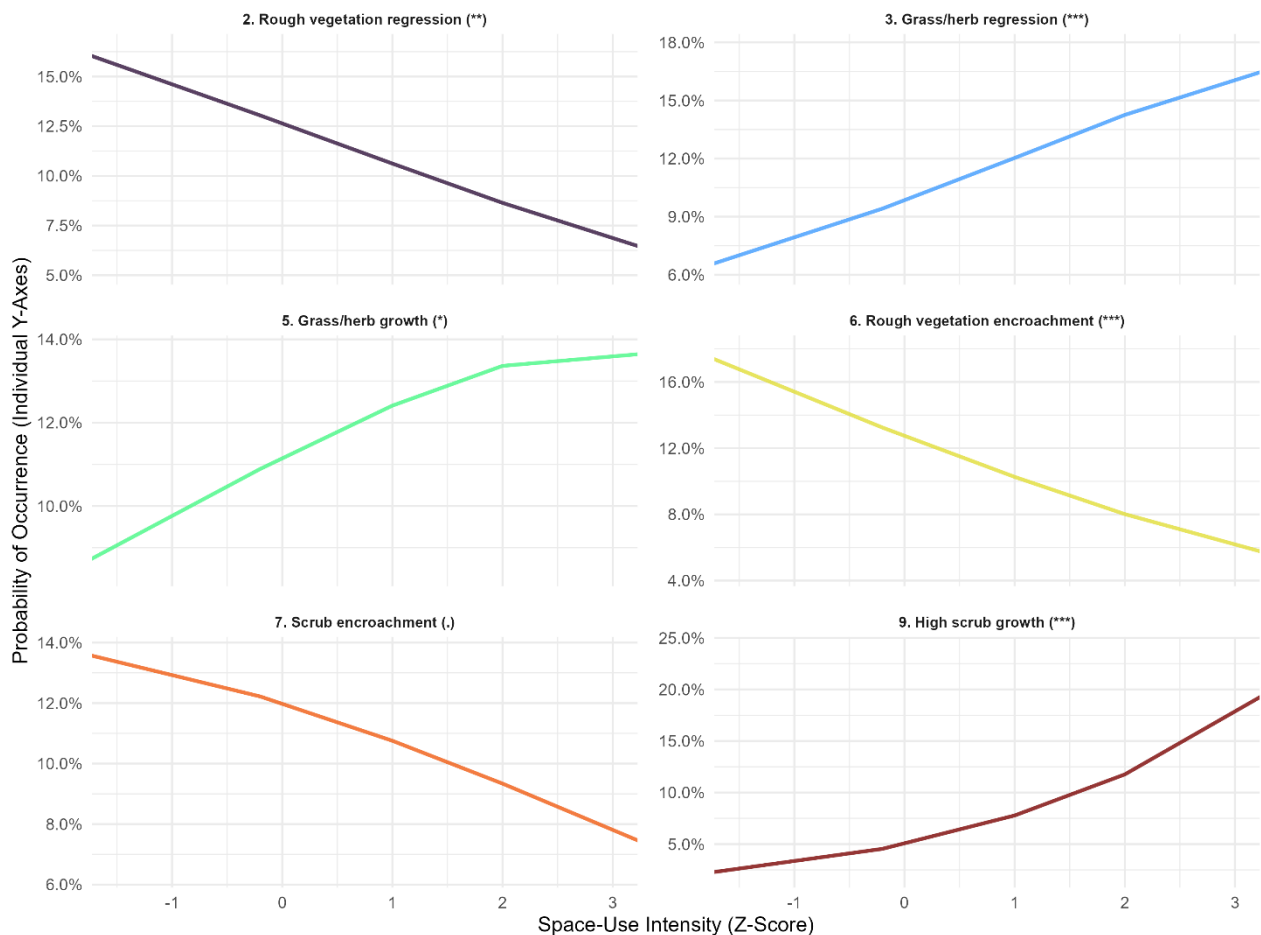


Figure 19. Predicted marginal effects of Space Use Intensity (SUI) on the probability of occurrence of specific vegetation successional processes, holding all abiotic covariates at their mean.

4.4.3. Abiotic Constraints on Succession

Besides Space Use Intensity, the abiotic landscape variables were also significant predictors of successional dynamics independent of the herbivore pressure.

Hydrology (Spring Groundwater Depth): Groundwater Depth was the strongest predictor across the reserve. An increase in this variable, representing a 1-SD shift from the reserve's average depth (2.0 m) to a deeper water table (+1 SD = 4.14 m), significantly increased the probability of the landscape remaining Stable (Slope = +0.0352, $p < 0.001$), undergoing Rough vegetation regression (Slope = +0.0361, $p < 0.001$), Grass/herb regression (Slope = +0.0641, $p < 0.001$), and Grass/herb growth (Slope = +0.0512, $p < 0.001$). Simultaneously, these drier and deeper conditions (+1 SD) limited woody succession, causing a highly significant decrease in the probability of Low scrub growth (Slope = -0.0552, $p < 0.001$), High scrub growth (Slope = -0.1055, $p < 0.001$), and Scrub encroachment (Slope = -0.0285, $p = 0.022$) (Figure 20). Conversely, variations in groundwater depth did not significantly alter the probability of Scrub regression or rough vegetation encroachment.

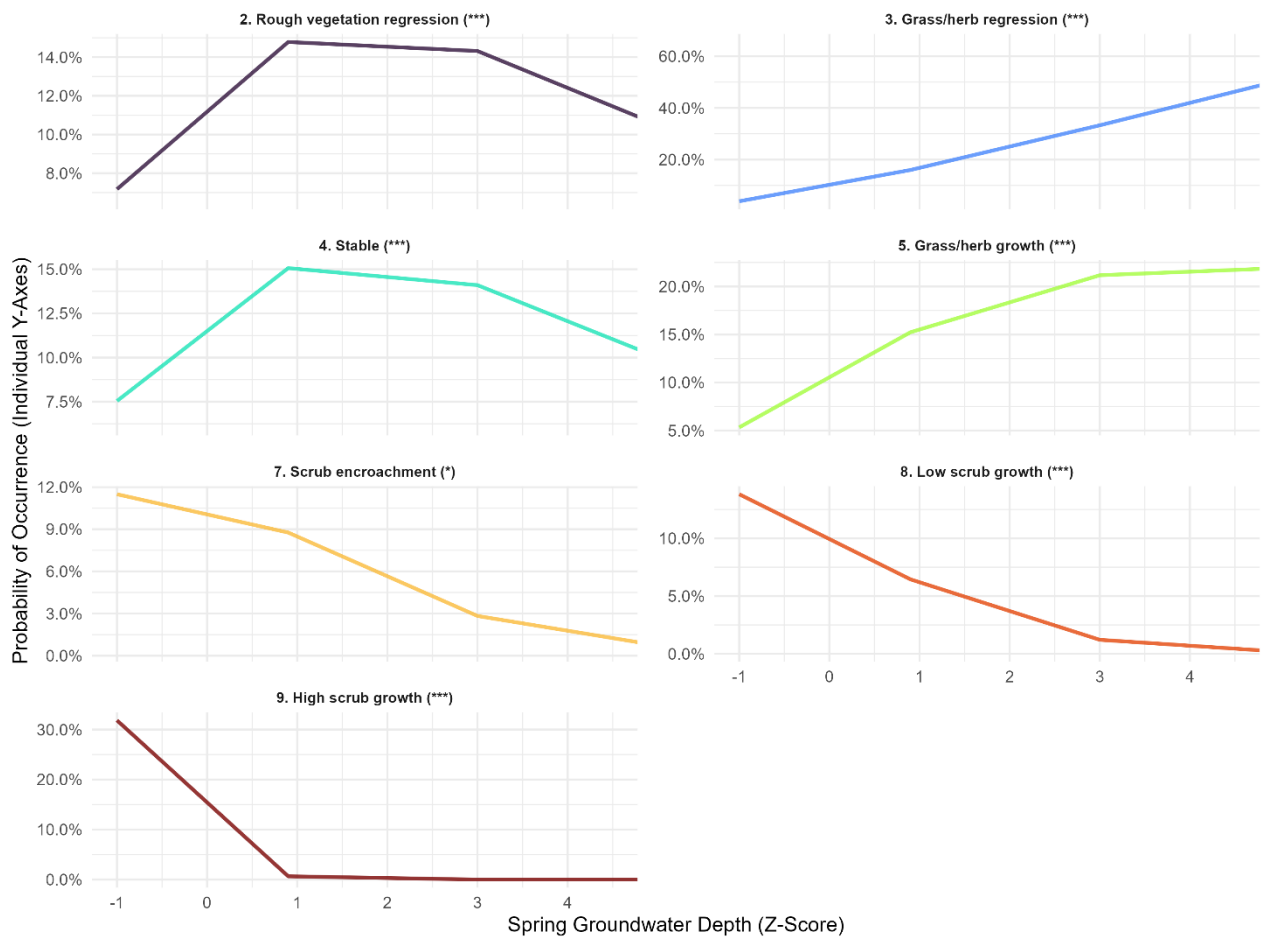


Figure 20. Predicted marginal effects of Spring Groundwater Depth on the probability of occurrence of specific vegetation successional processes. To isolate the independent effect of this hydrological driver, all other covariates, including Space Use Intensity (SUI), were held at their statistical mean.

Topography (Terrain Slope): A 1-SD steepening of the terrain (shifting from the 9.2° average to a steep 15.4° gradient) significantly increased the likelihood of Grass/herb growth (Slope = +0.0601, $p < 0.001$) and Grass/herb regression (Slope = +0.0389, $p < 0.001$). Conversely, steeper gradients significantly decreased the probability of all woody processes, including Scrub encroachment (Slope = -0.0395, $p = 0.002$), Scrub regression (Slope = -0.0273, $p = 0.028$), and Low scrub growth (Slope = -0.0292, $p = 0.018$) (Figure 21). Terrain slope did not significantly influence the occurrence of rough vegetation regression, rough vegetation encroachment, High scrub growth, or the probability of the landscape remaining Stable.

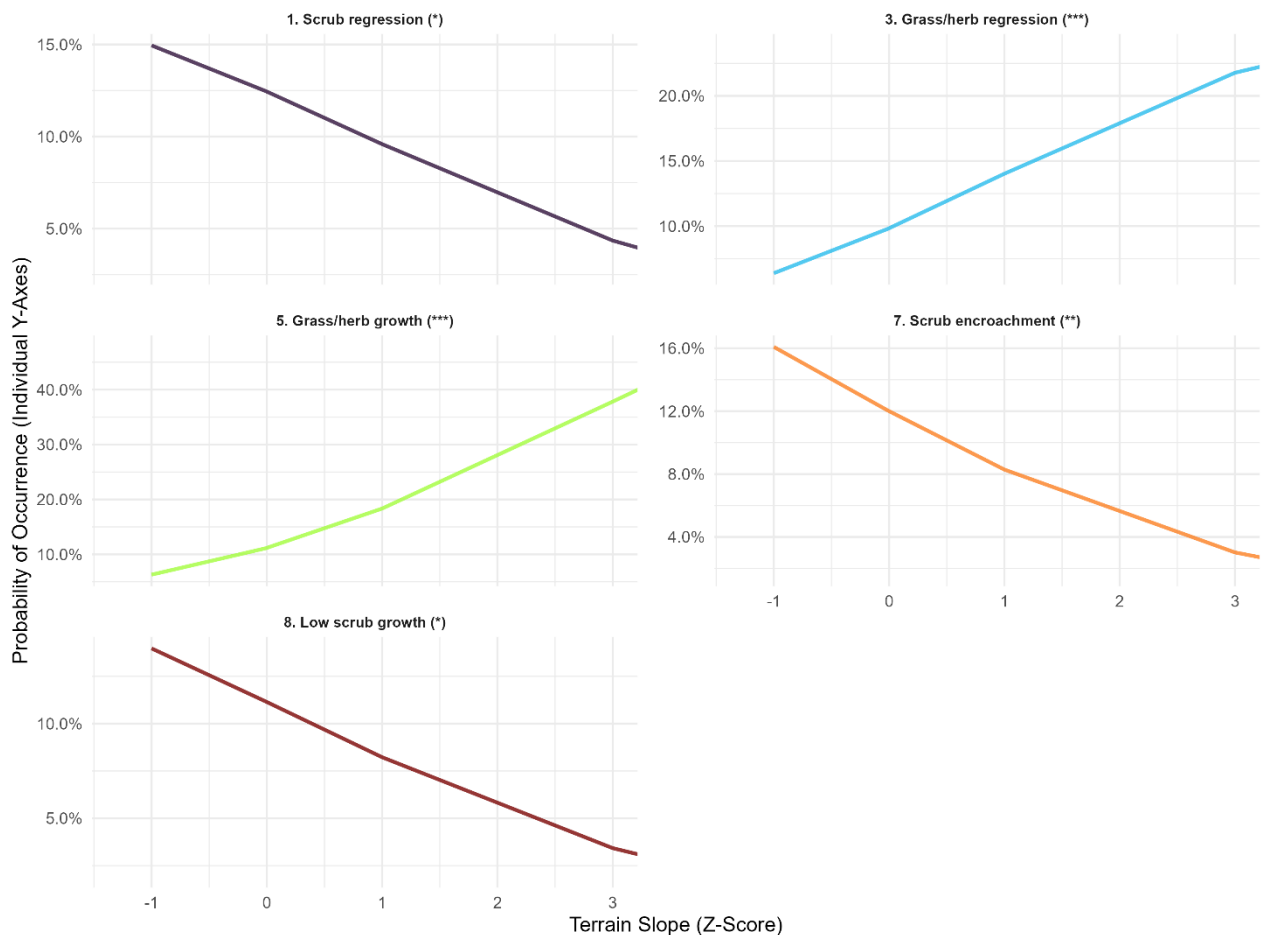


Figure 21. Predicted marginal effects of Terrain Slope on the probability of occurrence of specific vegetation successional processes. To isolate the independent effect of this topographical driver, all other covariates, including Space Use Intensity (SUI), were held at their statistical mean.

Microclimate (Solar Exposure): High solar insolation functionally mirrored the constraints of steep topography. More exposed terrain, such as southern slopes, promoted Grass/herb growth (Slope = +0.0414, $p < 0.001$) and Grass/herb regression (Slope = +0.0150, $p = 0.026$), while significantly decreasing the structural capability of the landscape to support Scrub encroachment (Slope = -0.0303, $p = 0.009$) (Figure 22). Solar exposure did not significantly impact the probability of Scrub regression, rough vegetation regression, rough vegetation encroachment, Low or High scrub growth, or the landscape remaining Stable.

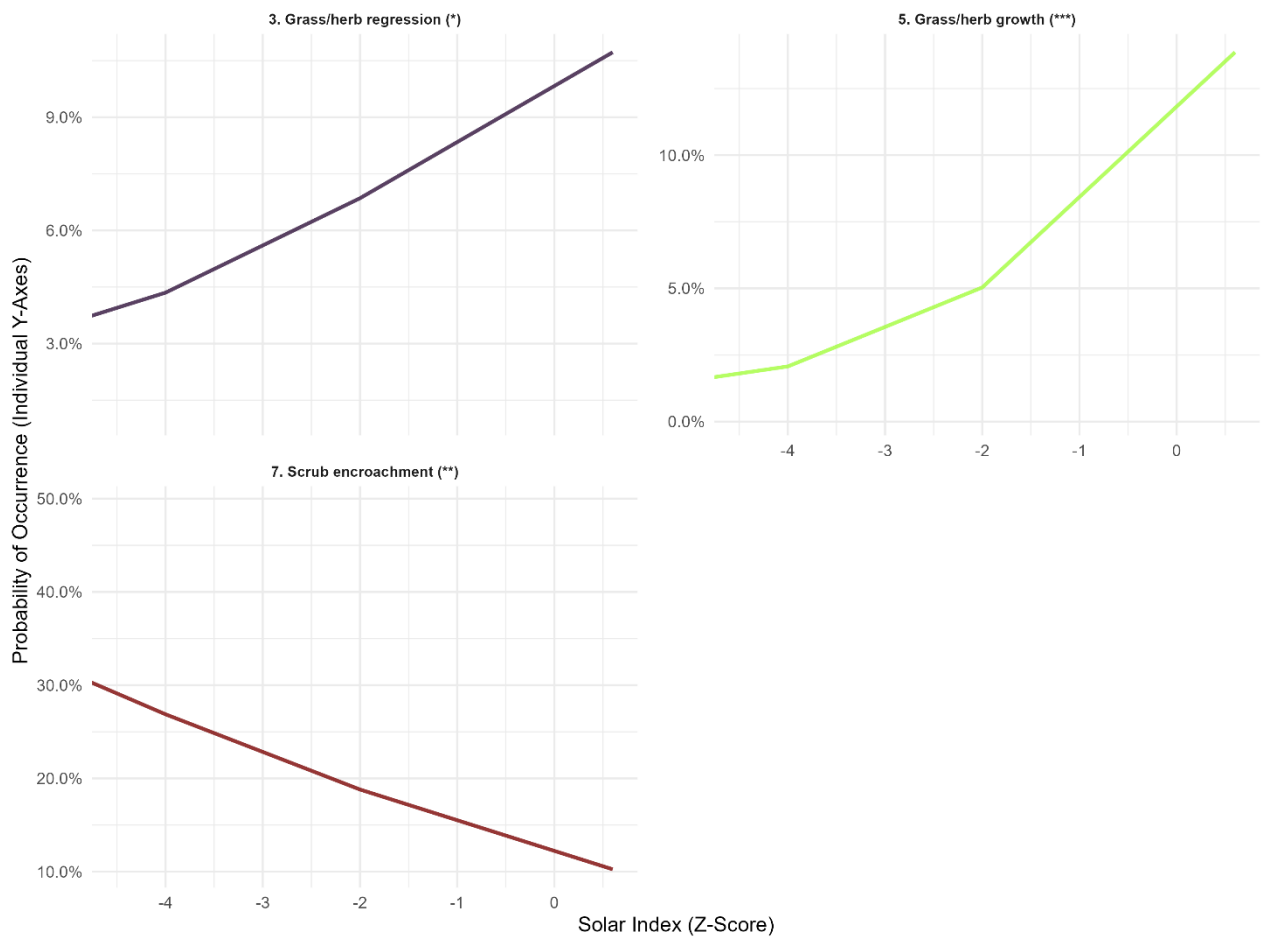


Figure 22. Predicted marginal effects of Solar exposure on the probability of occurrence of specific vegetation successional processes. To isolate the independent effect of this microclimatic driver, all other covariates, including Space Use Intensity (SUI), were held at their statistical mean.

5. Discussion

5.1 Spatial Constraints and Anthropogenic Landscapes

5.1.1 Home Range Saturation and the Impact of Corridor Expansion

The physical perimeter of fenced nature reserves fundamentally dictates the spatial ecology of large herbivores. By analysing the 95% AKDE saturation indices, this study revealed potential spatial constraints acting upon the studied populations.

Prior to the corridor opening in the winter of 2022-23, the equid group in the Westhoek was spatially restricted, exhibiting high saturation indices within their isolated northern and southern sectors. Following the removal of this barrier, the equids demonstrated a significant expansion in their absolute home range sizes, confirming our expectations under Hypothesis 1.3 (Landscape Connectivity). However, this spatial response was divergent between sub-herds. While the Shetland pony and the AN788 Konik sub-herd capitalized on the newly accessible area, the AN789 sub-herd remained conservative in its movement, showing minimal expansion despite experiencing high saturation prior to the opening. This social independence was also evident during the secondary spike in home range size and saturation observed for the Shetland pony and the AN788 Konik sub-herd during the autumn of 2024. While the specific reason for this late-stage expansion remains unclear, the fact that it was not mirrored by the AN789 sub-herd means it cannot be readily attributed to uniform environmental drivers, such as a reserve-wide depletion of forage. This highlights that spatial expansion in the Westhoek is not uniformly adopted by the equid group but is instead mediated by sub-herd social dynamics and localized site fidelity. A potential explanation for this spatial divergence between the Konik sub-herds may lie in their contrasting demographic compositions. The AN788 bachelor herd of stallions may inherently be more exploratory, whereas the AN789 mixed demographic herd (comprising mares, a stallion, yearlings, and foals) may favour a more site-conservative strategy. However, because this study monitored only a single representative sub-herd for each demographic category, this driver cannot be statistically confirmed.

Crucially, even though the home range size increased after the corridor opened, the overall saturation indices dropped significantly and remained below the 75% saturation threshold. This illustrates that the horses did expand their home range size, but not linearly with the expansion of the total reserve area. If they truly were saturated in the whole reserve, like in their southern and northern sectors previously, we would expect the saturation to be at the same level before and after the corridor opening. This suggests that the equids are likely not saturated when the whole reserve is connected, supporting Hypothesis 1.1 (Spatial Saturation) for the post-corridor landscape.

Conversely, the spatial dynamics observed in the Kalmthoutse Heide reflect a fundamentally different ecological baseline. This distinction is primarily driven by the scale of the available landscape, as the fenced area of the Kalmthoutse Heide is approximately three times larger than that of the Westhoek. Within this expansive area, the Galloway cattle exhibited baseline saturation levels that were comparable to the unconfined, post-corridor Westhoek equids. Furthermore, the cattle demonstrated seasonal fluctuations in their home range sizes. This seasonal variation is an

indicator of spatial freedom; if the herd were operating at the physical limits of the reserve, their home ranges would remain static year-round. Because their spatial footprint naturally expands and contracts across the seasons without reaching maximum capacity, it indicates that the cattle are likely not constrained by the physical perimeter of the reserve and thus not saturated. This further supports Hypothesis 1.1 across both study sites. While the Westhoek equids largely lacked this seasonal spatial variation, this should not be interpreted as a symptom of spatial limitation or saturation. Rather, it reflects a biological divergence, as equids are generally less sensitive to seasonal phenology than cattle, leading to more stable year-round spatial strategies (Hendler et al., 2026; Kristensen et al., 2026).

However, the findings regarding home range saturation must be interpreted with caution. While low saturation and seasonal variability are prerequisites for free spatial choice, they are not definitive proof of it. Unused areas may instead be the result of localized physical inaccessibility or social exclusion mechanisms, such as the potential territorial avoidance between the Equid sub-herds and the Scottish Highland cattle in the Westhoek.

Furthermore, the driver of spatial variance differed between the two reserves. Unlike the fractured equid sub-herds in the Westhoek, where social divergence drove spatial patterns, inter-individual variance among the Galloway cattle was notably low. Because the cattle operated as an unsaturated and rather cohesive herd unit year-round, temporal factors (inter-annual and seasonal shifts) dictated their spatial footprint more than social fragmentation or physical fencing.

5.1.2. The Influence of Anthropogenic Infrastructure on Spatial Ecology

Beyond physical confinement, anthropogenic infrastructure, specifically boundary fences and internal paths, exerted a significant, species-dependent, influence on spatial selection within both reserves.

Fence Aversion vs. Attraction

In the Westhoek, the boundary fence functioned as a spatial deterrent. The equids actively selected for greater distances away from the perimeter, particularly during spring and winter. However, this avoidance was sub-herd dependent: the Shetland pony exhibited strict, year-round aversion to the fence, whereas the Konik sub-herds only displayed avoidance during the colder months.

Because the integrated Resource Selection Function (iRSF) mathematically isolates the independent effect of distance-to-fence from categorical habitat selection, any spatial avoidance or attraction driven by vegetation-types near the fence is correctly attributed to habitat preference, not fence proximity. This methodological decoupling of vegetation from physical infrastructure is a critical distinction. Many previous studies observing fence interactions (Acciaro et al., 2024; Rech et al., 2025) do not isolate habitat covariates and frequently conflate structural avoidance or attraction with localized habitat selection. Because this decoupling was executed in this study, the distance covariate confirms that the physical structure of the fence itself, acts as a true spatial deterrent. This finding partially supports Hypothesis 2.3 (Anthropogenic Avoidance) regarding perimeter infrastructure and aligns with recent literature; for example, Rech et al. (2025) similarly

documented a generalized avoidance of boundary fences by free-roaming horses in a Danish rewilding area.

Conversely, the Galloway cattle in the Kalmthoutse Heide demonstrated a seasonal, shifting relationship with the reserve perimeter. While they avoided the fence during the summer, likely coinciding with the peak of tourist activity and associated perimeter disturbance, this effect inverted during the spring, where the cattle actively selected for proximity to the boundary. Because the iRSF strictly accounts for underlying vegetation, this spring attraction cannot be attributed to foraging behaviour. Instead, it may be a behavioural artifact of their seasonal management cycle, reflecting a temporary spatial anchoring to their release site upon returning to the reserve. Alternatively, this attraction may serve a functional movement purpose. In expansive landscapes such as open heathlands, prominent fence infrastructure can be utilized by large herbivores as a navigational landmark. Consequently, the cattle may actively use the perimeter fence as a reliable structural guide to efficiently navigate between disparate, high-quality spring grazing patches.

Ultimately, the contrast between the seasonal fence use of cattle in the Kalmthoutse Heide and the strict avoidance observed in other systems (Rech et al., 2025) underscores that the spatial impact of fences is not a universal constant. Instead, it is mediated by the specific anthropogenic disturbance gradients and management contexts surrounding a given reserve.

Paths as Navigational Corridors

While fences largely repelled the herbivores, internal paths frequently functioned as spatial attractants, a behaviour widely documented among various wildlife species seeking to minimize travel costs along movement corridors (Kays et al., 2017). In the Westhoek, the model indicated a population-level preference for paths during spring and winter. However, disaggregating the data revealed this was a mathematical artifact driven entirely by the Shetland pony, which exhibited a year-round attraction to the path network while the Konik sub-herds remained neutral.

Structurally, the bare, compacted ground and short vegetation characteristic of these trails are ideal for animal movement. Additionally, because the iRSF controls for habitat, this attraction indicates that the paths are utilized as low-resistance navigational corridors rather than foraging grounds. Because the majority of the mapped path network within the Westhoek grazing blocks consists of inaccessible service roads rather than busy recreational trails, this attraction is likely driven by the physical ease of movement rather than a high tolerance for human disturbance. The spatial divergence observed between the equids further supports this energy-conservation mechanism, likely functioning as a result of morphological constraints. Due to its smaller stature and shorter stride length, navigating through denser, off-trail vegetation likely imposes a higher energetic cost on the Shetland pony compared to the larger Konik horses. Conversely, the Koniks, possessing a larger body mass and longer legs, are likely better equipped to traverse the rougher matrix of the reserve with a lower energetic penalty, rendering them less dependent on these structural corridors. Consequently, the pony probably relies on the cleared service roads to minimize movement friction and travel efficiently between patches.

However, while the Konik sub-herds remained statistically neutral towards the broader network of service roads, the specific spatial path arrangement of the corridor may have introduced an

anthropogenic spatial filter. Specifically, unlike the otherwise quiet service roads in the Westhoek, the corridor is directly intersected by a heavily trafficked east-west public footpath. This localized zone of high human disturbance could function as a soft boundary or invisible barrier (Sibbald et al., 2011), reducing the functional permeability of the corridor. Because equid groups may remain spatially segregated even after formal physical barriers are removed (Hendler et al., 2026), and herd composition can influence space use in free-roaming systems (Laidlaw, 2023), this anthropogenic bottleneck provides a plausible secondary hypothesis for the spatial divergence observed between the Konik sub-herds. Specifically, the AN788 bachelor group may have been more willing to navigate this high-traffic intersection to access newly available foraging grounds, whereas the AN789 sub-herd may have been less likely to do so because it included juveniles. Thus, although the formal management barrier was removed, anthropogenic avoidance may still have limited corridor use for some demographic groups.

In the Kalmthoutse Heide, the role of paths as navigational highways was consistent. The Galloway cattle exhibited a year-round attraction to the path network, with minimal inter-individual variance. This behaviour aligns with spatial tracking in other managed landscapes; for instance, Tofastrud et al. (2019) documented a similar preference for unpaved forest roads among cattle traveling through coniferous forests in Norway. However, this explicitly contrasts with recent findings by Rech et al. (2025), who reported that cattle in a rewilding area showed neither attraction nor avoidance toward recreational paths. Consequently, the distinct path attraction observed in the Kalmthoutse Heide represents a novel contribution to the limited literature regarding how cattle interact with recreational paths, specifically within heath ecosystems. Collectively, the consistent attraction to paths exhibited by both the cattle and the Shetland pony forces the rejection of the broader path-avoidance assumption within Hypothesis 2.3.

However, to fully resolve the mechanisms driving this attraction in areas with genuine public access, future research must incorporate fine-scale temporal analyses. By determining whether path utilization occurs during peak recreational hours or is restricted to early mornings, evenings, and nocturnal periods, subsequent studies can test for temporal avoidance strategies. If it is found that path navigation is limited to dawn, dusk, or nocturnal periods, it would indicate that these herbivores are exploiting the low-resistance navigational benefits of the corridors while shifting their schedules to avoid direct contact with human recreationists. Such temporal analysis is necessary to definitively confirm whether the observed spatial attraction truly equates to human tolerance.

5.2 Seasonal Foraging Strategies and Sub-herd Divergence

5.2.1. Westhoek Population-Level Dichotomy: Grass vs. Scrub

At the population level, the equid habitat preferences in the Westhoek broadly conformed to a binary vegetational dichotomy, supporting Hypothesis 2.1 (Baseline-Relative Selection):

- They prefer open, grassy vegetation including *Duingrasland* (Dune grassland), *Duinvallei* (Dune slack), *Schaarsbegroeid* (Sparse vegetation), and *Grasruigte* (Tall herbaceous vegetation).

- They do not prefer taller, denser structural habitats, including dense scrub (*Duindoornstruweel* and *Opgaand struweel*), closed-canopy forest (*Bos*), and grass-poor open vegetation such as *Mosduin* (Moss dunes).

However, two notable exceptions to this general rule occurred at the population level, driven by seasonal shifts: First, during the summer, the equid group displayed a shared positive spatial inclination (resulting in a statistical trend) toward *Mosduin*. While this specific summer trend appears to contrast with historical baselines (Lamoot, 2004) that documented avoidance of moss dunes during the warmer months, this discrepancy is likely rooted in methodological differences. Because Lamoot (2004) specifically quantified grazing behaviour via direct observation, whereas the current study measures overall space use via continuous telemetry, it is probable that the equids are utilizing these moss dunes for non-foraging activities such as resting, traversing or thermoregulation.

Second, during the winter, the entire group exhibited a preference for *Kruipwilg_laagstruweel* (Creeping willow low scrub), temporarily breaking their generalized avoidance of scrub habitats. This winter exploitation probably represents an adaptive foraging and sheltering strategy. As the biomass and nutritional quality of open grasslands deplete during the colder months, equids can shift their habitat use from strict grazing to opportunistic browsing (I. J. Gordon & Illius, 1989).

Aside from these two seasonal anomalies, the overarching population-level patterns align strongly with historical observations in the Westhoek, confirming that free-roaming equids primarily function as grazers of open dune habitats while utilising scrub and woodland matrices only marginally (Hoffmann et al., 2005; Lamoot, 2004; Lamoot et al., 2005).

Importantly, while their habitat preferences remain largely stable throughout the year, the specific geographic utilization of the landscape is seasonally dynamic. As established in WP1, while their broader 95% home ranges showed no seasonal size variation, significant seasonality was observed in their geometric Core Fidelity (50% Overlap). This indicates that their affinity for specific core foraging patches fluctuates continuously, whereby the 50% core area overlap was significantly lower when transitioning from winter into spring compared to the transition from summer into autumn. This drop in fidelity confirms a core area relocation during the spring, as the equids abandon their winter refuges, such as *Kruipwilg_laagstruweel* (Creeping willow low scrub), to exploit new patches of early spring vegetation such as *Grasruigte* (Tall grass/herbaceous) or *Duingrasland* (Dune grassland). This spatial shift is hypothesized to be driven by a transition in food availability. By the end of winter, it is probable that the edible biomass within their winter refuges becomes depleted. As spring initiates a localized flush of high-quality vegetation across the broader landscape, the equids would actively relocate their core areas to track these newly available resources.

In contrast, the transition into autumn is characterized by significantly higher spatial stability, as the animals maintain nearly half of their core area foraging on the same summer grazing grounds. This stability may be a reflection of seasonal habitat selection and the persistence of food availability. It is plausible that the habitats selected during the summer, such as *Duingrasland* (Dune grassland), *Duinvallei* (Dune slack) and *Schaarsbegroeid* (Sparse vegetation), continue to offer sufficient forage mass into the early autumn. Assuming these core areas have not yet reached critical

depletion, and without a sudden attractive alternative flush emerging elsewhere on the landscape during autumn, the equids would not be environmentally forced to relocate. Instead, they can repetitively use these specific, established resource patches as the growing season concludes. This fluctuation of core area fidelity partially confirms the spatial shift predictions of Hypothesis 1.2 (Seasonal Dynamics) for the equid group, despite their absolute home range sizes remaining static.

5.2.2. Westhoek Morphological and Social Drivers of Sub-herd Divergence

As established in Section 5.1.1, the Westhoek equid group exhibited overarching seasonal spatial stability, leading to a partial rejection of Hypothesis 1.2 (Seasonal Dynamics) regarding absolute home range size variance. However, while their macro-scale outer boundaries remained seasonally stable, internal social and morphological dynamics played a critical role in driving distinct, micro-scale habitat divergence between the sub-herds.

Equine social hierarchies are complex and typically determined by age, herd residency, and reproductive class, rather than strictly by body size or height alone (Komárková et al., 2014; Sigurjónsdóttir et al., 2003; Vries et al., 1994). Within these hierarchical structures, competitive displacement frequently occurs, wherein dominant sub-herds monopolize optimal feeding locations, pushing subordinate individuals or smaller, crowded groups toward less profitable forage (Ingólfssdóttir & Sigurjónsdóttir, 2008; Linnartz & Linnartz-Nieuwdorp, 2017; Lisa Nash et al., 1987).

As observed by Laidlaw (2023), horse populations tend to fragment into distinct sub-groups centred around long-term adult associations. Disaggregating the habitat models revealed how social displacement, combined with morphological differences, could have influenced specific spatial selection between the collared Konik individuals and the Shetland pony:

- **Sparse Vegetation and Foraging Efficiency:** The Shetland pony demonstrated a consistently higher preference for *Schaarsbegroeid* (Sparse vegetation) across all seasons. In the context of coastal dune ecosystems, Sparse vegetation is characterized by low plant density. This divergence is plausibly related to morphological constraints on forage acquisition and selectivity. Allometric grazing theory predicts that smaller ruminant herbivores can forage more efficiently where edible biomass is more dispersed or structurally patchy, because their smaller bite dimensions allow finer-scale selection (Illius & Gordon, 1987). This allometric theory extends to equids, where feeding mechanics and mouth morphology have been shown to directly shape ingestive behaviour in ponies (Bordin et al., 2024). On that basis, the stronger preference of sparse vegetation by Shetland ponies can be interpreted as an advantage in selecting edible shoots from patchy vegetation compared with the larger Konik horses. Social processes may also contribute, since dominance can affect feeding access in equids, but direct evidence that Koniks displace Shetlands into sparse vegetation is currently lacking.
- **Low Scrub Exploitation:** An interesting deviation from historical literature was observed regarding *Kruipwilg_laagstruweel* (Creeping willow low scrub). While previous studies concluded a strong generalized avoidance of scrub by Shetland ponies in the Westhoek (Lamoot, 2004), the high-resolution categorization of different scrub types in this study

revealed that the pony actively preferred this specific low scrub during spring and summer. Crucially, unlike other scrub types found in the Westhoek, creeping willow is devoid of thorns or spines and contains a lower proportion of tough, woody tissue. This accessible plant morphology, combined with the pony's smaller body size, likely affords the animal the agility to navigate the patches more easily, forage more efficiently on the softer biomass, and rest more comfortably within this habitat than the larger Koniks.

- **Anomalous Scrub Selection:** During the summer, the pony demonstrated an unexpected preference for *Duindoornstruweel*. Interpreting this summer scrub anomaly requires caution. Because the Shetland data relied on a single monitored summer season, this preference may simply be a statistical artifact of limited temporal sampling. Alternatively, it may reflect true behavioural shifts driven by competitive exclusion. Crucially, because the co-habiting Highland cattle were uncollared, their potential competitive influence is missing from the models. If the larger Koniks and these untracked Highland cattle partly monopolized the optimal grasslands during the summer peak, the Shetland pony may have been competitively forced to seek refuge or forage in this sub-optimal dense scrub.

5.2.3. Kalmthoutse Heide Population-Level Selection: Requirement of the Forageable Layer

In the Kalmthoutse Heide, the Galloway cattle's habitat selection was fundamentally dictated by the presence of a forageable layer. Overall, the herd consistently directed their space use toward habitats characterized by structural variety, specifically areas offering grass understories or tree encroachment. These vegetation layers likely offer the highest-quality food sources in the reserve. For instance, *droog schraalland met boomopslag* (dry grassland with tree encroachment) was preferred during the spring, likely due to the additional high-protein food source provided by the emerging buds of deciduous trees, such as willow (*Salix* spp.) and birch (*Betula* spp.) (Spedener et al., 2024).

Conversely, they maintained an avoidance of vegetation types providing poor forage, such as pure, unencroached heathlands and dense scrub, particularly during spring and summer. During autumn, however, this avoidance disappeared, suggesting a progressive reduction in habitat selectivity as the growing season advanced and high-quality forage became uniformly scarce across the landscape mosaic. This forced individuals to adopt more divergent, opportunistic spatial strategies, resulting in higher inter-individual variability (a pattern also observed in the continuous variable analysis in Section 5.2.4). This targeted selection of resource-rich matrices confirms Hypothesis 2.1 (Baseline-Relative Selection) and aligns with established literature confirming that cattle in heath landscapes utilize pure heath only as a secondary, marginal component when herbaceous quality declines (I. Gordon, 1989; Pratt et al., 1986; Putman et al., 1987).

These fine-scale behavioural trends correlate with the macro-scale spatial dynamics established in WP1. During the spring, the cattle exhibited the smallest seasonal home ranges. This spatial concentration is likely a consequence of their highly selective foraging behaviour, as the herd anchors itself to specific patches of the early spring flush. As the season progresses into summer and this initial flush depletes, selectivity decreases, forcing the herd to broaden its foraging effort. Consequently, their summer home ranges expanded significantly while maintaining a high spatial overlap with their spring core areas. Interestingly, while selectivity continued to drop during the

autumn, the home range size did not undergo further expansion. Instead, the spatial footprint shifted: the incomplete overlap between the summer and autumn ranges indicates that the herd abandoned depleted summer zones to exploit new, peripheral areas. Finally, the spatial overlap between the autumn ranges and the subsequent spring ranges of the following year was the lowest of any seasonal transition. This pronounced disconnect suggests a spatial reset following their winter management removal; rather than tethering to their previous autumn locations, the cattle immediately target the most profitable spring flush upon re-entering the reserve, initiating the cycle anew. These dynamic fluctuations in absolute size, spatial location, and core overlap validate Hypothesis 1.2 (Seasonal Dynamics) for the bovine herd.

5.2.4. Topographical and Distance to Water Constraints on Spatial Use

Topography

Beyond vegetational characteristics, spatial distribution across both reserves was significantly influenced by topographical variation, though the seasonal drivers differed between the equid group and the cattle.

In the Westhoek, the iRSF revealed a preference for flatter terrain during the summer and autumn seasons, driven primarily by the Konik sub-herds. Because the model strictly controls for categorical vegetation and distances to water, paths and fences, this spatial choice may be driven by two factors. First, navigating steep, loose dune sand incurs a high metabolic cost, which the Koniks likely avoid during summer to minimize heat stress, and during autumn to maximize net energy retention. Second, as suggested by recent studies on Konik horses in wetland ecosystems (Anna et al., 2023), the use of flat, lower-elevation meadows often peaks during the summer as these habitats retain soil moisture and greener forage after higher, drier sites wither. Because our model's distance to standing water variable does not capture localized soil moisture, the Koniks' preference for flat terrain may function as a spatial proxy for these drought-resistant foraging patches. Conversely, while the Shetland pony mirrored this preference for flatter terrain during the autumn, it deviated from the Koniks by remaining topographically neutral during the summer. This seasonal divergence suggests either that the pony's smaller body mass affords greater agility, reducing the relative metabolic penalty of moving on steeper slopes, or that the solitary pony is being competitively displaced into less desirable, steeper topography by the Konik sub-herds or the Scottish highland cattle (Ingólfssdóttir & Sigurjónsdóttir, 2008; Linnartz & Linnartz-Nieuwdorp, 2017; Lisa Nash et al., 1987).

The topographical distribution of the Galloway cattle in the Kalmthoutse Heide mirrored the seasonal high-to-low selectivity progression established in Section 5.2.3. Topography exerted a strong influence during the spring, where the Galloway cattle demonstrated a significant attraction to flatter terrain. In heathland ecosystems, cattle typically concentrate on flatter areas during the spring flush because these locations often harbour the most accessible and nutritionally rewarding grass-rich patches, allowing for highly selective foraging when overall quality is high (Henkin et al., 2012; Pratt et al., 1986; Putman et al., 1987; Vries et al., 1994). Conversely, steeper heath areas are associated with lower-quality vegetation and higher locomotion costs, reducing the forage return per unit of effort (Bokdam & De Vries Wallis, 1992; Wallisdevries, 1996). As the year progresses into summer and autumn, declining overall forage quality and quantity forces a reduction in selectivity, promoting a more even utilization of the landscape, including the less profitable, steeper zones (Henkin et al., 2012; Kohler et al., 2006; Putfarken et al., 2008). Collectively, the avoidance of steep slopes by both the cattle (in spring) and Koniks (in

summer/autumn) leads to the acceptance of Hypothesis 2.2 (Abiotic Constraints) regarding topography.

Distance to Water

Regarding distance to water, neither reserve demonstrated a classical dependency on water sources, highlighting that water availability is not a limiting ecological factor in these coastal and heathland systems. This finding forces the rejection of the proximity to water assumptions within Hypothesis 2.2 (Abiotic Constraints).

In the Westhoek, the equid group generally demonstrated spatial neutrality toward water bodies year-round. Because small ponds are highly abundant and widely distributed across the reserve, there is no physiological necessity for the equids to anchor their spatial movements to a singular water source. The sole exception occurred during the spring, when the Shetland pony actively selected for larger distances from water sources. This spatial avoidance may represent a strategy of competitive displacement, bypassing water sources to minimize agonistic encounters with Koniks. Alternatively, it may reflect the pony's seasonal spatial dynamics; exhibiting the lowest core site fidelity during the winter-to-spring transition, the pony's statistical distance from water may simply be a byproduct of post-winter exploratory behaviour into the peripheral landscape.

Similarly, in the Kalmthoutse Heide, the Galloway cattle showed no spatial attraction to water, instead actively preferring longer distances from water sources during the spring and summer. While, in heterogeneous grazing systems, cattle distribution is frequently driven more by forage acquisition and terrain navigability than by proximity to water alone (Kohler et al., 2006; Putfarken et al., 2008; von Müller et al., 2017), this still contrasts with established literature documenting year-round attractions to ponds in other pastoral systems (Kristensen et al., 2026; Rech et al., 2025), underscoring the complexity of the Kalmthoutse Heide's water management. Ultimately, because water availability is not a limiting ecological factor in either reserve, proximity to water does not dictate fine-scale herbivore distribution.

5.3 Herbivore-Driven Engineering of Vegetation Structure

While WP1 and WP2 established how the Westhoek equid group navigates and selects habitats, WP3 evaluates the reciprocal ecological impact by analysing how the prolonged spatial presence of these herbivores actively engineers the successional vegetation trajectory of the reserve. However, before interpreting these dynamics, a methodological limitation must be acknowledged: the presence of unmeasured herbivory. While the Konik horses and the Shetland pony were tracked to create the Space-Use Intensity map, the Westhoek is also co-habited by an untracked herd of Scottish Highland cattle. Because these bovines were uncollared, their spatial footprint and consumptive pressure are missing from the models. Consequently, the Space-Use Intensity metric represents equid-driven engineering rather than the complete, multi-species impact. Despite this constraint, modelling vegetation height changes against cumulative equid space-use intensity and abiotic constraints provides a spatial narrative regarding the benefits and limits of top-down control.

The Stress-Maintained Baseline

The probability of vegetation remaining structurally stable was exclusively driven by groundwater depth, peaking significantly in drier terrain. This stability likely reflects the spatial dominance of moss dunes (*Mosduin*) in areas with deep water tables. In these desiccated zones, the moss-dominated pioneer vegetation represents an inherently stable, stress-maintained state with minimal potential for successional encroachment. Additionally, the unpalatability of moss dunes ensures this stability is maintained. While the equid group does not spatially avoid these zones year-round, they likely do not forage on the moss layer due to its negligible nutritional value. Because the moss escapes consumptive top-down pressure, the vegetation is not structurally altered by grazing, leaving the severe abiotic drought stress as the sole dictator of its permanent pioneer state.

The Stress-Driven Herb-Grass Cluster

Herb/grass regression and herb/grass growth are two tightly coupled processes that are spatially interlinked across the landscape. Because these structural shifts frequently co-occur at a fine spatial scale, they exhibit similar statistical responses to both biotic and abiotic drivers. Rather than occurring independently, they form a complex, fine-scale matrix of simultaneous regression and growth (Figure 23). As a clustered dynamic, this matrix is fundamentally driven by environmental stress; both classes demonstrate a significantly higher probability of occurrence in patches characterized by elevated space use intensity, steeper slopes, deeper groundwater tables, and higher solar exposure. This strong response to microclimate, topography and groundwater depth confirms the expectations of Hypothesis 3.2 (Abiotic Drivers), which predicted that environmental stress would actively drive the spatial dynamics of shallower-rooted vegetation.

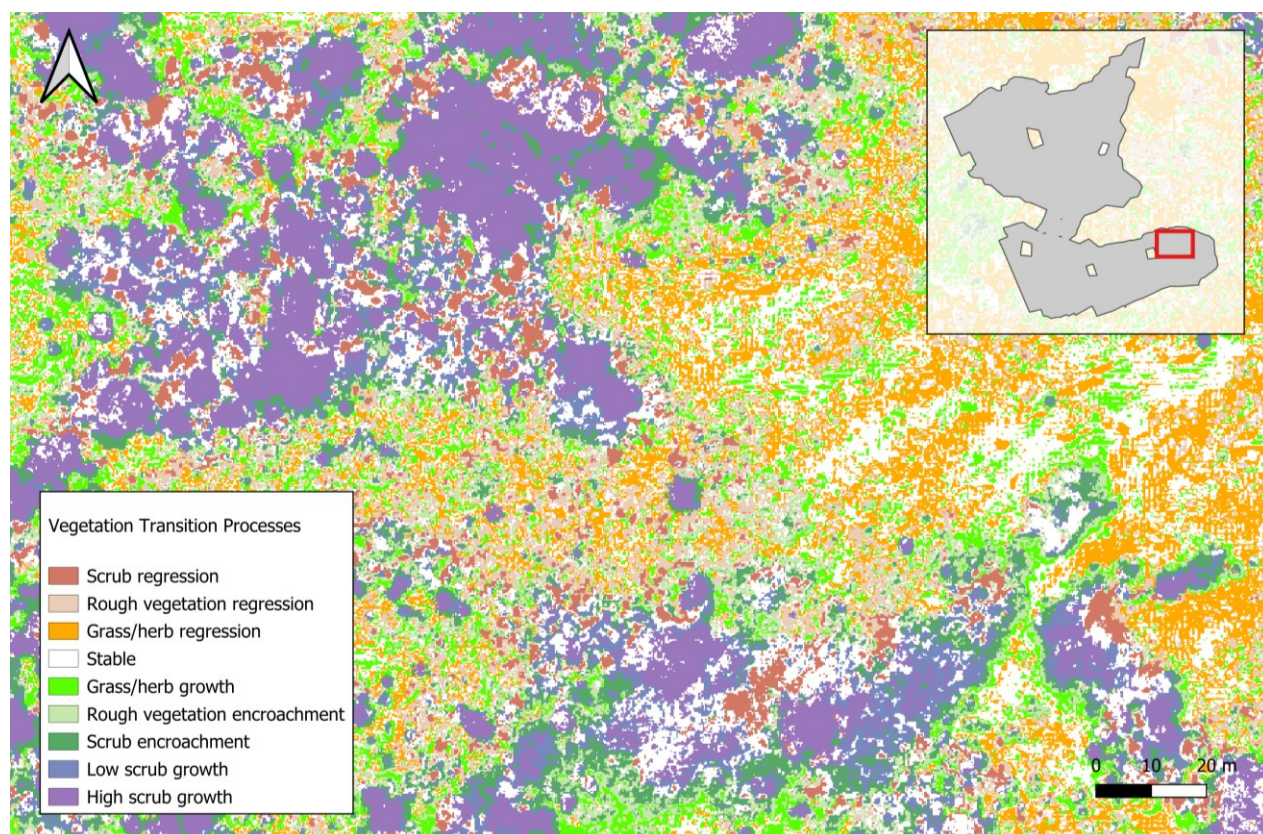


Figure 23. Fine-scale spatial clustering of herbaceous vegetation dynamics. This localized spatial subset illustrates the

tightly coupled distribution of 'Grass/herb growth' and 'Grass/herb regression' within the Westhoek reserve. Rather than occurring as broad, independent homogeneous patches, these two processes co-occur at a highly granular scale, forming a stress-driven successional cluster governed by shared biotic and abiotic landscape drivers.

Herbivory as a Successional Barrier

Regarding rough vegetation, increased space-use intensity was correlated with a significantly lower probability of rough vegetation encroachment. Because equid presence was the sole tested variable capable of suppressing this encroachment, it underscores their essential role as landscape engineers, as they function as an effective and singular barrier preventing the initial formation and spread of rough vegetation. Given that WP2 established that equid spatial pressure is disproportionately concentrated in open habitats like *Duingrasland*, this pressure may effectively lock these grasslands into an arrested successional state. This finding validates the primary component of Hypothesis 3.1 (Terrain Use Impact), confirming that high cumulative space use actively suppresses early successional advancement.

In contrast to the coupled herb-grass matrix (which requires environmental stress), scrub encroachment demonstrated the exact opposite spatial requirements. The probability of initial woody establishment peaked strictly in low-stress environments, characterized by flatter terrain, reduced solar exposure, shallower groundwater tables, and a negative statistical trend regarding equid space-use intensity. The reliance on shallower groundwater for woody establishment further supports the hydrological predictions within Hypothesis 3.2 (Abiotic Drivers).

Herbivory as a Successional Facilitator

A seemingly counterintuitive dynamic emerges once rough and woody vegetation successfully breaches these initial barriers. Increased space-use intensity was associated with a lower probability of rough vegetation regression and a significantly higher probability of high scrub growth (alongside a positive, though non-significant, trend for low scrub growth, $p = 0.146$). This indicates that once rough vegetation and scrub are established, intense equid presence is not only insufficient to drive their structural collapse but can even facilitate their successional advancement.

The failure to induce structural regression is likely driven by mature plant defences. As rough vegetation and woody scrub mature, the accumulation of indigestible plant fibres (such as lignified material) together with the development of larger and denser thorns, reduces forage palatability and nutritional quality. This aligns with the findings of Provoost & Declerck (2021), who documented that low-to-moderate grazing pressure is generally unable to reduce mature scrub cover or limit its expansion.

Concurrently, the successional facilitation is likely driven by a synergistic combination of localized nutrient enrichment and mechanical soil disturbance. As demonstrated by Lamoot et al. (2004), free-roaming equids in the Westhoek do not show latrine behaviour and defecate in the areas they graze. This results in the addition of critical nutrients (nitrogen, phosphorus, and potassium) to the soil. However, this fertilizing effect can be further amplified by the physical impact of the equids. Intense space use inevitably leads to trampling, which compacts the soil and affects many different abiotic soil characteristics such as pore size, soil moisture and soil aeration. These compaction-

induced physical changes drive shifts in N mineralization by fundamentally altering the activity of soil biota (Drewry et al., 2008; Hamza & Anderson, 2005; Powers et al., 2005). For instance, reduced pore size in a compacted soil can increase the water holding capacity and accelerate the N mineralization of existing organic layers in the soil, converting previously inaccessible organic complexes into bioavailable mineral salts, such as nitrates (Schrama et al., 2013). This nutrient surplus can function as a fertilising agent that stimulates the vertical growth of established scrub and rough patches that have already escaped top-down browsing limits. Additionally, increased space use intensity could also relieve established rough vegetation and scrub from resource competition with lower herbs and grasses (Bokdam & Gleichman, 2000). Consequently, this dynamic forces a partial rejection of Hypothesis 3.1 (Terrain Use Impact); while herbivory effectively prevents initial encroachment, it fails to achieve the regression of established, late-stage succession.

Abiotic Constraints on Late-Stage Succession

Because intensive space use fails to dismantle late-stage succession, the reduction of mature vegetation is not driven by top-down herbivory, but rather by intrinsic biotic processes such as natural senescence and aging, alongside localized anthropogenic management interventions (i.e., mechanical scrub removal by nature managers). However, the spatial models demonstrate that where vegetation undergoes natural die-back, these processes are mediated and accelerated by abiotic stressors.

Rough vegetation regression is strongly linked to deeper groundwater tables, demonstrating that the die-back of these vegetation types is driven by abiotic drought stress. Furthermore, the growth of high scrub is restricted solely by deeper groundwater, whereas the growth of low scrub faces dual constraints: it is prevented by both deeper groundwater and steeper topographical slopes. Interestingly, the dynamics of scrub regression are also strictly governed by topography. Slope steepness emerged as the only significant predictor for scrub regression, with die-off events being predominantly confined to flatter areas. Consequently, flatter topographical zones operate as dynamic areas where low scrub can both grow and regress. Functionally, this topographical dynamic closely mirrors the stress-driven herb/grass cluster discussed earlier. Just as shallow-rooted vegetation forms a tightly coupled matrix of spatial turnover, low scrub on flat terrain forms a parallel, spatially coupled matrix of simultaneous growth and regression. Ultimately, this environmentally mediated, bottom-up control over late-stage succession confirms the final predictions of Hypothesis 3.2 (Abiotic Drivers).

The Legacy Effect of Abiotic Constraints

It is important to acknowledge that the low probability of scrub growth in areas with deep groundwater tables is heavily influenced by initial state dependence. Because deep groundwater can function as a long-term abiotic barrier to woody establishment, these dry zones likely harboured little baseline scrub at the start of the study period. However, rather than confounding the model, this baseline limitation reinforces the ecological conclusion: the abiotic stress of the dune ridges with deep groundwater tables acts as a continuous filter, where deep groundwater not only stunts the vertical growth of any existing woody vegetation, but has historically prevented its initial establishment.

5.4 Methodological Strengths and Limitations

5.4.1. Analytical Strengths: Autocorrelation and DOF Filtering

A primary strength of this study lies in its use of Continuous-Time Movement Modelling (ctmm) and the integrated Resource Selection Function (iRSF). Historically, wildlife tracking studies have struggled with inherent temporal autocorrelation. Traditional habitat selection models often violate statistical assumptions by treating these points as independent.

By using the ctmm package, this study successfully fitted continuous-time movement models that mathematically accounted for this autocorrelation. Furthermore, extracting the Autocorrelated Kernel Density Estimates (AKDE) allowed for an accurate representation of space use that does not underestimate home range sizes. Crucially, the application of Degrees of Freedom (DOF) filtering ensured that only datasets containing sufficient independent movements were retained for the seasonal models. This quality control prevents fragmented or insufficient data from skewing the habitat selection outputs.

5.4.2. Telemetry Constraints, Sample Sizes, and Spatial Artifacts

Despite the robust statistical framework, the dataset faced several logistical constraints. Most notably, the biological divergence observed in the Westhoek regarding the Shetland pony must be interpreted with caution. Because the tracking data relied on a single collared Shetland pony ($N = 1$), it is mathematically impossible to state with certainty whether the observed behaviours (e.g., active preference for low scrub, distinct path attraction) represent true species-level traits or simply the idiosyncratic preferences of this specific individual or sub-herd. Future studies require a larger sample size of collared ponies to confirm population-level behavioural divergence.

A related constraint concerns the analytical aggregation of the three collared Konik horses. From a behavioural ecology perspective, it is plausible to view these individuals not as representatives of a uniform 'Konik' trait, but rather as proxies for three functionally independent sub-herds operating with distinct internal dynamics. However, for the analytical framework of this study, these individuals were aggregated to represent a single Konik demographic unit. This methodological choice was primarily driven by functional ecology and applied conservation goals. First, because all three Konik sub-herds share the same baseline morphology and biomechanics, grouping them isolates the spatial impact of these breed-level physical traits, allowing for a functional comparison against the smaller Shetland pony. Second, from an applied conservation perspective, landscape managers require generalized, breed-level insights to design effective grazing strategies. Disaggregating the Koniks into isolated sub-herds would fracture the data, precluding the ability to draw robust, actionable conclusions regarding how large equids, as a broader ecological group, engineer the landscape. Consequently, while this aggregation successfully captures the functional spatial trends required for landscape management, the resulting outputs must be recognized as a statistical average that may partially mask distinct internal dynamics.

Furthermore, while the spatial models successfully accounted for and corrected the external boundaries of the reserves, the calculation of AKDE home ranges inherently introduces minor spatial artifacts regarding internal infrastructure. Because AKDE generates a continuous probability density distribution, the home range estimates can artificially spill over small, internal physical barriers. For instance, where small internal fenced exclosures existed within the reserve that the herbivores could not access, the AKDE smoothing process may still calculate a localized probability of occurrence over these inaccessible patches.

A secondary spatial artifact was introduced during the preparation of the categorical habitat rasters. To prevent statistical confounding with the continuous 'Distance to Water' covariate, open water pixels were categorically removed and algorithmically replaced using a nearest-neighbour focal modal filter (see Section 3.3.3). While this gap-filling procedure was statistically necessary to provide a continuous, unbroken raster for the Resource Selection Functions (RSF), growing the neighbouring pixels into these water gaps could overestimate the availability of riparian or edge habitats.

Finally, as detailed in Section 3.2.3, the lack of an exact administrative record for the Westhoek corridor opening necessitated the use of a telemetry-derived proxy. While this data-driven workaround allowed for robust temporal stratification, the inherent reliance on initial animal movement rather than a physical management log introduces minor temporal noise. Consequently, the exact timing of the immediate pre- and post-corridor spatial expansions must still be interpreted with caution.

5.4.3. Inter-Reserve Discrepancies and Future Directions

The comparative nature of this study was slightly limited by discrepancies in data availability between the two reserves. Most significantly, while the Westhoek benefited from drone flights in both 2020 and 2025, allowing for the comprehensive WP3 vegetation analysis, the Kalmthoutse Heide lacked a subsequent second drone flight at the time of writing. Consequently, the true structural impact of the Galloway cattle on the heathland could only be inferred via spatial preference (WP2) rather than empirically measured (WP3). Furthermore, as previously noted, the Westhoek vegetation models were constrained by unmeasured herbivory, as the spatial footprint of the untracked Scottish Highland cattle could not be integrated into the analysis.

To build upon this research, future studies should prioritize flying a secondary drone mission over the Kalmthoutse Heide to definitively quantify the cattle's capacity for successional suppression. In the Westhoek, deploying GPS collars on the Scottish Highland cattle is critical to resolve the unmeasured herbivory gap and map the true, multi-species cumulative Space-Use Intensity. Finally, while spatial telemetry successfully identifies where the animals forage, coupling this spatial data with localized diet analysis (e.g., eDNA metabarcoding of dung) would provide definitive proof of exactly which plant species are driving these spatial selections.

5.5. Implications for Conservation Management

While the iRSF and vegetation models demonstrate how the large herbivores select habitats and engineer the landscape, the ultimate value of these findings lies in their translation to applied conservation. Evaluating these spatial preferences against the primary management goals of the Westhoek and Kalmthoutse Heide reveals critical insights regarding grazer effectiveness, herd composition and additional interventions.

5.5.1. *Vergrassing* and *Verstruweling* in the Westhoek: A Dual Management Approach

In coastal dune ecosystems, management largely focuses on halting two successional pathways: the dominant spread of grasses and tall herbs (*vergrassing* or *verruiging*), and the establishment of dense woody scrub (*verstruweling*). The models from this study provide a verdict on the equids' utility for these goals.

If the management objective is to battle *vergrassing* and maintain open dune matrices, the equid group is an effective conservation practice. Their spatial preference for grassy patches and their ability to prevent rough vegetation and scrub encroachment confirm that they can successfully lock these areas into an open, early successional state. However, if the primary objective is to reverse *verstruweling*, the equids do not offer a standalone solution. Because the herd avoids dense scrub and cannot force the regression of mature woody vegetation, managers cannot rely on equids to clear established thickets. Consequently, conservation agencies must accept a dual-strategy approach: relying on equids as a biological preventative measure against initial rough vegetation and scrub establishment, while continuing to utilize targeted mechanical intervention (e.g., chainsaw clearing or heavy machinery) to remove mature, high scrub.

5.5.2. Morphological Diversity in the Westhoek: The Case for the Shetland Pony Sub-Herd

Perhaps one of the most actionable insights from the Westhoek concerns the internal composition of the grazing group. Historically, management has often viewed grazers at the species level (e.g., "horses" vs. "cattle"). However, this study revealed significant spatial divergence driven by morphology and social structure, specifically regarding the smaller Shetland pony sub-herd.

Unlike the larger Konik sub-herds, the Shetland sub-herd demonstrated an active preference for creeping willow low scrub (*Kruipwilg_laagstruweel*) during the spring and summer. Furthermore, it exhibited a greater capacity to utilize sparse-swarded vegetation types, such as *Schaarsbegroeid* (Sparse vegetation). Because smaller equids possess different biomechanical characteristics and smaller bite sizes, they are likely more capable of profitably exploiting these sparse swards and low-tier scrub types that larger Koniks ignore or cannot survive on.

For conservation managers, this highlights the value of maintaining a morphologically diverse grazer group. Rather than stocking a reserve exclusively with a single breed of large horses, intentionally mixing body sizes (e.g., maintaining a ratio of smaller ponies to larger Koniks) effectively broadens the total ecological impact. However, managers should also account for inter- and intraspecific social dynamics when mixing these herds. The summer spatial data revealed an anomalous use of dense scrub (*Duindoornstruweel*) by the Shetland pony. While this single-season observation requires cautious interpretation, it highlights how competitive displacement could

present both a welfare risk and a management opportunity. It is hypothesized that during periods of high resource competition, dominant Konik sub-herds or Highland cattle may force subordinate individuals into sub-optimal habitats. Therefore, while a morphologically diverse herd is highly beneficial for broadening total ecological impact, overall stocking densities should be carefully calibrated.

5.5.3. Alignment of Cattle Space Use Preferences with Heathland Conservation Goals

The spatial baseline of the Galloway cattle in the Kalmthoutse Heide provides a promising indication for current heathland management protocols in the face of modern ecological pressures. As established, widespread atmospheric nitrogen deposition and the loss of historical disturbances have triggered rapid structural degradation in these ecosystems, primarily through aggressive grass encroachment and woody colonization. The spatial models demonstrate that the herd's distribution aligns with the management of these threats. The cattle consistently selected for vegetation types characterized by a forageable layer (e.g. grass or tree encroachment). Conversely, they exhibited an avoidance of unencroached, pure heathlands.

However, it is crucial to distinguish between spatial preference and structural impact. Because the Kalmthoutse Heide analysis relied on habitat selection models (iRSF) rather than diet preference or long-term vegetation monitoring, the data cannot definitively quantify the effectiveness of the encroachment suppression itself.

Nevertheless, these findings represent a critical, positive validation of the current grazing strategy. While long-term structural monitoring is required to confirm the ultimate success of the suppression, the data confirms that the cattle are systematically directing their consumptive pressure toward the degraded margins and transitional zones that require intervention, while bypassing the fragile and pristine heathland habitats.

5.5.4. Minimum Reserve Size and Strategic Infrastructure

The spatial models reveal that anthropogenic infrastructure should not be viewed merely as a constraint, but rather as an active tool to direct herbivore distribution and maximize conservation impact. Most fundamentally, the saturation data provides structural indications for the spatial scale required to maintain natural, unconstrained grazing behaviour, which varies significantly depending on the ecosystem and the focal grazer species.

In the Westhoek coastal dune ecosystem, the analysis demonstrated that small, enclosed compartments of under 100 hectares (such as the isolated 67-hectare and 98-hectare sectors) forced the equid group into spatial saturation. Following the corridor opening, individual home ranges peaked at approximately 125 hectares. Consequently, to allow for large-scale spatial expansions and natural sub-herd divergence, it is advised that conservation managers implementing extensive equid grazing in coastal dunes consider targeting a reserve size of at least 125 hectares.

Conversely, the spatial requirements in the Kalmthoutse Heide lowland heath ecosystem operate on a vastly different scale. Because the seasonal home ranges of the Galloway cattle peaked at approximately 420 hectares, it is recommended that future heathland grazing blocks aim to maintain a contiguous area of at least 420 hectares to prevent the herd from becoming artificially constrained by the perimeter.

If existing nature reserves fall below these ecosystem-specific targets, the removal of internal barriers (such as the corridor intervention in the Westhoek) can serve as a critical macro-scale mitigation strategy. By connecting previously isolated sectors, managers can effectively diffuse localized grazing pressure, prevent over-utilization of saturated core areas, and allow the herds to optimally redistribute their consumptive effects across the broader landscape.

Furthermore, this spatial manipulation is equally viable at the micro-scale. The models demonstrated that internal paths could function as effective spatial attractants, particularly for the Galloway cattle in the Kalmthoutse Heide and the Shetland pony in the Westhoek. This finding refutes the path-avoidance component of Hypothesis 2.3 (Anthropogenic Avoidance), which predicted that grazers would disproportionately select areas further away from path infrastructure. Consequently, the deliberate spatial planning of these path networks represents an underutilized, proactive management strategy. Rather than laying recreational paths solely based on human convenience, managers can strategically design these trails to intersect or connect isolated, encroached areas. By doing so, the paths can function as biological funnels, drawing grazers into specific target areas.

While paths serve as effective spatial attractants, the models reveal a different dynamic regarding standing water. Given that the equids in the Westhoek remained statistically neutral toward distance to water bodies, and the Galloway cattle in the Kalmthoutse Heide avoided them during the growing season, proximity to water does not dictate herbivore distribution in these specific reserves. If this lack of spatial dependency is driven by the existing high abundance and wide distribution of natural water sources, it establishes that preserving an abundant, widespread and even distribution of water bodies could be beneficial for achieving a balanced, landscape-scale terrain use that naturally prevents localized clustering and intense space use around individual water bodies.

6. Conclusions

This study evaluated the spatial ecology and ecosystem engineering capacity of free-roaming large herbivores in two structurally distinct, nutrient-poor landscapes: the coastal dunes of the Westhoek and the lowland heathlands of the Kalmthoutse Heide. By integrating continuous-time movement modelling, integrated resource selection functions, and remote-sensing vegetation dynamics, this research bridged the gap between individual animal movement and landscape-scale vegetational changes. The final evaluation of the working hypotheses yields a nuanced understanding of conservation grazing.

6.1. Work Package 1: Boundary-Constrained Space Use

The first objective sought to quantify the baseline spatial ecology and saturation of the targeted grazers.

- **Hypothesis 1.1 (Spatial Saturation) is accepted.** The spatial models confirm that neither the equid group in the Westhoek (post-corridor) nor the Galloway cattle in the Kalmthoutse Heide are biologically saturated. The herbivores are not constrained by the physical perimeters of the reserves, indicating they exercise active and targeted spatial choices.
- **Hypothesis 1.2 (Seasonal Dynamics) is partially accepted.** The Galloway cattle exhibited relatively high seasonal fluctuations in home range size, reflecting dynamic adjustments to resource availability. Conversely, the Westhoek equids exhibited relatively static year-round home range sizes, reflecting a biological divergence where equids are less sensitive to seasonal phenology. However, the equids did exhibit significant seasonal shifts in their geometric core areas, confirming that while their total area remains static, their internal foraging focus shifts dynamically.
- **Hypothesis 1.3 (Landscape Connectivity) is accepted.** The restoration of landscape connectivity in the Westhoek via the winter 2022-23 corridor opening caused a significant expansion in the absolute home range sizes of the equids. However, this spatial expansion was not uniformly adopted, highlighting that landscape connectivity is mediated by sub-herd social dynamics and localized site fidelity.

6.2. Work Package 2: Fine-Scale Habitat Selection

The second objective evaluated the fine-scale habitat preferences of the grazers and their underlying environmental constraints.

- **Hypothesis 2.1 (Baseline-Relative Selection) is accepted.** Herbivores in both reserves exhibited distinct, highly targeted habitat preferences. The Westhoek equids disproportionately selected for open, grassy vegetation over dense scrub, though morphological divergence likely allowed smaller Shetland ponies to exploit sparse vegetation and low scrub more profitably. Meanwhile, the Kalmthoutse Heide cattle

operated as biological filters, targeting habitats with a forageable layer (e.g. grass or tree encroachment) and avoiding unencroached, pure heathlands.

- **Hypothesis 2.2 (Abiotic Constraints) is partially accepted.** The hypothesis regarding topography is accepted: the cattle (during the spring), the Konik horses (during summer and autumn) and the Shetland pony (during autumn) actively selected for flatter terrain, likely to minimize metabolic costs. However, the hypothesis regarding proximity to water is rejected. Neither reserve demonstrated a classical dependency on surface water. The equids generally exhibited spatial neutrality, and the cattle actively preferred longer distances from water during spring and summer, proving water proximity is not a limiting constraint in these reserves.
- **Hypothesis 2.3 (Anthropogenic Avoidance) is partially rejected.** While boundary fences functioned as a spatial deterrent for the equids (during spring and winter, driven primarily by the Shetland pony), they functioned as a spatial attractant for the Galloway cattle in spring. Similarly, internal path networks functioned as spatial attractants for both the Shetland pony and the Galloway cattle. Therefore, rather than universally avoiding human infrastructure, large herbivores can potentially use path networks as low-resistance navigational corridors, and boundary fences as structural and navigational landmarks.

6.3. Work Package 3: Spatial Ecology and Vegetation Dynamics

The final objective linked herbivore spatial presence to structural vegetation changes in the Westhoek.

- **Hypothesis 3.1 (Terrain Use Impact) is partially accepted.** High cumulative space use by equids acts as an effective preventative barrier against the initial formation and spread of rough vegetation. However, the hypothesis is rejected regarding the regression of mature succession. Once rough vegetation and scrub breach the initial herbivory barrier, intense space use pressure is insufficient to force its regression and can even facilitate its vertical growth via a synergistic combination of localized nutrient deposition, mechanical soil disturbance, and reduced competition.
- **Hypothesis 3.2 (Abiotic Drivers) is accepted.** The dismantling of late-stage, mature succession is driven exclusively by bottom-up abiotic stressors rather than top-down herbivory. Spring Groundwater Depth had the most pronounced effect on vegetation dynamics, dictating the stability of pioneer matrices, driving rough vegetation regression, and serving as the primary natural stressor preventing the continuous growth or presence of low and high scrub. Furthermore, the dynamics of shallower-rooted grasses and herbs were dictated by high environmental stress, with these matrices growing and regressing in areas characterized by deep groundwater, steeper terrain slopes, and high solar exposure.

6.4. Synthesis

Ultimately, this thesis demonstrates that the impact of large herbivores as ecosystem engineers is not uniform or absolute. Space use by free-roaming herbivores is a tool for arresting early succession and targeting degraded habitats. However, their top-down biological control is bounded by the morphological diversity of the grazer group, internal social networks, human infrastructure (such as paths and fences), and the overriding abiotic constraints of the physical landscape (such as topography and distance to water). For conservation management, this often mandates a strategic, dual-management approach that couples the ecological impact of diverse herbivore groups with targeted mechanical interventions.

7. Summary

English version

The use of free-roaming large herbivores is a cornerstone of nature conservation in Europe. It is relied upon to arrest successional encroachment and maintain the structural diversity of open landscapes. In nutrient-poor ecosystems, such as coastal dunes and lowland heathlands, widespread atmospheric nitrogen deposition and the loss of historical disturbances have triggered fast structural degradation. This primarily manifests as grass encroachment (*vergrassing* or *verruiging*) and the establishment of dense woody scrub (*verstruweling*), which outcompete specialized pioneer species and reduce overall biodiversity. While conservation grazing is widely deployed to mitigate these threats, the precise spatial mechanisms by which these animals select habitats, interact with physical infrastructure, and subsequently engineer their environments remain complex and context dependent. This study evaluated the spatial ecology and ecosystem engineering capacity of large herbivores in two structurally distinct landscapes: the coastal dunes of the Westhoek (grazed by a mixed equid group of Konik horses and Shetland ponies and a herd of Highland cattle) and the lowland heathlands of the Kalmthoutse Heide (grazed by a herd of Galloway cattle).

To bridge the gap between individual animal movement and landscape-scale successional change, this research utilized a multi-layered methodological framework divided into three distinct Work Packages (WP). First, to map boundary-constrained space use and spatial saturation (WP1), Continuous-Time Movement Modelling (ctmm) was applied to GPS telemetry data. This approach mathematically corrected for inherent temporal autocorrelation and utilized Degrees of Freedom (DOF) filtering to extract robust Autocorrelated Kernel Density Estimates (AKDE). Second, to evaluate fine-scale habitat selection and underlying environmental constraints (WP2), integrated Resource Selection Functions (iRSF) were deployed. Crucially, the iRSF models utilized each animal's AKDE home range as the availability baseline, ensuring habitat selection was evaluated strictly relative to the accessible landscape while simultaneously accounting for continuous variables such as topography, distance to water, and distance to anthropogenic infrastructure (paths and fences). Finally, to link this spatial behaviour to structural landscape alterations (WP3), high-resolution vegetation height maps from 2020 and 2025 were analysed in the Westhoek. By categorising spatial pixels into vegetational transition states (Stable, Regression, or Encroachment), the cumulative space-use intensity of the equids was modelled against abiotic stressors to determine the true drivers of vegetation dynamics.

The spatial models (WP1) revealed fundamental divergences in baseline spatial ecology, driven by species-level traits and herd dynamics. The spatial tracking demonstrated that neither the equid group in the Westhoek (post-corridor) nor the Galloway cattle in the Kalmthoutse Heide are biologically saturated; their home ranges are not completely dictated by the physical perimeter of the reserves, indicating active and targeted spatial choices. The Galloway cattle exhibited relatively high seasonal fluctuations in home range size, reflecting dynamic adjustments to resource availability. Conversely, the Westhoek equids exhibited relatively static year-round home range sizes, reflecting a biological divergence where equids are less sensitive to seasonal phenology. However, the equids did exhibit significant seasonal shifts in their geometric core areas, confirming

that while their total area remains static, their internal foraging focus shifts dynamically. Furthermore, while low inter-individual variance drove a rather cohesive herd dynamic in the cattle, high inter-individual variance among the equids drove distinct sub-herd divergence. Additionally, WP1 evaluated the impact of restoring landscape connectivity in the Westhoek via a corridor opening in the winter of 2022-2023. While the opening caused a significant expansion in the absolute home range sizes of the equids, this expansion was not uniformly adopted by the entire group, highlighting that landscape connectivity is mediated by localized site fidelity and internal social structures.

Evaluating fine-scale habitat selection (WP2) further reinforced these species-level divergences. In the Kalmthoutse Heide cattle operated as biological filters, actively targeting habitats with a forageable layer (e.g. grass or tree encroachment) and avoiding unencroached, pure heathlands. This selection was more concentrated during the spring flush and broadened progressively as the growing season concluded. In the Westhoek, equids disproportionately selected for open, grassy vegetation over dense scrub, though morphological divergence likely allowed smaller Shetland ponies to exploit sparse swards (e.g. *Schaarsbegroeid*) and low scrub (*Kruipwilg_laagstruweel*) more profitably. This divergence indicates that smaller equids, utilising different biomechanical characteristics and smaller bite sizes, can exploit niches that larger equids ignore or cannot survive on, thereby broadening the total ecological impact on the landscape.

Beyond categorical habitat types, spatial distribution was significantly modulated by continuous abiotic and anthropogenic constraints. Proximity to water proved to be a non-limiting factor in both reserves; neither the equids nor the cattle demonstrated a dependency on standing surface water, displaying spatial neutrality or active avoidance. Topographically, the cattle (during the spring), the Konik horses (during summer and autumn) and the Shetland pony (during autumn) actively selected for flatter terrain, likely to minimize metabolic locomotion costs. Conversely, while the Shetland pony mirrored this preference for flatter terrain during the autumn, it deviated from the Koniks by remaining topographically neutral during the summer. This seasonal divergence suggests either that the pony's smaller body mass affords greater agility, reducing the relative metabolic penalty of moving on steeper slopes, or that the solitary pony is being competitively displaced into less desirable, steeper topography by the Konik sub-herds or the Scottish highland cattle. Regarding human infrastructure, the models forced a reassessment of generalized anthropogenic avoidance. While boundary fences functioned as a spatial deterrent for the equids (during spring and winter, driven primarily by the Shetland pony), they functioned as a spatial attractant for the Galloway cattle in spring. Similarly, internal path networks functioned as spatial attractants for both the Shetland pony and the Galloway cattle. Therefore, rather than universally avoiding human infrastructure, large herbivores can potentially use path networks as low-resistance navigational corridors, and boundary fences as structural and navigational landmarks.

While WP1 and WP2 established how the Westhoek equid group navigates and selects its habitats, WP3 evaluates the reciprocal ecological impact: how the prolonged spatial presence of these herbivores actively engineers the successional vegetation trajectory of the reserve. By modelling vegetation height changes against cumulative equid space-use intensity and abiotic constraints, a spatial narrative emerges regarding the benefits and limits of top-down control. The vegetation modelling established that high cumulative space use by equids acts as an effective preventative barrier against the initial formation and spread of rough vegetation. However, the data

simultaneously defined the limits of this top-down biological control. Once woody or rough vegetation successfully breaches the initial herbivory barrier, intense equid space use pressure becomes insufficient to force its regression. In fact, driven by a synergistic combination of localized nutrient deposition, mechanical soil disturbance, and reduced competition, intense equid space use can even facilitate the vertical growth of established high scrub. The dismantling of late-stage, mature succession is driven exclusively by bottom-up abiotic stressors rather than top-down herbivory. Spring Groundwater Depth had the most pronounced effect on vegetation dynamics, dictating the stability of pioneer matrices, driving rough vegetation regression, and serving as the primary natural stressor preventing the continuous growth or presence of low and high scrub. Furthermore, the dynamics of shallower-rooted grasses and herbs were dictated by high environmental stress, with these matrices growing and regressing in areas characterized by deep groundwater, steeper terrain slopes, and high solar exposure.

For conservation management, this thesis provides clear, data-driven mandates regarding the use of free-roaming large herbivores. Ultimately, this study demonstrates that the impact of these large herbivores as ecosystem engineers is not uniform or absolute. The spatial dynamics confirm that space use can be an effective targeted tool for arresting early succession, maintaining open matrices and targeting degraded habitats. However, because it cannot dismantle established thickets, reversing mature woody encroachment requires a strategic, dual-management approach that couples biological space use with targeted mechanical interventions. Furthermore, the spatial divergence of the Shetland pony underscores the critical value of morphological diversity. Specifically, this divergence indicates that smaller equids, utilising different biomechanical characteristics and smaller bite sizes, can exploit niches that larger equids ignore or cannot survive on, thereby broadening the total ecological impact on the landscape. Finally, the attraction to path infrastructure and the dispersion effect of corridors highlights proactive management opportunities. Rather than viewing human infrastructure as a disturbance, managers can strategically design internal path networks and corridors to function as biological funnels, drawing grazers into specific target areas and maximize ecological engineering across the broader landscape.

Dutch version

Het inzetten van vrij rondlopende grote herbivoren vormt een hoeksteen van het natuurbeheer in Europa. De bedoeling is om via extensieve begrazing natuurlijke processen te herstellen, zoals het tegenhouden van snelle vegetatiesuccessie en het in stand houden van de structurele diversiteit van open landschappen. Hierdoor wordt dit type beheer ook wel procesbeheer genoemd. In voedselarme ecosystemen, zoals kustduinen en laaglandheiden, heeft de wijdverspreide stikstofdepositie en het wegvallen van historische verstoringen geleid tot een snelle structurele achteruitgang. Dit uit zich voornamelijk in de vestiging van sterk competitieve grassen en kruidachtigen (vergrassing of verruiging) en de vestiging van dicht struikgewas (verstruweling), waardoor gespecialiseerde pioniersoorten worden verdrongen en de biodiversiteit afneemt. Hoewel begrazing voor natuurbeheer op grote schaal wordt ingezet om deze bedreigingen te verminderen, blijven de precieze ruimtelijke mechanismen waarmee deze dieren habitat selecteren en interageren met fysieke infrastructuur complex en contextgebonden. Deze studie evalueerde de ruimtelijke ecologie en het vermogen tot ecosysteembeïnvloeding van grote herbivoren in twee structureel verschillende landschappen: de kustduinen van de Westhoek (begraasd door een gemengde groep paardachtigen bestaande uit Konikpaarden en Shetlandpony's en een kudde Schotse hooglanders) en de laaglandheide van de Kalmthoutse Heide (begraasd door een kudde Galloway-runderen).

Om de kloof tussen de bewegingen van individuele dieren en successieveranderingen op landschapsschaal te overbruggen, maakte dit onderzoek gebruik van een meerledig methodologisch kader dat was onderverdeeld in drie afzonderlijke werkpakketten (WP). Ten eerste werd Continuous-Time Movement Modelling (ctmm) toegepast op GPS-telemetriegegevens om het gebruik van ruimte met grensbepalingen en ruimtelijke verzadiging in kaart te brengen (WP1). Deze benadering corrigeerde wiskundig voor inherente temporele autocorrelatie en maakte gebruik van Degrees of Freedom (DOF)-filtering om robuuste Autocorrelated Kernel Density Estimates (AKDE) te extraheren. Ten tweede werden geïntegreerde Resource Selection Functions (iRSF) ingezet om de habitatkeuze op kleine schaal en de onderliggende milieubepalingen te evalueren (WP2). De iRSF-modellen gebruikten specifiek het AKDE-gebied van elk dier als beschikbaarheidsbasis, waardoor de habitatkeuze strikt werd geëvalueerd ten opzichte van het toegankelijke landschap, terwijl tegelijkertijd rekening werd gehouden met continue variabelen zoals topografie, afstand tot water en afstand tot antropogene infrastructuur (paden en hekken). Ten slotte werden vegetatiehoogtekaarten met hoge resolutie uit 2020 en 2025 in de Westhoek geanalyseerd om dit ruimtelijk gedrag te koppelen aan structurele landschapsveranderingen (WP3). Door ruimtelijke pixels te categoriseren in vegetatiele overgangstoestanden (Stabiel, Regressie of Toename), werd de cumulatieve ruimtegebruiksintensiteit van de paarden gemodelleerd tegen abiotische stressfactoren om de werkelijke drijvende krachten achter de vegetatiedynamiek te bepalen.

De ruimtelijke modellen (WP1) brachten fundamentele verschillen in de ruimtelijke basisecologie aan het licht, die worden bepaald door eigenschappen op soortniveau en de dynamiek binnen de kudde. Uit de ruimtelijke tracking bleek dat noch de paardachtigen in de Westhoek (na de corridor opening) noch de Galloway-runderen op de Kalmthoutse Heide biologisch verzadigd zijn. Hun leefgebieden worden dus niet volledig bepaald door de fysieke grenzen van de reservaten, wat wijst op actieve en doelgerichte ruimtelijke keuzes. De Galloway-runderen vertoonden relatief grote

seizoensgebonden schommelingen in de omvang van het leefgebied, wat wijst op dynamische aanpassingen aan de beschikbaarheid van voedselbronnen. Omgekeerd vertoonden de paardachtigen in de Westhoek het hele jaar door relatief stabiele leefgebieden, wat wijst op een biologisch verschil waarbij paardachtigen minder gevoelig zijn voor seizoensgebonden fenologie. De paardachtigen vertoonden echter wel significante seizoensgebonden verschuivingen in hun kerngebieden, wat bevestigt dat, hoewel hun totale gebied stabiel blijft, hun interne foerageerfocus dynamisch verschuift. Bovendien zorgde een lage interindividuele variatie voor een vrij samenhangende kuddedynamiek bij de runderen, terwijl een hoge interindividuele variatie onder de paardachtigen leidde tot duidelijke divergentie tussen subkuddes. Daarnaast evalueerde WP1 de impact van het herstel van de landschapsconnectiviteit in de Westhoek via de opening van een corridor in de winter van 2022-2023. Hoewel de opening een aanzienlijke uitbreiding van de absolute omvang van de leefgebieden van de paardachtigen veroorzaakte, werd deze uitbreiding niet uniform door de hele groep overgenomen, wat benadrukt dat landschapsconnectiviteit wordt gemedieerd door lokale locatietrouwheid en interne sociale structuren.

De evaluatie van de habitatkeuze op kleinschalig niveau (WP2) bevestigde deze verschillen op soortniveau nog eens extra. Op de Kalmthoutse Heide fungeerden de runderen als biologische filters: ze zochten actief habitat op met een begraasbare laag (bijvoorbeeld gras- of boomopslag) en vermeden zuivere heidegebieden zonder begraasbare laag. Deze selectie was het sterkst tijdens de voorjaarsgroei en werd geleidelijk breder naarmate het groeiseizoen ten einde liep. In de Westhoek kozen paardachtigen onevenredig vaak voor open, grasrijke vegetatie boven dicht struikgewas, hoewel morfologische verschillen de kleinere Shetlandpony's waarschijnlijk in staat stelden om ijle vegetatie (bijv. Schaarsbegroei) en laag struikgewas (Kruipwilg laagstruweel) gunstiger te exploiteren. Deze divergentie geeft aan dat kleinere paardachtigen niches kunnen exploiteren die grotere paardachtigen negeren of waarin ze niet kunnen overleven door gebruik te maken van andere biomechanische eigenschappen en kleinere beetgroottes, waardoor de totale ecologische impact op het landschap wordt verbreed.

Naast de categorische vegetatie werd de ruimtelijke verspreiding aanzienlijk beïnvloed door voortdurende abiotische en antropogene beperkingen. Nabijheid van water bleek in beide reservaten geen beperkende factor te zijn; noch de paardachtigen, noch de runderen vertoonden een afhankelijkheid van stilstaand oppervlaktewater, maar toonden ruimtelijke neutraliteit of actieve vermijding. Topografisch gezien kozen de runderen (in de lente), de grotere Konik-paarden (in de zomer en herfst) en de Shetlandpony (in de herfst) actief voor vlakker terrein, waarschijnlijk om de metabolische bewegingskosten te minimaliseren. Hoewel de Shetlandpony deze voorkeur voor vlakker terrein in de herfst deelde, week hij in de zomer af van de Koniks door topografisch neutraal te blijven. Deze seizoensgebonden divergentie suggereert ofwel dat de kleinere lichaamsmassa van de pony voor meer wendbaarheid zorgt, waardoor het relatieve metabolische nadeel van voortbeweging op steilere hellingen afneemt, ofwel dat de solitaire pony door de Konik-kuddes of de Schotse hooglander kudde competitief wordt verdrongen naar minder gunstige, steilere topografie. Wat de menselijke infrastructuur betreft, dwongen de modellen een heroverweging af van de visie van algemene antropogene vermijding. Terwijl de omheiningen van het reservaat fungeerden als een ruimtelijke barrière voor de paardachtigen (in de lente en winter, voornamelijk gedreven door de Shetlandpony), fungeerden ze als een ruimtelijk aantrekkingspunt voor de Galloway-runderen in de lente. Gelijkaardig werkten de interne paden als ruimtelijke aantrekkingspunten voor zowel de Shetlandpony als de Galloway-runderen. Dit toont aan dat grote

herbivoren, in plaats van menselijke infrastructuur universeel te vermijden, padennetwerken potentieel kunnen gebruiken als navigatiecorridors, en omheiningen als structurele oriëntatiepunten.

Terwijl WP1 en WP2 vaststelden hoe de paardachtigen in de Westhoek navigeren en hun habitat selecteren, evalueert WP3 de wederzijdse ecologische impact: hoe de langdurige ruimtelijke aanwezigheid van deze herbivoren actief het successietraject van de vegetatie in het reservaat beïnvloedt. Door veranderingen in vegetatiehoogte te modelleren tegen de achtergrond van cumulatieve ruimtegebruiksintensiteit en abiotische beperkingen, ontstaat een ruimtelijk verhaal over de voordelen en beperkingen van top-downcontrole door grazers. De vegetatiemodellering toonde aan dat een hoog cumulatief ruimtegebruik door paardachtigen fungeert als een effectieve preventieve barrière tegen de initiële vorming en verspreiding van ruige vegetatie. De gegevens definieerden echter tegelijkertijd de grenzen van deze top-down biologische controle. Zodra houtige of ruige vegetatie de initiële herbivoriebarrière met succes doorbreekt, volstaat intens ruimtegebruik niet meer om de terugtrekking ervan af te dwingen. Gedreven door een synergetische combinatie van lokale nutriëntenafzetting, mechanische bodemverstoring en verminderde concurrentie, kan intensief ruimtegebruik door paardachtigen zelfs de verticale groei van gevestigd hoog struikgewas bevorderen. De ontmanteling van vegetatie in een laat, volwassen stadium wordt uitsluitend aangedreven door bottom-up abiotische stressfactoren in plaats van top-down herbivorie. De diepte van het grondwater in het voorjaar had het meest uitgesproken effect op de vegetatiedynamiek: het bepaalde de stabiliteit van pioniersmatrices, stimuleerde de terugtrekking van ruige vegetatie en fungeerde als de belangrijkste natuurlijke stressfactor die de voortdurende groei of aanwezigheid van laag en hoog struikgewas voorkwam. Bovendien werd de dynamiek van ondieper gewortelde grassen en kruiden gedicteerd door hoge omgevingsstress, waarbij deze matrices groeiden en afnamen in gebieden die gekenmerkt worden door diep grondwater, steilere hellingen en een hoge blootstelling aan de zon.

Voor natuurbeheer biedt deze thesis duidelijke, op gegevens gebaseerde aanbevelingen met betrekking tot het gebruik van vrij rondlopende grote herbivoren. Uiteindelijk toont deze studie aan dat de impact van deze grote herbivoren als ecosysteemingenieurs niet uniform of absoluut is. De ruimtelijke dynamiek bevestigt dat ruimtegebruik een effectief, gericht instrument kan zijn om vroege successie te stoppen, open matrices in stand te houden en gedegradeerde habitats aan te pakken. Omdat grazers echter geen gevestigd struikgewas kunnen ontmantelen, vereist het terugdringen van volgroeide houtige begroeiing een strategische, dubbele beheersaanpak die biologisch ruimtegebruik koppelt aan gerichte mechanische ingrepen. Bovendien benadrukt de ruimtelijke divergentie van de Shetlandpony de cruciale waarde van morfologische diversiteit. Specifiek geeft deze divergentie aan dat kleinere paardachtigen, door gebruik te maken van andere biomechanische eigenschappen en een kleinere hapgrootte, niches kunnen benutten die grotere paardachtigen negeren of waarop ze niet kunnen overleven, waardoor de totale ecologische impact op het landschap wordt verbreed. Ten slotte wijst de aantrekkingskracht van paden en het verspreidingseffect van corridors op nieuwe, proactieve beheersmogelijkheden. In plaats van menselijke infrastructuur als een verstoring te beschouwen, kunnen beheerders strategisch interne padennetwerken en corridors ontwerpen die als biologische trechters fungeren, waardoor grazers naar specifieke doelgebieden worden geleid en de ecologische manipulatie (engineering) in het bredere landschap wordt gemaximaliseerd.

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8.1 Statement on the use of Generative AI

During this master's dissertation, Undermined, Elicit, Search Rabbit and Connected Papers were used for searching scientific literature among other standard search engines. Gemini 3.1 Pro was used to improve spelling and grammar and to help write the code for the analysis in R.

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10. Attachments

To ensure full transparency and reproducibility of the analyses presented in this dissertation, all code has been made available digitally. This repository contains the R scripts used for the statistical modelling of both the spatial dynamics (WP1 and WP2) and the transitional vegetation trajectories (WP3), alongside the relevant data tables and figures.

These files can be accessed permanently via the following Google Drive repository:

- **Digital Access Link:** <https://drive.google.com/drive/folders/1whesq2-XO0htv6F08SvILZE88A3-05Oc?usp=sharing>