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Drivers and impacts of large herbivore foraging behaviour in a rewilded landscape

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Abstract

Rewilding is increasingly being proposed in conservation discourse, as a means to reverse present ecological declines. Despite its increasing prominence however, there is little known of its ecological outcomes. The historic role of large herbivores in shaping a wild landscape is a particularly important area of research in the context of modern rewilding in temperate Europe, but opportunities to deduce the extent of herbivore influence has been rare. The Knepp Wildland Project offers an opportunity to address this gap. The deliberate abandonment of agricultural land, has allowed self-willed habitat to develop, this has been complemented by the reintroduction of large herbivore species, present in near-natural grazing conditions.

This project aimed to ascertain the drivers and impact of large herbivores forage selection and intensity within this rewilding project. A network of thirty-eight camera traps were active for twenty-five trap days in summer and winter to record herbivore movements, as well as seven 2km walked line transects, active over the same study periods. Five $1m^2$ vegetation quadrats were sampled within each camera trapped field to ascertain floral diversity, while LiDAR data was collected within $30m^2$ patches to record structural heterogeneity and vegetation height.

Herbivore foraging was found to be non-uniform, with overlaps in forage selection between study species creating clear pressure points, conversely other areas are developing under minimal pressure. No sequential patterns occurred when considering when the fields were taken out of agriculture, indicating this is not a driver in forage selection. Floral diversity was negatively correlated to Longhorn cattle foraging intensity, but had no influence on any other species, with individual plant species characteristic of habitat types appearing to be a better gauge. Increased habitat heterogeneity was positively correlated with Roe deer foraging intensity while negatively correlated to Longhorn cattle, while no other species were driven by structural variables.

These results largely support an open mosaic habitat as the most likely destination for Knepp's landscape under current conditions, while providing a baseline for a long-term study into the nuances of the cyclic nature of herbivore-plant interactions. The results also detail the individual niches of the large herbivore species present and the importance of diverse grazing in a rewilding context.

1. Introduction

As the world wakes up to an environmental crisis, new solutions to address the downward spiral of biodiversity loss are regularly proposed (Barnosky *et al.,* 2011; Corlett, 2016). Conservation management and government commitments have continually failed to reverse these trends, with estimates suggesting that global extinction rates could exceed current predictions (Barnosky *et al.,* 2011; Ceballos *et al.,* 2015). In the UK, the recent state of nature report concluded that the UK is ranked 189th in terms of intactness of biodiversity, with 56% of species in decline (Hayhow *et al.,* 2016). These results, coupled with political uncertainty around environmental policy (Swimbank, 2017; Hilson, 2018), has fuelled the belief that widespread land abandonment, as has been seen in mainland Europe, could increase following Brexit, as insecurities over subsidies continue (Queiroz *et al.,* 2014; Cadywould, 2017). This developing situation is forcing environmental stakeholders towards a new way of conservation thinking (Navarro & Pereira, 2012).

One prominently discussed novel solution is rewilding (Sandom, Donlan & Svenning, 2013; Merckx & Pereira, 2015). Rewilding is presented as an optimistic strategy for conservation (Donlan *et al.* 2006; Seddon *et al.*, 2014), seeking to restore natural processes through a minimum intervention approach, benefitting biodiversity and ecosystem services (Cerqueira *et al.,* 2015; Hodder *et al.,* 2010). This approach therefore, aims to create landscape scale change in both conservation methods and outcomes, while creating a connected network of self-willed biologically rich protected areas (Soulé & Noss, 1998; Donlan, 2005; Sandom, Donlan & Svenning, 2013). Rewilding is often supported by the reintroduction of keystone species that support ecosystem functionality, such as wolves (*Canis iupus*), wild boar (*Sus scrofa*) and large herbivores (Sandom, Macdonald, & Feber, 2015). It has been a catalyst for a shift in appetite within conservation debate, leading the creation of numerous 'rewilding' projects, which have spawned under its umbrella (Donlan, 2013). The projects encompass a range of habitats, species focus and above all scale (Jepson, 2016). While many environmentalists point to the potential benefits of rewilding, it is not without criticism (Caro & Sherman, 2009; Nogués-Bravo et al., 2016).

The earliest definitions of rewilding are in the context of restoring large areas of wilderness and the engineering roles of large predators in North America (Soulé & Noss, 1998), with most early work focusing on this large-scale re-establishment of past landscapes and trophic cascades, termed Pleistocene rewilding (Donlan *et al.,* 2006). This involves implementation on

a large scale to enable fully functioning ecological processes, for example predator-prey relationships, to flourish and human intervention to be negligible (Donlan *et al.,* 2006; Taylor & Ayres, 2014). In the urban and agricultural centres however, this is simply not feasible, so alternative adaptations have spawned allowing for spatial constrictions (Snyder, 2017; Prior & Brady, 2017). Particularly in Europe, rewilding has seen a shift into a more passive approach, centred around naturalistic grazing, reduced management and where possible, re-establishing ancient species assemblages for their functional traits within an ecosystem (Vera, 2000). There has also been more of a transfer into an agricultural context (Navarro & Pereira, 2012), with rewilding described as "a process in which a formerly cultivated landscape develops without human control" (Höchtl, Lehringer, & Konold., 2005).

The exponential growth in scholarly research and media discourse, has led to rewilding increasingly being utilised to capture public imagination, heightening scrutiny (Lorimer *et al.,* 2015). One criticism placed upon it, is the lack of consensus that exist by proponents of the concept, especially relating to the plasticity of its definition (Jørgensen, 2015; Nogués-Bravo et al., 2016). There is also a paucity of research on its outcomes, leading to scepticism and acknowledgment that the concept needs further research to make it fit for policy (Nogués-Bravo et al., 2016; Pettorelli et al., 2018). Furthermore, the term is very wildlife focused, and has been criticised for distancing itself from socio-ecological issues particularly around agriculture (Jørgensen, 2015).

The upsurge in interest in rewilding over the past decade has seen new leaders begin to emerge in the discipline, broadly helping to address these criticisms. Rewilding Europe (2018) have a working definition focusing not only on prominence of wild spaces and natural process, but also in the opportunities to reconnect society to nature that rewilding can offer. Similarly, the group Rewilding Britain (2018) place "People, communities and livelihoods" at the heart of their vision for the future of rewilding, as well as emphasising rewilding as a long-term strategy.

A lot of the uncertainty over the application of rewilding can found by looking at the aesthetics of rewilded landscapes (Vera, 2000; Hodder & Bullock, 2005; Prior & Brady, 2017). The debate was elevated by Dutch scientist Frans Vera, who questioned the 20th century assumption that forest cover establishes when an undisturbed situation occurs in Europe, leading to the belief that closed canopy forest was the dominant landscape in Neolithic times (Vera, 2000; Mitchell, 2005). Instead, Vera hypothesised that an open mosaic of grassland and woodland formed the majority Europe's habitat, raising the possibility that large herbivores were the

driver for these grassland-woodland cycles. One of the main arguments Vera (2000) proposed is based on the lack of regeneration of oak (*Quercus robur*) and hazel (*Corlyus avellana*) within unmanaged forest canopies. These species are highly represented in Holocene fossil records, underpinning his suggestion that they thrived in this era because of grazing pressure, which reduce competition from more shade tolerant species (Vera, 2000). This theory has caused a rethink between conservation practice in Europe, and a debate on the impact and use of large herbivores in the context of rewilding (Hodder *et al.*, 2005; Hodder & Bullock, 2009; Vera, 2009; Smit *et al.*, 2015).

Analysis of pollen records between Ireland, where large herbivores were highly restricted, and Britain and Europe from pre-Neolithic times however is in contradiction to Frans Vera's (2000) theory (Bradshaw, 2004; Mitchell, 2005). The analysis concluded that vegetation patterns were not altered by the presence or absence of large herbivores, observing that this means they could not have been the main driver towards landscape structure and forest composition (Bradshaw, 2004; Mitchell, 2005). Conversely, analysis of dung associated beetle fossils by Sandom *et al.* (2014) highlighted that abundance and diversity of large herbivores is associated with high structural diversity. Results suggest evidence of a closed or partially closed forest in the early Holocene, semi-open vegetation and forest in the last Interglacial and closed woodland seemingly becoming more prevalent following megafauna extinctions at the end of the Pleistocene. On both sides, there is agreement that uncertainty exists in our knowledge of historic large herbivore abundance and behaviour (Hodder & Bullock, 2005; Hodder *et al.*, 2009).

While there is debate over the role of large herbivores in creating histroic landscapes, research of modern environments suggests that large herbivores are driven by and impact vegetation at varying scales (Olff & Richie, 1998). Herbivores influence growth, recruitment, and mortality rates of plants, doing so in ways correlated with plant diversity and density (Gibson & Brown, 1991; Nathan & Muller-Landau, 2000; Herrero-Jáuregui & Oesterheld, 2018). The absence of large herbivores can result in significant changes in ground floral composition and abundance, while selective browsing signifcantly influences establishment of woody vegetation communities (Newman, Mitchell & Kelly, 2014; Hanley, 1997). As well as this, it has been observed that homogenisation of floral communities can increase over time when herbivores are absent (Newman, Mitchell & Kelly, 2014; Falk *et al.,* 2015). Even when present in an environment the spatial selection and foraging preferences of free roaming herbivores alter all the factors given (Anderson & Briske, 1995).

Spatial selection can be driven by seasonality, migration, age of the individual and indivdual idiosyncratic traits (van Beest *et al.,* 2013), as well availability and quality of forage to suit individual species preferences (van Beest *et al.,* 2010). On top of this, group size, mate selection as well as anthropogenic pressure and predation risk have all been shown to alter herbivore movment patterns and forage perferences (Leblond, Dussault & Ouellet., 2013; Bagchi *et al.,* 2018). Percieved threats, whether through anthropogenic pressure and/or predation can force significant changes in movement patterns and avoidance behaviour, as well as increased exploitation of refuges (Fortin *et al.,* 2005; Matson, Goldizen, & Putland., 2005; Leblond, Dussault & Ouellet., 2013).

Predation forms an important part in creating non uniform patterns in herbivore foraging, research from Yellowstone national park (YNP), highlighted how the impact of reintroducing wolves on large herbivores was a key driver in shaping the landscape (Hernández & Laundré, 2005; Laundre, Hernandez & Ripple, 2010). In YNP, Red deer browsing pressure was reduced in riparian vegetation within areas of high predation risk (Hernández & Laundré, 2005). The presence of a predator keeps large herbivores moving, altering the composition of the landscape as a result and triggering trophic cascades (Laundre, Hernandez & Ripple, 2010). Many rewilding projects occur at a scale to small to support large predators however or because of the potential conflict and cost of predator proofing a site, the means comparisions into the impact of predation risk within this context are rare. At Oostvadersplaasen in the Netherlands, a flagship rewilding experiment, depsite the absence of predation it has been found that naturalistic grazing practises have encouraged natural herbivore movement cycles, meaning grazing is not equal across the site, causing long grass and fobs to grow in areas with less grazing pressure (Cornelissen *et al.,* 2004). These habitats benefited small mammal communities, which in turn benefitted the avian species that predated on them, evidencing the complexity of large herbivore spatial selection beyond merely predation risk and showing trophic cascades are not limited to apex predators (Cornelissen *et al.,* 2004).

The drivers and impacts of large herbivore selection occur and vary in both their positive and negative effects through a range of mechanisms, including the abundance and species of herbivore (Olff & Richie, 1998). For example, at natural densities, free roaming large herbivores have been shown to increase plant species richness (McNaughton, 1985) this is also true when domesticated grazers are stocked at low densities (Wierren, 1995), conversely high densities of both wild and domestic large herbivores can cause a reduction in floral diversity (Hanke *et al.,* 2014; Bressette, Beck, & Beauchamp, 2012). This is caused by unselective

grazing, as well as increased pressure triggering detrimental soil disturbances, and reduced plant cover, with only a few tollerant species inhabiting effected areas (Kairis *et al.,* 2015). Impacts are also influenced by scale, with both local disturbance by herbivores and selective grazing having the potential to increase diversity at a local scale, however a strong selection of tollerant and robust plant species could reduce overall diversity when considering a larger scale (Anderson & Briske, 1995).

The heightened impact of large herbivores across spatial scales when compared with smaller species is also important to consider, as local effects such as disturbance and seed dispersal occur on a much larger scale as body size increases (Bakker et al., 2006). The consistency of effects also differentiates between size, large herbivores are for example more consistent than smaller herbivores in their effects on a landscape, this is usually due to their preferred use of abundant typically low-quality food sources such as grasses (Mobaek et al., 2009; Anderson & Briske, 1995). It should be noted however, that these increases in plant diversity could ultimately disappear due to herbivore induced succession, leaving only a few defended or tolerant species (Hidding, Tremblay & Côté., 2013; Sabo *et al.,* 2017). In the context of rewilding, the need for grazing refuges as a defence following abandonment has been discussed (Smit *et al.,* 2015). This would allow natural defences to develop without herbivory, increasing the chances of initial sapling survival, with defences on abandoned agricultural areas likely to be initially absent (Smit *et al.,* 2015).

The extinction or absence of megafauna that would have once roamed European landscapes also adds a complication (Ripple *et al*., 2016). The extinctions of the auroch (*Bos taurus primigenius*) and the absence of european bison (*Bison bonasus*) and wild boar, and even the straight-tusked elephant (*Palaeoloxodon antiquus*), leave herbivore-plant interactions with important functional gaps in its relationship. Allowing nature to be rewilded in the absence of these influential megafauna therefore poses a problem. The most common solution is the use of proxies, which can act as a functional analogue to the absent species where their reintroduction is not possible due to extinction, or feasible due to economics or potential human-wildlife conflict (Decker *et al.,* 2010; Dickman, 2010; Linnartz & Meissner, 2014; Helmer *et al.,* 2015; Haidt *et al*., 2018). Programmes are also underway to back breed towards extinct species such as the auroch (Helmer *et al.,* 2015). Projects such as Oostvaderplaasen and the Knepp Wildland Project have both used aspects of these approaches to test some of the naturalistic grazing and rewilding outcomes within Europe, that are currently being debated (Vera, 2009; Tree, 2017).

The Knepp Wildland Project is situated on a former arable farm, which began leaving its fields to nature in 2000, stepping back to see how vegetation evolves (Greenaway, 2011; Tree, 2017). This was subsequently followed by the reintroduction of a suite large herbivore some as proxies for absent species and others native species (Greenaway, 2011; Tree, 2017). As well as early evidence of increased biodiversity, the project has also been held up as a model due to its economic model by using ecotourism, hosting green businesses and selling organic free-range meat from the project each year as a means of making the site profitable (Greenaway, 2011). Although still in its early stages, the Knepp wildland project represents an ideal environment to test some of the theories previously mentioned using a real time case study.

1.1. Aim

Based at the Knepp wildland project, this study aims to ascertain the extent to which large herbivore foraging varies spatially, and assess the potential drivers and impacts of this in the context of rewilding.

1.2. Hypotheses

a) There will be significant differences in foraging intensity rates between large herbivores species at Knepp

b) Foraging intensity patterns will be non-uniform with preferential foraging areas present for all large herbivore species

c) There will be a sequential pattern in forage selection between years of agricultural abandonment, with browsing and mixers feeder favouring earlier years and grazers favouring later years.

d) Floral diversity will be significant driver in forage selection for grazing species but not for mixed feeding and browsing species

e) Structural heterogeneity will positively correlate with forage selection for species with a browsing preference and negatively correlate with forage selection for grazing species

2. Method

2.1. Study site

The Knepp Wildland Project is an innovative rewilding scheme situated south of Horsham, West Sussex, UK (50.9717° N, 0.3629° W). Knepp extends across approximately 1,400ha of formerly intensive agricultural land within a region of heavy clay soil Low Weald, now transformed into a lowland mosaic habitat. The Estate is made up of three blocks (Northern, Middle, and Southern) each under different management regimes. The wild land project began in 2000 with land phased out of production over subsequent years. This study focused on the 450ha southern block which in contrast to the other two blocks, was not reseeded, but allowed to regenerate naturally between 2000-2006, as fields were removed from production.

From 2008, the reintroduction of free roaming herbivores occurred, including Longhorn cattle (*Bos primigenius*), Tamworth pig (*Sus scrofa domesticus*), Exmoor pony (*Equus ferus caballus*), Red deer (*Cervus elaphus*), and Fallow deer (*Dama dama*). These herbivores are native or act as proxies to former native herbivore that are now absent or extinct. For example, Exmoor ponies, Longhorn cattle and Tamworth pigs act as proxy for animals like the Tarpan (*Equus ferus ferus*), the Auroch and Wild boar. Fallow deer have occurred in England in the Pleistocene, but did not inhabit England during the Holocene until the Normans introduced them. Red deer are native and have been reintroduced, while Roe deer (*Capreolus capreolus*) naturally colonized the site in small densities. The suite of herbivores introduced fulfil separate niches through their different techniques of grazing, browsing and rooting.

The herbivores at Knepp are free roaming within the southern block and have been described as having a near natural grazing state (Greenaway, 2006). Many of the grazing principles have been adapted from the naturalistic grazing regimes at the Oostvaardersplassen project in the Netherlands (Vera, 2009). Animals are taken off the land as part of the sites economic model as well as using this to manage herbivore numbers by acting as a proxy for predators that would usually regulate population numbers

2.2.1 Herbivore Movement

Herbivore movement data were collected using a mixed method approach. Most of the data being compiled via a network of camera traps. Thirty-four cameras were set up in seventeen fields within the southern block of Knepp in winter with Thirty-eight cameras in nineteen fields in summer, using stratified random sampling to decide which fields, taking into consideration

habitat type and the year each field was taken out of production. Each field contained two cameras. Where possible placing cameras in adjoining fields or fields that share access paths was minimised, to reduce data replication and spatial auto correlation.

Table 1: Summer and Winter camera trapped field within Knepp's southern block and their habitat classification

Site Number	Field Name	Habitat Classification	Winter	Summer
1	Wildflower Meadow	Permanent Pasture	X	X
2	Bentons Place	Grassland		X
3	Brookhouse 6	Grassland	X	X
4	New Barn Lane 1	Grassland	X	X
5	Tench Ford	Grassland	X	X
6	Brookhouse E	Grassland/Scrub	X	X
7	Dial Post 1	Grassland/Scrub	X	X
8	Fresco East	Grassland/Scrub	X	X
9	Oaklands 1	Grassland/Scrub	X	X
10	Oaklands 4	Grassland/Scrub	X	X
11	New Barn 2	Scrub	X	X
12	New Barn 6	Scrub	X	X
13	Smokehouse 1	Scrub/Woodland		X
14	Twenty-Seven Acres	Scrub/Woodland	X	X
15	Waterworks West	Scrub/Woodland	X	X
16	Woggs	Scrub/Woodland	X	X
17	Wagstaff Wood	Woodland	X	X
18	Wickwood	Woodland	X	X
19	Woggs Bottom Wood	Woodland	X	X

The camera traps were active between February-March 2018 and May-June 2018 enabling seasonality to be a factor within the dataset. During both data collection phases, the cameras recorded for 25 traps days beginning from the first full day of recording following set up, amounting to 425 days of sampling effort in winter and 475 in summer. All camera traps were placed at a location deduced to provide the greatest coverage of the entire field and set to record for 10 seconds with a 3-minute interval between triggers. The cameras were placed 1m above

the ground, however, this varied greatly depending on availability of a suitable site, as well as sward height and seasonality, between 0.5m and 1.25m.

To avoid replication of individual animals, 30-minute intervals following the first trigger of a species were implemented, using the assumption that triggers that contained the same number of animals within that time were the same, with the largest number animals within a frame being taken as the overall total. When colouration, gender, age or other significant features could identify animals as new to the frame with 100% certainty an accumulation was used.

Walked line transects supplemented camera trap data. Seven 2km transects were set up with the predominate factor for their location being overall site coverage. Transects were walked weekly for 6 weeks with a target time of 45 minutes per transect implemented for continuity. Transects were undertaken over the same period as the cameras were active. Distance sampling was used to record data, while species location was recorded using Mapit GIS as a mobile way of recording GPS position as well as distance and bearing of each species. Transects were walked at varying times each week. Camera traps are advantageous for their 24hr coverage however, they possess many blind spots, so transects complemented the camera trap data to build a more robust picture of herbivore distribution on site. For both methods, Date, Time, Species ID, Number of individuals, Behaviour and GPS location were recorded. Recorded behaviours included Walking, Running and Resting as well as Grazing, Browsing and Rooting.

2.2.2. Vegetation Surveys

Within each camera-trapped field, five $1m^2$ quadrats were sampled with each species present being recorded on a DAFOR scale. Three of the quadrats were located randomly within each field, while the other two quadrats were placed within a 5-metre circumference of the camera traps within the field. Recordings of opportunistic sightings were added to obtain as complete a species list as possible. Vegetation sampling was conducted using the National Vegetation Classification as a base, therefore species data within the scrub layer and site characteristics were recorded as single observations, also using the DAFOR scale.

2.2.3 Vegetation Structure

LiDAR was used to gather data on vegetation structure. The data were collected using a ZEB-REVO hand held mobile, laser-scanning devise. Each field was surveyed using a 30m x 30m square plot randomly generated in Arc Map 10.5. Each plot was situated a minimum of 30m from the field boundary. To ensure complete coverage of the plots, they were walked along

parallel 2m intervals with any gaps identified and covered using a Garmin e-trex 30 GPS. Where the vegetation was impenetrable on foot, the feature was surveyed by walking around it. LiDAR data were processed using the GeoSLAM Hub software. A ply file was created, using 75% of points, with a spatial decimation of 10mm, with points shaded by height, and point normals set. It was also set to 'Single Floor'. The output file was cleaned and analysed in Cloud Compare before R studio was used to calculate basic statistics including mean vegetation height and standard deviation as a measure of habitat heterogeneity from each plot.

2.3. Statistical analysis

2.3.1. Foraging Intensity

Foraging intensity was calculated for both camera traps and walked line transects using the accumulative abundance of individuals each trap/survey day in each field divided by the number of trap/survey days. This was conducted separately for six large herbivore species in the study. For this calculation, all observed behaviours of 'resting' were removed.

To assess the first hypothesis a Kruskal-Walis test was undertaken using the 'asbio' (2018) package in R studio to ascertain the significant difference between foraging intensity scores for each species, this test was chosen as it allowed the analysis of multiple groups and caters for data that is non-parametric. A post-hoc Dunn test was then conducted as it allowed a more detailed look at significance between the pairwise comparisons for each species.

ArcMap 10.5 was used to create a dot density map where a foraging intensity value of 0.1 was the equivalent to one dot within each field. The map utilised the foraging intensity value from both the camera trap data and transect data. The map included all six large herbivore species enabling patterns to be inferred specifically crossovers in species foraging.

ArcMap 10.5 was also used to create individual maps for each large herbivore foraging intensity using the same data as above. This time a gradient colour scale was used to indicate the level of intensity within each field. The gradient scale was unique to each species relative foraging intensity.

Using the same 'asbio' (2018) package, a Chi-squared goodness of fit tested statistical preferences for each camera trapped field and each species. This test was chosen due to its ability to compare differences in an observed and expected value and enable a measure of preference between multiple results to be easily identified. Here, the accumulative abundance of each herbivore species foraging, within each field, over the twenty-five summer and twenty-

five winter camera trapped period was the observed value and the mean of all fields was the expected value if all things were equal, with the fields grouped by habitat classification with habitats classified as Permanent Pasture (Figure 1a), Grassland (Figure 1b), Grassland/Scrub (Figure 1c), Scrub (Figure 1d), Scrub/Woodland (Figure 1e), and Woodland (Figure 1f), depending on the percentage coverage of grass, scrub and tree cover. The accumulative abundance was chosen instead of the foraging intensity score, to avoid values below 1 being present in the analysis. The same test was repeated, this time the fields were grouped by the year taken out of production with the test replicated to assess temporal influences on the foraging behaviours.

Figure 1: Camera trap images displaying example habitats to fit six classifications. a) Permanent pasture, b) Grassland, c) Grassland/Scrub, d) Scrub, e) Scrub/Woodland, f) Woodland

Photo Credit: Thomas Dando

2.3.2. Floral diversity

DAFOR data from vegetation quadrats were pooled and converted into an abundance score. Dominant vegetation scored five and rare vegetation scored one within each quadrat and the sum of these across all field produced a total abundance score. The Simpsons D-1 diversity indices used this abundance score for each species and total species richness to deduce its diversity value between zero and one. The Simpsons D-1 indices was selected over many similar indices for its ability to differentiate to a greater extent between.

A Pearson correlation coefficient analysed this diversity score in each field with the associated foraging intensity score for each of the six large herbivore species to test for the degree of correlation and statistical significance. The abundance data for 'representative' species of scrub and grassland habitats aka Perennial ryegrass and Bramble within each surveyed field then replaced species diversity before being analysed using the same Pearsons correlation coefficient. Both tests were undertaken in ggplot 2 (2018) within R studio.

2.3.4. Vegetation structure

Mean vegetation height and standard deviation followed the same method as floral diversity, with a Pearsons correlation coefficient used to analyse the degree of correlation between foraging intensity and these two variables in R studio.

3. Results

3.1. Large Herbivore Population

Stocking data (figure 2) shows Longhorn cattle and Fallow deer have been the most abundant species since large herbivore reintroduction to the site, with Longhorn cattle peaking at 264 individuals in 2013/2014, to a level of 94 in 2016/2017. The final year of the figures (2016/2017) represents the most abundant Fallow deer have been, with 164 individuals present within the southern block. Tamworth pig numbers have been decreasing in number since their initial reintroduction with a current low of 7, compared to 35 upon the initial reintroduction. Exmoor ponies and Red deer and have been consistently between ten and fifteen animals. Overall population numbers have been consistent for the duration of the project, with between 200 and 300 animals present in six of the seven years since 2010/2011, with only 2013/2014 showing an upward spike in numbers.
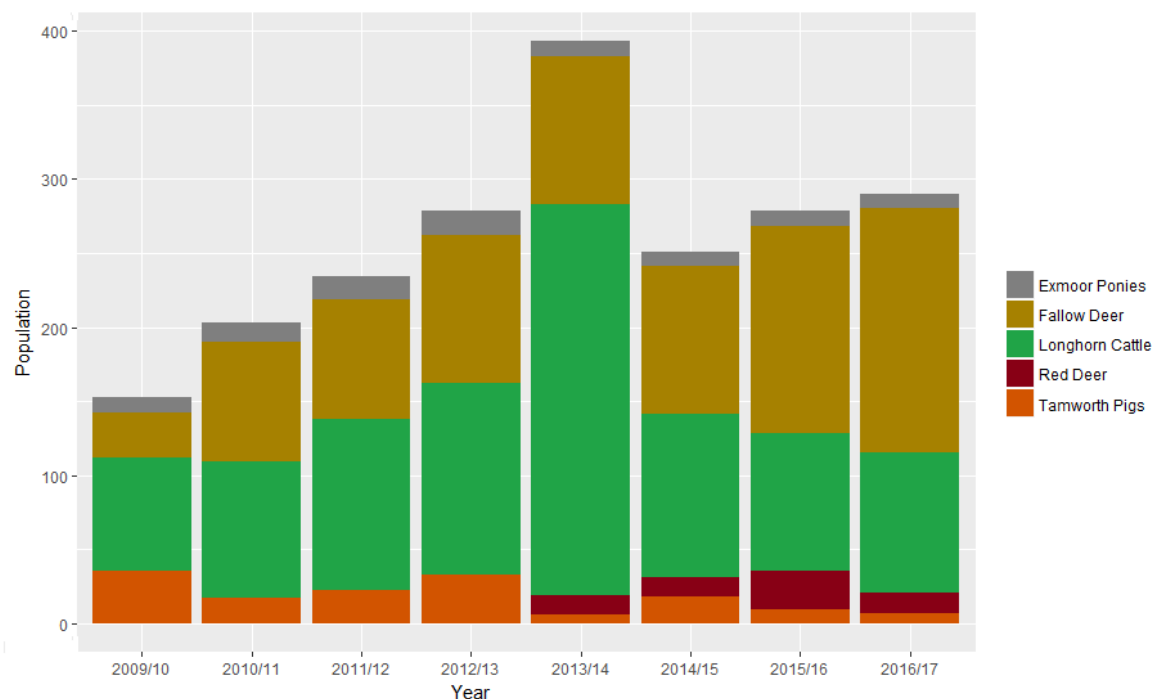
Figure 2: Stocking levels of five reintroduced large herbivores within Knepp wildland projects southern block

3.2. Foraging Intensity

A comparison of mean foraging intensity scores from both camera trap and transect data (figure 3) revealed that there is significant difference in foraging intensity between species within the southern block (X^2=24.255, df=9, p=0.003). The two most abundant species, Fallow deer and

Longhorn cattle have the highest foraging intensity rates across the site at 2.04 animals per day (apd) and 1.6 apd respectively, while Roe deer have the lowest intensity value of 0.27 apd.
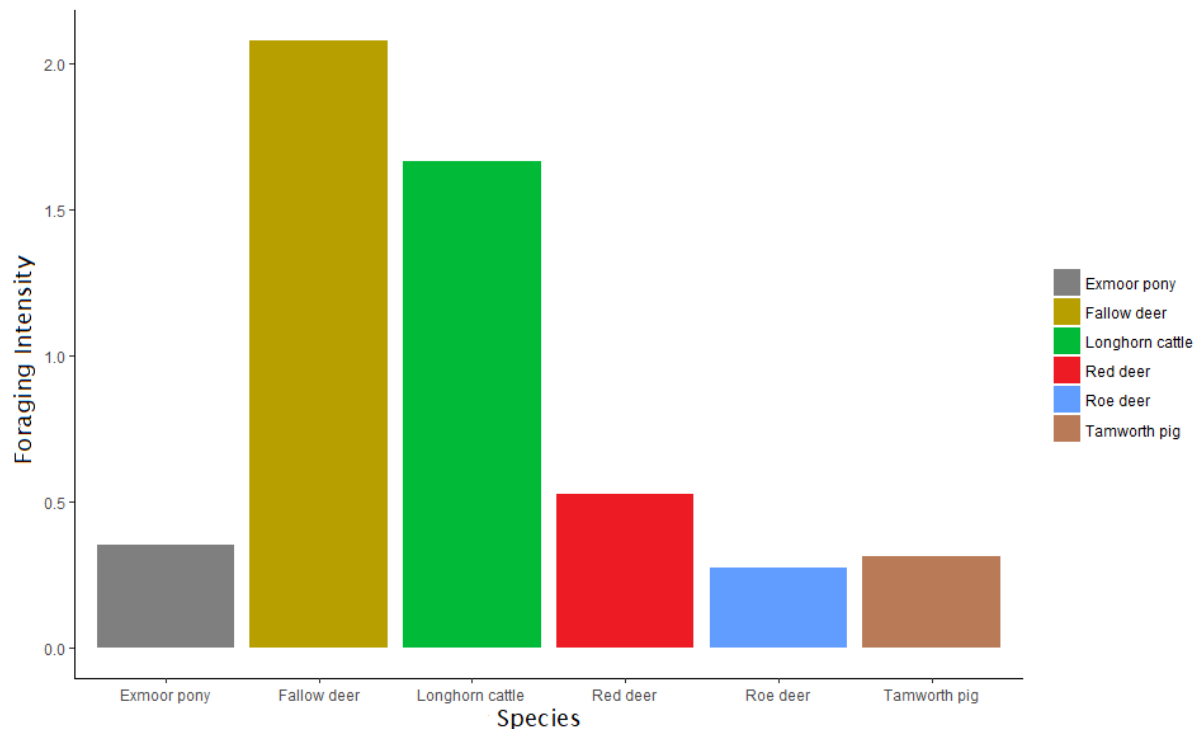

Figure 3: Mean foraging intensity value for the six-study species within Knepp wildland projects southern block

A Dunn post-hoc test (table 2) indicated Longhorn cattle and Fallow deer foraging intensity to be significantly greater than Roe deer (p=0.003; p≤0.001), Tamworth pigs (p=0.002; p≤0.001) and Exmoor ponies (p≤0.001; p≤0.001). While Fallow deer also returned a significant result when analysed against Red deer (p≤0.001). No other results were significant.

*Table 2: Matrix of differences in mean foraging intensity between each species. *significance value <0.05*

Species	Fallow deer	Exmoor pony	Longhorn cattle	Red deer	Roe deer	Tamworth pig
Fallow deer	0	1.08*	0.53	1.58*	1.82*	1.81*
Exmoor pony		0	1.27*	0.22	0.02	0.01
Longhorn cattle			0	1.05	1.29*	1.28*
Red deer				0	0.24	0.23
Roe deer					0	0.01
Tamworth pig						0

3.3. Spatial Intensity

The patterns of species foraging as shown by figure 4, indicates that foraging intensity is not uniform across Knepp with pressure points of high forage intensity clearly identifiable. The trend is clearest in the northeast of the block where there are intense areas of multi species foraging, compared to central areas where the dot density is sparse. Other isolated intense patches are present in the western and southern area.
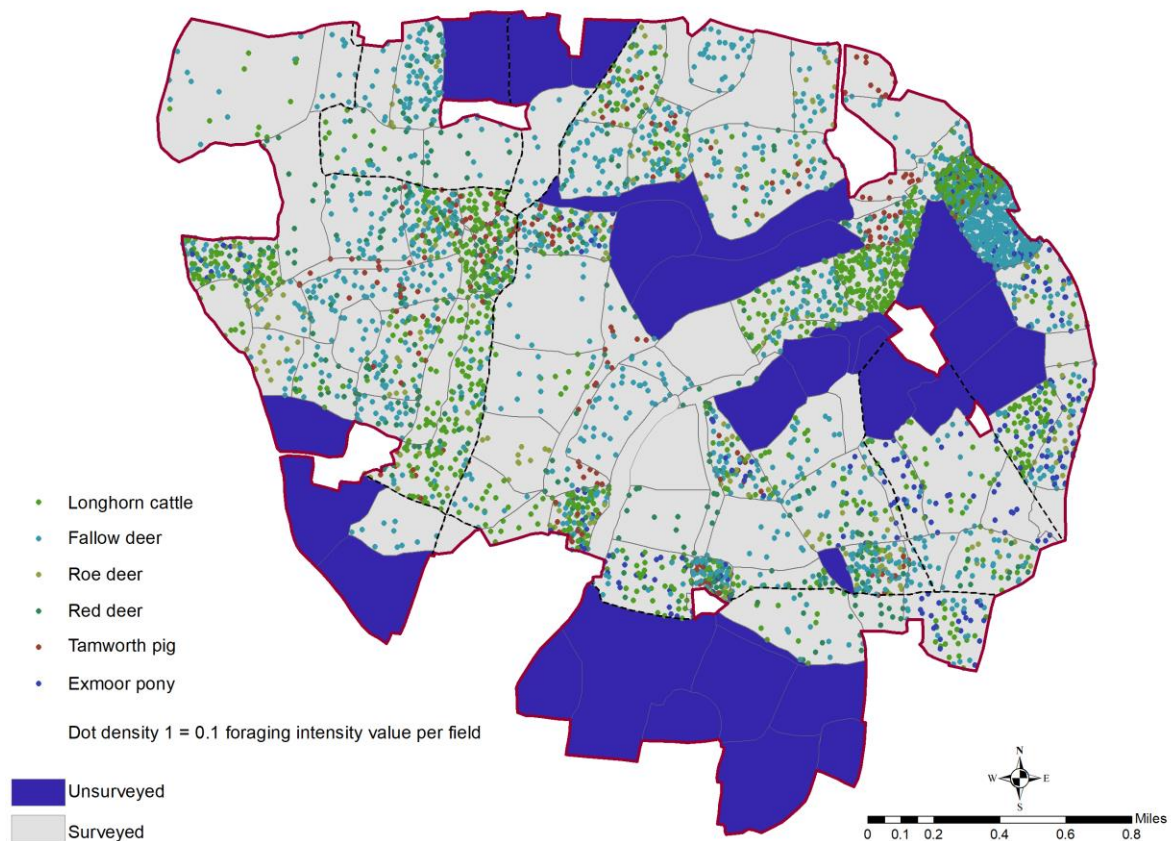

Figure 4: Dot density map of foraging intensity for the six large herbivore study species in Knepp's southern block. One dot equals a foraging intensity value of 0.1 within each field. Dots are randomly distributed within the appropriate field to produce a representation of overall site intensity

When extrapolated to individual species, figure 5a indicates that Longhorn cattle have several intense areas of foraging. These areas have high spatial separation, with noticeably lower intensity values in between. The greatest intensity, depicted by the darkest colour, was a field called Tench ford in the northeast, which has a foraging intensity score of 21.9 apd. Similarly, the Exmoor ponies (figure 5c) had their highest levels of foraging intensity at Tench ford, 1.82 apd, with this lower value being reflective of their smaller population within the site. The Exmoor ponies had a noticeably restricted range of foraging compared to all other species studied, which is in direct contrast to the mixed feeders such as, Fallow deer, Roe deer and Red

deer (figures 5b, 5d, 5e) which all foraged across a much wider area. The highest rate of forage for Fallow deer (figure 5b) overlapped that of the Longhorn cattle and Exmoor ponies, with an intensity value of 9.8 apd at Tench ford and 39.1 apd in the adjacent field, Lucas, the highest two values for this species. Roe deer (figure 5d) displayed increased foraging intensity in the southwest and Red deer (figure 5e) foraged most intensively in the eastern section of the block. Tamworth pigs (figure 5f) followed a similar distribution to Red deer, albeit they were largely absent from the northeast of the block.
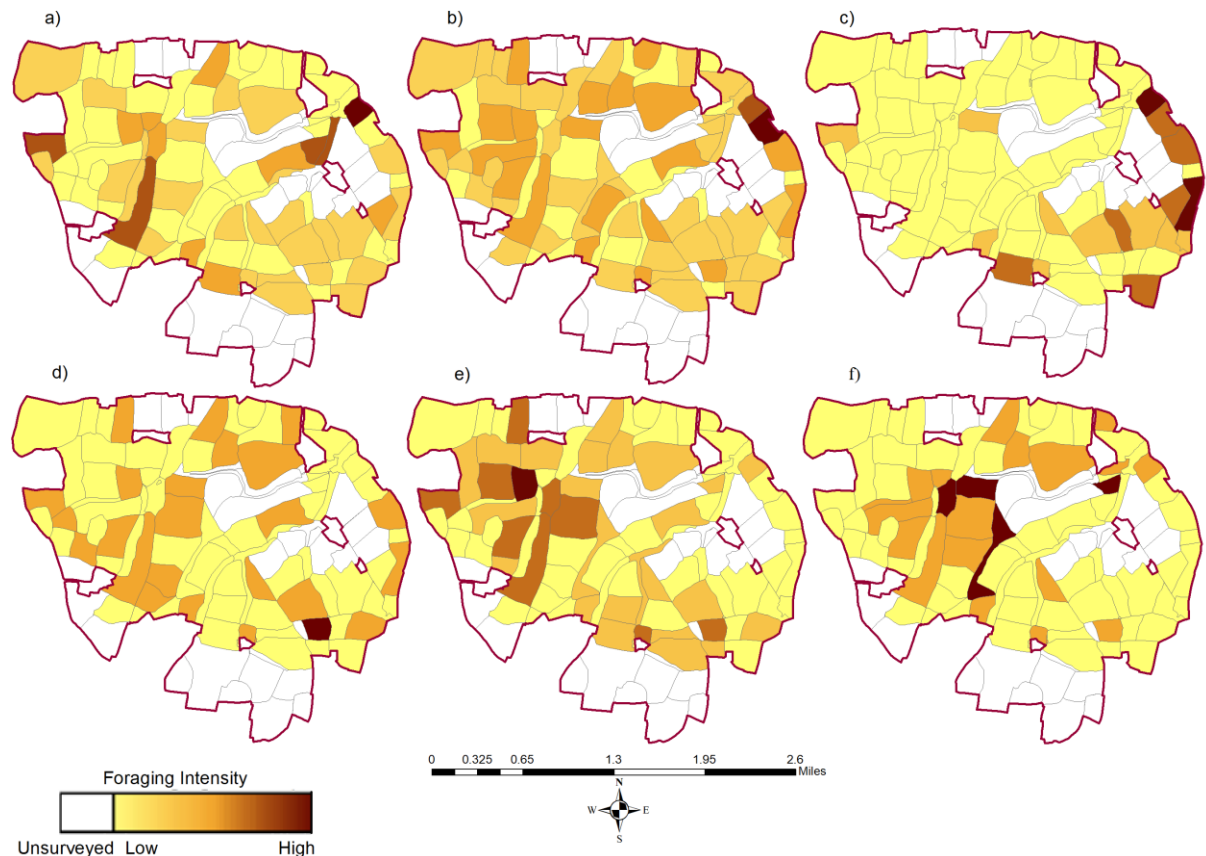
Figure 5: Individual foraging intensity maps for each of the six large herbivore study species. a) Longhorn cattle, b) Fallow deer, c) Exmoor pony, d) Roe deer, e) Red deer, f) Tamworth pig. (Intensity scale relative to each species).

3.4. Foraging site selection

When Individual field sites were groups by habitat type, analysis showed Longhorn cattle to have a significant preference for three out of four grassland fields with site 5 being the most preferred area in the southern block ($X^2 = 5067.82$, df = 18, p≤0.001: figure 6a), all grassland and permanent pasture sites were positively selected. Every other site was negatively selected except for site 9 ($X^2 = 235.98$, df = 18, p≤0.001: figure 6a), an area of mixed grassland and scrub. Fallow deer also displayed a significant preference for foraging in site 5 ($X^2 = 749.46$,

df = 18, p≤0.001: figure 6b), however unlike the Longhorns this was the only grassland area to be positively selected. Scrub habitat in site 10 (X^2 = 97.21, df = 18, p≤0.001: figure 6b) and habitat defined as being mixed scrub and woodland also being preferred sites (X^2 = 114.44, df = 18, p≤0.001: figure 6b), while every habitat type had at least one site to be negatively selected. Exmoor ponies followed a similar pattern to Longhorn cattle albeit foraging at a much lower intensity with grasslands sites being the only area significantly preferred, once again including site 5 (X^2 = 423.5, df = 18, p≤0.001: figure 5c), but also site 4 X^2 = 578.57, df = 18, p≤0.001: figure 6c). Roe deer followed the opposite trend, negatively selecting all grassland habitats while significantly preferring denser vegetated areas such as the mixed scrub and woodland site 15 (X^2 = 105.83, df = 18, p≤0.001: figure 6d). Red deer were the most generalist of all species and the only species to significantly prefer a woodland habitat (X^2 = 33.76, df = 18, p = 0.01: figure 6e), while Tamworth pigs also showed generalist tendencies by positively selecting a site of each habitat classification, however none were significant (figure 6f).
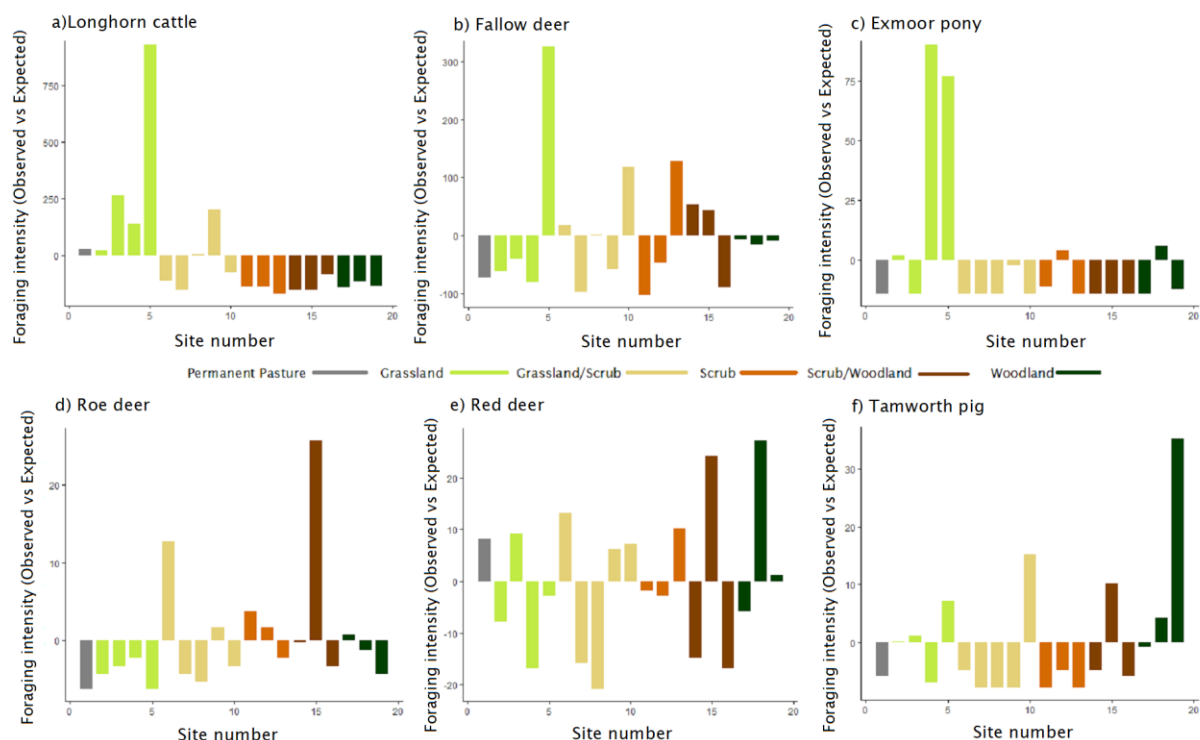

Figure 6: Chi-squared goodness of fit results for foraging intensity across each camera trapped field site displayed as residual frequency of observed vs expected value. Sites classified by habitat

3.5. Temporal site selection

When considering the year field sites came out of production, results found that Longhorn cattle had clear preferences between years. Fields left to nature in 2004 (X^2 = 21.62, df = 7, p = <0.01: figure 7a), 2005 (X^2 = 26.99, df = 7, p≤0.001: figure 7a) and 2006 (x2 = 34.31, df =

7, p≤0.001: figure 7a) were significantly foraged with greater intensity than fields from 2000 (X^2 = 134.35, df = 7, p≤0.001: figure 6a) and woodland (X^2 = 97.56, df = 7, p≤0.001: figure 7a) areas which were negatively selected. These results displaying a preference for areas of the site that have had less time to establish themselves. A pattern is less obvious for Fallow deer, which displayed a significant preference for 2005 (X^2 = 60.73, df = 7, p≤0.001: figure 7b) and 2000 (X^2 = 28.64, df = 7, p≤0.001: figure 7b) field sites while negatively selecting areas of permanent pasture (X^2 = 24.84, df = 7, p = <0.01: figure 7b), as well as fields removed in 2004 (X^2 = 22.67, df = 7, p = <0.01: figure 7b) and 2002 (X^2 = 16.75, df = 7, p = 0.02: figure 7b). Like the other primary grazer, the Longhorn cattle, Exmoor ponies foraged significantly more intensively on fields removed in 2006 (X^2 = 55.12, df = 7, p = <0.001: figure 7c). Both roe deer (X^2 = 81.24, df = 7, p≤0.001: figure 7d) and Red deer (X^2 = 20.32, df = 7, p = <0.01: figure 7e) displayed a higher foraging rates in fields removed in 2000 with analysis revealing no statistical significance for any other group. This was the same for Tamworth pigs, which displayed increased foraging intensity in woodland areas (X^2 = 18.06, df = 7, p = 0.02: figure 7f) but no significant positive or negative selection elsewhere.
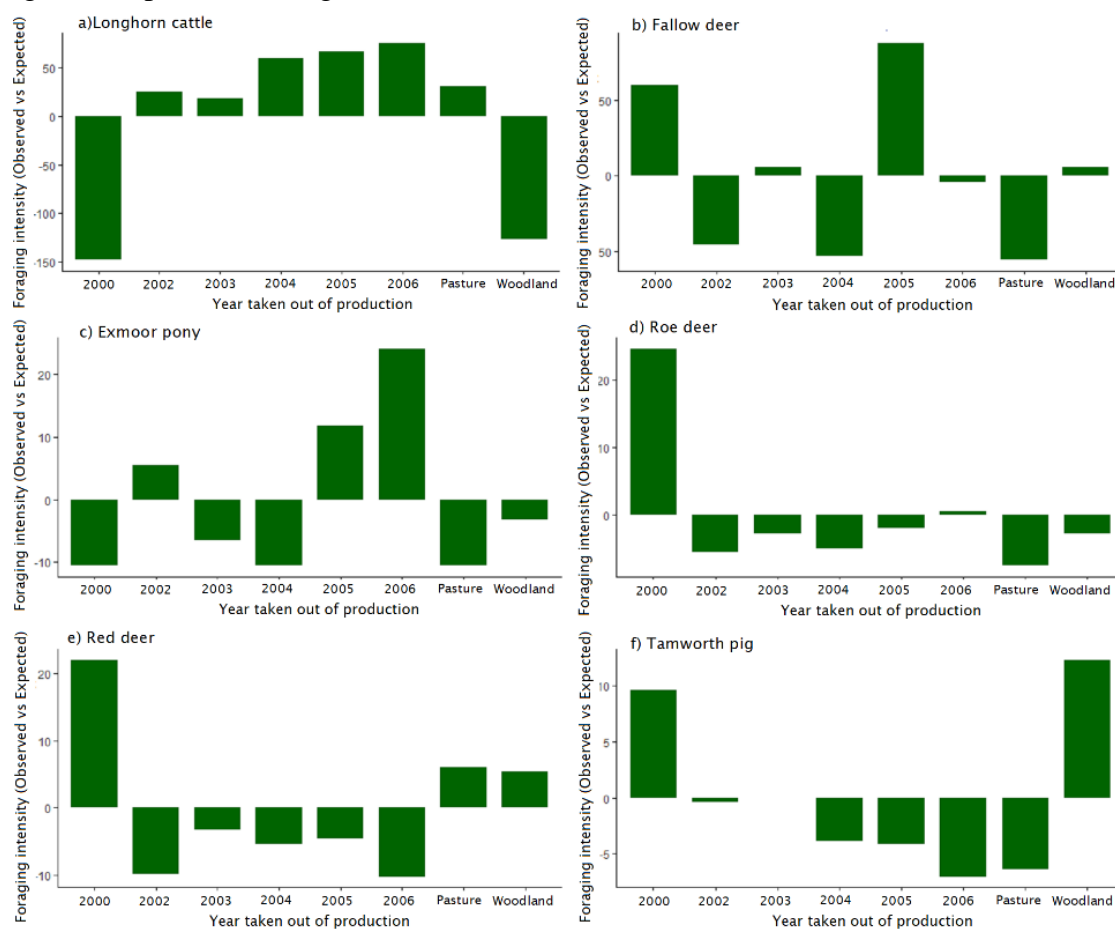

Figure 7: Chi-squared goodness of fit results for foraging intensity vs year taken out of production, displayed as residual frequency of observed vs expected value.

3.6. Floral diversity

Analysis from the Pearsons correlation showed no significant relationship between foraging intensity and floral diversity for five out of the six study species (figure 8). The only statistically significant result was a negative correlation displayed by Longhorn cattle (r=-0.4581, n=17, p=0.0485: figure 8a) with foraging intensity, reducing as floral diversity increased.
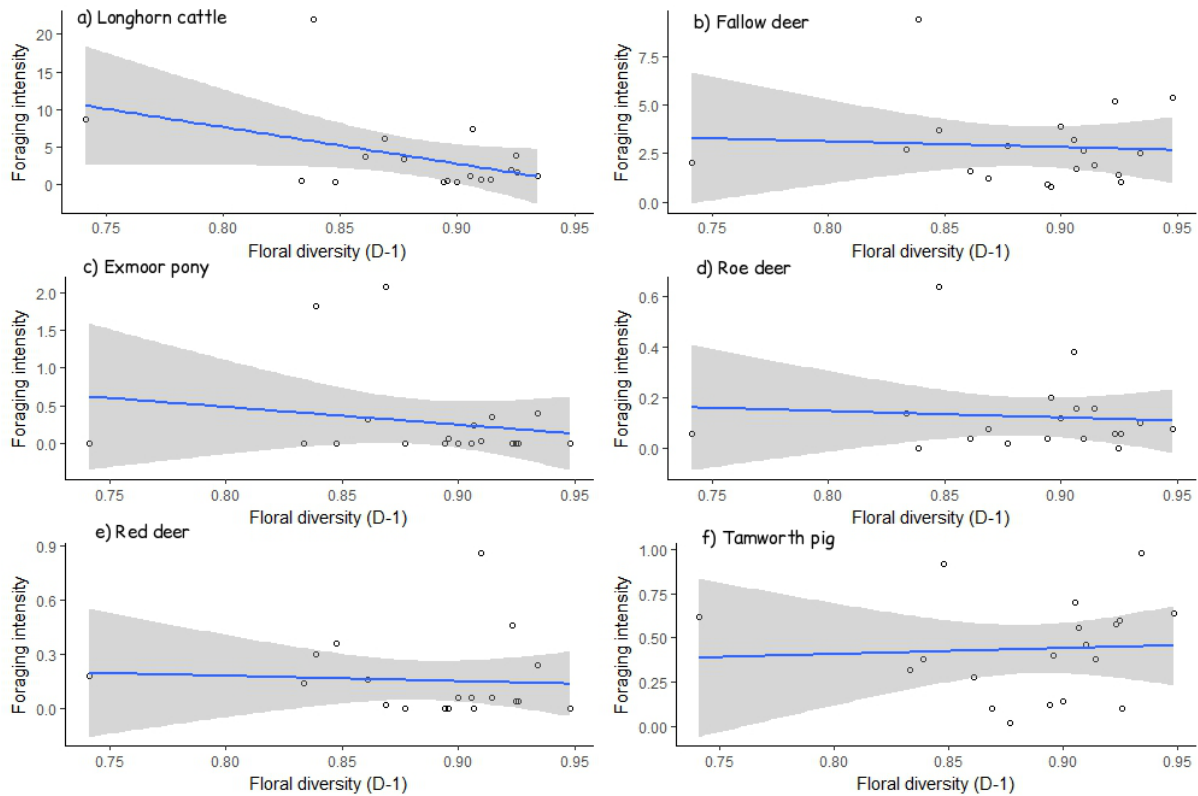

Figure 8: Scatter plot-displaying relationship between foraging intensity and floral diversity for six study species at camera-trapped sites.

Considering herbivore habitat selection, Longhorn cattle displayed a significant positive correlation with *lolium perenne* abundance (r=0.466, n=17, p=0.044; figure 9) and a significant negative correlation with *Rubus fruticosus* (r=0.472, n=17, p=0.04; figure 9). No other species returned a significant result; however, Fallow deer and Exmoor ponies both positively selected areas with increased *lolium perenne* abundance, and negatively selected *Rubus fruticosus,* while this trend was reversed for Roe deer and Red deer. Tamworth pigs were the only study species to positively select both.
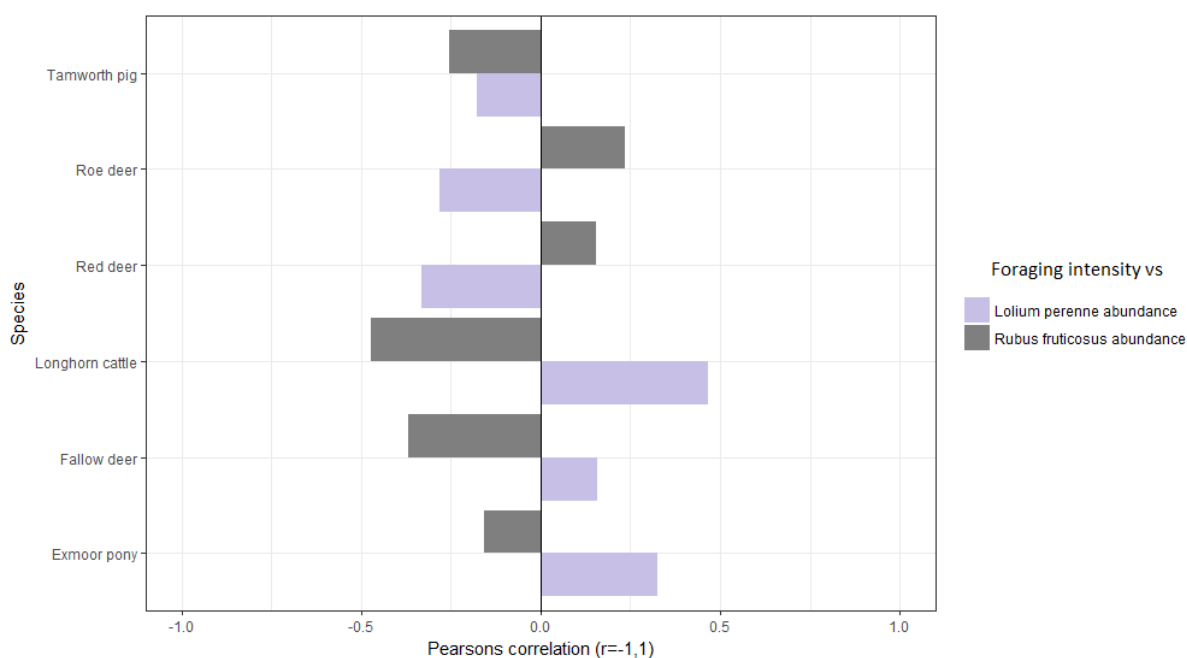
Figure 9: Pearsons correlation score for each of the six large herbivores comparing foraging intensity with lolium perenne and rubus fruticosus abundance

3.7. Structural diversity

Analysis of LiDAR data (figure 10) showed a significant negative correlation between Longhorn cattle foraging intensity and habitat heterogeneity (r=-0.6016, n=14, p=0.0137). The opposite relationship occurred for roe deer (r=0.6159, n=14, p=0.0110), where a significant positive correlation was observed, with foraging increasing as heterogeneity increases. Exmoor ponies (r=-0.4214, n=14, p=0.104) had a negative correlation however this was not significant. Fallow deer (r=-0.0818, n=14, p=0.7633), Tamworth pigs (r=-0.1158, n=14, p=0.6694) and Red deer (r=0.1661, n=14, p=0.5387) all had correlations close to zero indicating no relationship exists.

Analysis of mean vegetation height (figure 10) revealed no significant relationship for any species, although similar trends for Fallow deer (r=-0.0654, n=14, p=0.8098), Red deer (r=0.1218, n=14, p=0.6532), and Exmoor ponies (r=-0.4211, n=14, p=0.1042) compared to their heterogeneity results can be seen. The Pearsons value of roe deer (r=0.2492, n=14, p=0.352) demonstrated a positive correlation but it is non-significant. Tamworth pigs had a positive correlation compared to a negative relationship with heterogeneity (r=0.0914, n=14, p=0.7362), however neither was significant, while Longhorns displayed the strongest correlation (r=-0.4938, n=14, p=0.0518) with increased height resulting in lower foraging intensity.
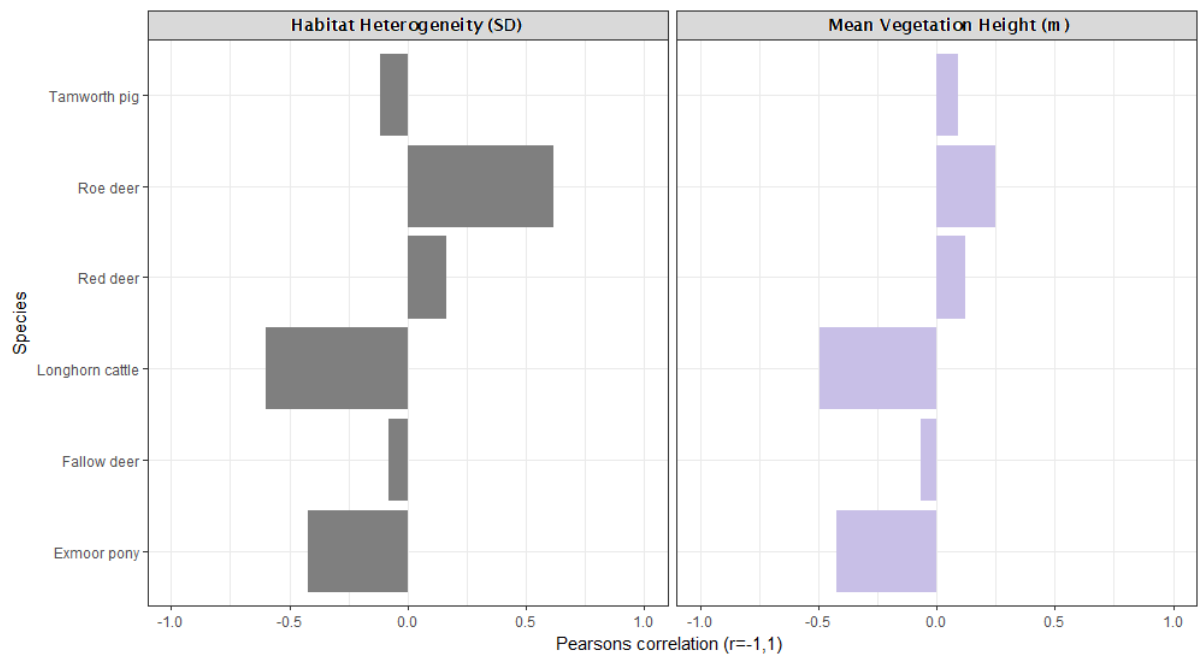
Figure 10: Pearsons correlation score for each of the six large herbivores comparing foraging intensity with Habitat Heterogeneity (SD) and Mean Vegetation Height (m)

4. Discussion

The methodology in this study has allowed the collection and analysis of data to ascertain the movement patterns and foraging intensity rates of six large herbivore species and begin to discuss the drivers and impacts of these results, while making suggestions for how Knepp can address these results in a rewilding context. The non-uniform spatial patterns of foraging and how this is linked to species behavioural traits in line with other literature will be discussed, as well as beginning to assess the environmental factors within the site itself that could be driving these results in the context of vegetation diversity, and structure. The paucity of literature on herbivore-plant interactions within the context rewilding and the impact this cyclic relationship has on the wider landscape makes this an important gap in which this study will fit.

4.1. Foraging intensity

Disparity in foraging intensity was found between species; this was an expected outcome and means the first hypothesis can be accepted. An explanation can be found when looking at the abundance of each species within the site; intensity followed the same order as population size with Fallow deer displaying the highest rate of intensity and Tamworth pigs the lowest. The only exception to this are Red deer, which have a higher foraging intensity than Exmoor ponies despite being less numerous. This is counter intuitive to what was expected, as Red deer tend to prefer habitat with more cover than Exmoor ponies, thus making them less detectable. One reason could be the group behaviour of each species and flight responses. Exmoor ponies on site had an average of 4 individuals per camera trap recording in both winter and summer and were observed on transects to be present in one group, while occupying the same sites for long periods. This contrasts with Red deer which recorded 2.6 individuals per recording in winter and 1.4 in summer. This implies that Red deer move more frequently and at lower densities than Exmoor ponies, but triggered cameras at a greater frequency and over wider range of the site, accounting for a higher overall foraging intensity score. While by moving as one group, Exmoor ponies triggered cameras at a lower rate, limiting the overall intensity score but condensing it to a smaller area.

Both Red deer and Exmoor ponies had a foraging intensity score less than one. These two species fulfil key roles within the system, Red deer through grazing, browsing, trampling, nutrient cycling, and seed dispersal as well as being the only species to regularly inhabit riparian environments (Bugalho, Milne, & Racey., 2001; Fløjgaard *et al.,* 2017). Their density, spatial distribution and feeding preferences are therefore key to their ecosystem

function (Gill & Beardall., 2001; Fløjgaard *et al.,* 2017). However, this effect requires herbivores at relatively high densities, which is not currently the case at Knepp, limiting these engineering effects (Fløjgaard *et al.,* 2017). Exmoor ponies can forage on tougher grasses than any other herbivore on site, and are adept at foraging with greater sensitivity, meaning they can forage on a different group of plants to most other species on site, helping to stimulate biodiversity other areas of the site (Putman *et al.,* 1987).

4.2. Spatial intensity and site selection

The lack of uniformity in the spatial foraging patterns across Knepp is coherent with the second hypothesis. The main reason for reintroducing the mix of herbivores that are present on site is the functional niches they each fulfil, whether through grazing or browsing, herd behaviours, body size, home range size or more intricately the individual food plants and predator avoidance strategies of each species (Vera, 2009; Helmer *et al.,* 2015). The mixed spatial patterns create and then maintain a diverse selection of habitat, in a cyclic relationship between foraging pressure and vegetation development (Hodder *et al.,* 2005). In the data, there is also a disparity between intensity of foraging among the habitat classification, suggesting more than just the presence of a grassland or increased scrub is driving herbivores to each site. Furthermore, the overlap of favoured areas for Longhorn cattle, Fallow deer and Exmoor ponies, is also unexpected, as the three-aforementioned species all have different grazing preferences yet have all positively selected the same site (Hosten, Whitridge, & Broyles, 2007).

The formation of pressure points will be a critical factor in how the landscape develops. Studies suggest that these heavily foraged areas will not be allowed to develop from a homogeneous grassland (Hester, 1996; Olff & Richie, 1998; Sansom, 1999), while the areas of the site with lower intensity will allow for scrubby species and young trees to establish themselves over time (Smit *et al.,* 2015). This study is too short in time to make firm predictions, however if these patterns continue the landscape would likely develop into something akin to a wood pasture system, with heavily grazed open areas interspersed with isolated tree's, already established mixed aged woodland, coupled with occasional scrub development.

The three species of deer displayed a wide spatial distribution, which is expected due to their adaptability, with all three preferring a mosaic pattern of open areas for feeding, interspersed with scrub, forest or woodland for cover and browse, meaning more of the site is favourable to them (Harris & Yaden, 2008). The relatively low foraging intensity and densities of the largest browser on site, the Red deer, means browsing pressure and bark stripping above 1.8m would

be expected rare at Knepp (Mayle, 1999). Similarly, Red deer browsing helps to control dense shrubs and brambles, lower intensity of foraging therefore increases the chance of scrub development (Clutton-Brock, Coulson, & Milner., 2004), although this is countered to an extent by high Fallow deer intensity which browse at similar heights.

Longhorn cattle and Exmoor ponies that were almost exclusively observed grazing, displayed restricted distribution. The intensity drop off between the favoured grassland sites and the fields that separated them would indicate that both species have established a few 'home' fields within the site that their grazing regime moves between, with the intermittent areas only used lightly to forage. Despite the Longhorn cattle's relatively large population size, in terms of foraging they are only affecting the vegetation at a small proportion of the site albeit at a very high rate. The same is true for Exmoor ponies, although their lower population and herd behaviour might be a contributing factor in limiting their distribution to a few fields near one another (Gates, 1977).

4.3. Temporal site selection

When fields were released to nature was shown not to be a reliable gauge of driving foraging behaviour for most species, a rejection of the third hypothesis. The expectation was fields that have longer to develop structural complexity will be more akin to a mix of scrub or young woodland while the last areas to be released would be more homogenous and dominated by grasses creating sequential affects as years progress. The absence of this pattern could be related to the lack of time between their releases not allowing enough time for habitats to develop in isolation. Similarly, the unexpected outcomes could indicate the presence of false positive and/or false negative statistical values. Despite this, the clear preference for woodland and fields from 2000 for Roe deer, Red deer and Tamworth pig does fit aspects of this theory as 2000 fields should be the most structurally complex. It also relates to what we know about each of these species preferred habitats and feeding preferences, with Roe deer and Red deer enjoying woody browse, shrubs and bramble (Harris & Yalden, 2008) with the Tamworth pig's adept at foraging both in woodland and pasture (Schley & Roper, 2003). For the rest of the species these relationships were less clear, indicating while the earliest fields and woodland areas have developed into structurally heterogeneous habitats, fields between 2003-2006 offer far more variety than a simple linear annual rate of successional development. The variety of development rates is also symptomatic of herbivore driven change within a landscape (Olff & Richie, 1998), therefore the further time moves from the initial reintroduction of herbivores,

the less the time period of habitat development pre-herbivore reintroduction will be representative of the habitats aesthetics.

4.4. Floral diversity

The lack of relationship displayed by floral diversity and foraging intensity, highlights that a biodiversity rich landscape is not necessarily a driver for forage selection and a rejection of the fourth hypothesis. The only species where a significant relationship was observed was Longhorn cattle, where a negative correlation occurred. This can be further explained by the positive trend displayed by increased *lolium perenne* abundance. This emphasises that habitat dominated by grassland is favourable to Longhorn cattle, although as we have seen from previous results this can vary between grassland sites, so we would need to look deeper into the subtle nuances of favoured food plants and anthropogenic influences to fully explain this relationship. One of the drivers for Longhorn reintroduction over other cattle proxies was their increased prevalence as a browser however this is not evidenced. Longhorn cattle not only positively select grassland habitats but also display reduced foraging the more prevalent bramble and browse becomes. Browsing could occur with increased frequency as habitats develop, and grassland becomes limited to a few isolated patches forcing Longhorn cattle to utilise these areas. Conversely, the low rates of floral diversity in areas preferred by Longhorn cattle, could be caused by the intense grazing from the Longhorn cattle creating a homogenisation of the habitat, meaning to an extent they are both being driven by and driving floral diversity rates.

While no significant correlation could be found in other species, trends were apparent and in line with previous analyses. Red deer and Roe deer displayed a positive relationship with fields where preferred food plant *rubus fruticosus* is more prevalent. While Exmoor pony and Fallow deer had a positive relationship with increased *lolium perenne* abundance which confirms what has been discussed thus far with field selection if not overall habitat selection the case of Fallow deer (Harris & Yalden, 2008). If this one-year snapshot were repeated over a number of years as habitat developed further, it would be expected that these relationships would become more pronounced.

Foraging intensity was not influenced by floral diversity in this study; however, as mentioned floral diversity is influenced by forage intensity (Olff & Richie, 1998). This emphasises the cyclic relationship between herbivore-plant interactions and highlights the importance of herbivory to support and manipulate floral diversity in a landscape. If this study were repeated,

it would be pertinent to assess the changing nature of floral diversity and the associated forage intensity from both sides of this relationship, to deduce in a rewilding context how under grazed and over grazed areas of the site change over time.

4.5. Structural diversity

Increased structural heterogeneity was shown to be a significant factor in Roe deer foraging behaviour. As the most elusive and smallest of the three deer species at Knepp, the trends being seen whereby roe deer are favouring the more sheltered and structurally diverse habitats fit their description as predominately a low height browsing animal that shy's away from human activity and potential threats (Bonnot *et al.,* 2014). They currently have a very small population size within the southern block; although it's actual number is unknown with recordings in this study limited to individual animals and infrequent sightings across much of the site. Their preference for more closed habitats means herbivore movement data could be under representing their population size due to lack of visual penetration. The negative relationship for Longhorn cattle further emphasised their presence as an open habitat-grazing animal on the project, which scarcely moves into denser vegetation except for periods of rest. The absence of a relationship for Tamworth pigs, Red deer and Fallow deer supports their role as mixed feeders, present in both more structurally homogenous grassland environments as well as denser mixed vegetation, intensity varying slightly between species. These results accept the fifth hypothesis.

Mean vegetation height was found to have no significant impact for any species, while this is surprising, the absence of woodland areas in this analysis condenses the difference between height values across the study fields which may have reduced the chance of correlation being seen. The Longhorn cattle and Exmoor ponies had a negative relationship with height, explained by their prevalence in short grassland habitats, while all other species had a correlation value near zero. For Roe deer, this indicates that the heterogeneity of a habitat is more important than height when selecting foraging sites. This result could mean as more of the site develops Roe deer abundance will increase as favourable mosaics within fields establish, enabling a greater carrying capacity for this species.

4.6. Landscape Impacts and Rewilding

For the most part the results here show each species to be fulfilling a different niche, despite overlaps in favoured fields as discussed earlier. Analysis clearly separates each species along a spectrum of grazer to browser although the impact of each species is largely dependent on population size. With each species fulfilling a niche, a mosaic of habitats was expected to

develop and indeed that is what is currently being seen at Knepp, with each field developing very differently, regardless of when it was released from production.

This study would indicate large herbivores are responsible for this structural diversity. On current trends, this data and secondary literature would appear to suggest Knepp is developing towards something akin to a wood pasture system with areas being kept open by intensive grazing, and reduced pressure in other areas encouraging scrub encroachment providing a refuge for isolated saplings (Vera, 2000; Vera, 2009). One of the main drivers in this development will be the population size of each large herbivore on site. Currently that is a management decision, however in the absence of predation, and drought as well as presence of control for disease outbreaks, adding a degree of randomness to determining the annual population size would increase the projects applicability within the context of rewilding, while also altering the timeline of succession within each field at Knepp. The overall result may well end up being the same but fluctuations in each herbivore species population could encourage this to happen at varying speeds across the site and create a more diverse system along the way.

The absence of predation is likely to be common in most sites within the UK that follow naturalistic grazing principles, therefore this research is applicable to any site where free roaming herbivore are present regardless of scale. Where predation is present alternative factors such as the landscape of fear as well as natural population variations would be key to understanding the extent to which predator-prey relationships could influence the results seen in this study.

Much of this study has been analysed and discussed in the context of large herbivore foraging being influenced by factors within their habitat, however, every hypothesis posed here could easily be reversed to look at how factors of habitat, such as diversity and development are driven by large herbivore foraging. This relationship as previously mentioned is very much cyclic, with habitat selection being both driven by and driving landscape scale change, whether that be reinforcing the status quo or simply influencing the rate of succession. Knepp presents an ideal baseline to study such interactions, and it is hoped that this study can form a baseline for teasing out some of the answers by providing the first block in what needs to be a multi-year study if the predictions from this data can lead to solid conclusions.

4.7. Future research

This study should be taken as a baseline for herbivore foraging behaviour both in terms of intensity and spatially, however to fully understand the complexity of relationships a multiyear study needs to be conducted.

More data looking into individual food plants of herbivore species could allow us to solidify the reasoning for each herbivore occupying specific fields, instead of at a habitat scale. The increased focus on vegetation could allow the questions posed here to be looked at from the point of view of vegetation development as opposed to herbivore movement.

An important step will also be to look at anthropogenic influences on site selection and the relationship this may have on habitat development, particularly regarding seasonality as seasonal foraging preferences may be altered by increased visitation pressure in the summer months.

Finally, a similar study conducted at a rewilding site in a comparable environment where predation is present, would be important step to deduce the level of impact predator-prey relationships have on herbivore movement, and subsequently foraging, and the knock-on effect within a landscape because of these trophic interactions.

5. Conclusion

In conclusion, the six large herbivores at Knepp displayed differences in forage selection and intensity, with clear pressure points and species overlaps present. Both population number and individual species traits such as herd dynamics dictated intensity of foraging, and therefore impact. Time since agricultural abandonment was not a reliable driver for these trends, while floral diversity negatively correlated with Longhorn cattle foraging intensity and found no evidence of being a driver for any other species. Vegetation structure in the measure of standard deviation was positively correlated to Roe deer foraging intensity and negatively to Longhorn cattle, once again, it was not a significant driver in foraging intensity for any other species. Vegetation height did not significantly correlate with any species foraging intensity. The results have shown herbivore foraging behaviour to be mostly in line with what we know about feeding habits, with Longhorn cattle and Exmoor pony being open habitat grazers. Fallow deer being a mixed feeder but more prominent in open habitats than both Roe deer and Red deer which occupy largely scrub and closed habitats although not exclusively. Tamworth pigs were shown to forage in both woodland and grassland pasture.

The impact of these behaviours based on current populations would be a reinforcing of the mixed mosaic habitat present within the southern block, with grassland areas being firmly established while scrub and subsequently isolated tree's and potentially young woodland increases in areas with less pressure. The result being something like a wood pasture system as Vera (2000) described. Introducing randomness to herbivore population numbers to provide a proxy for natural variations should be encouraged.

In the context of rewilding, this project has displayed that free roaming large herbivore foraging is a key driver in habitat creation, with a mixed suite of herbivores being important to creating the previously described mosaic that has the potential to be biologically diverse. Similar studies should be encouraged on large sites that have the potential to support carnivores to add the landscape of fear as a factor varying forage behaviour. It will also be critical to focus on the reverse of the relationship studied here and looking more specifically, at how vegetation is influenced, particularly by foraging intensity and population size over an extended period.

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Appendix 1

Appendix Table 1: Camera trap output displaying mean number of animals per recording and the number of camera triggers per species for each study period

Camera trap	Summer		Winter	
Species	Number of individuals per trigger	Number of triggers	Number of individuals per trigger	Number of triggers
Longhorn cattle	7.9	322	3.4	160
Fallow deer	1.96	911	2.68	254
Exmoor pony	4	51	3.95	24
Roe deer	1.02	69	1.27	22
Red deer	1.46	167	2.64	39
Tamworth pig	2.35	60	1.42	14

Appendix 2
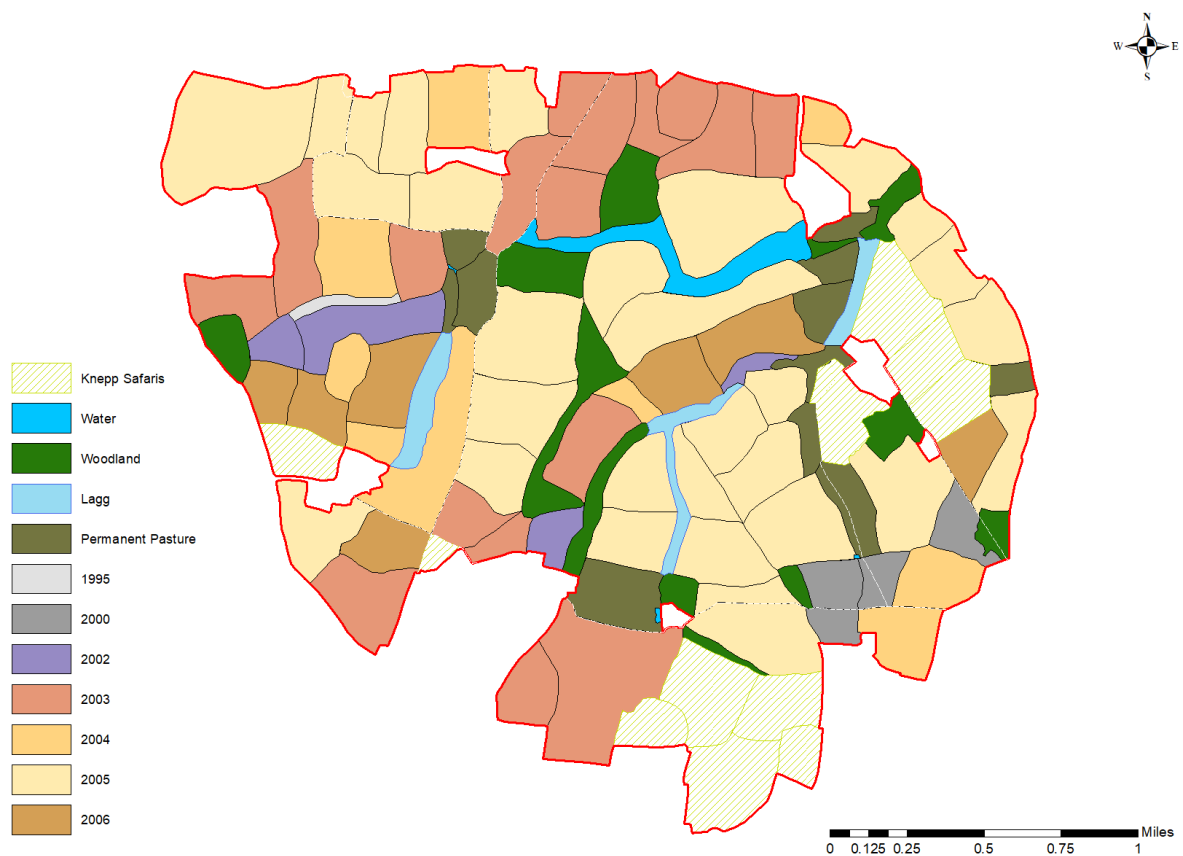
Appendix Figure 1: Map of Knepp's southern block, displaying the year fields were taken out of production and land classification

Appendix 3
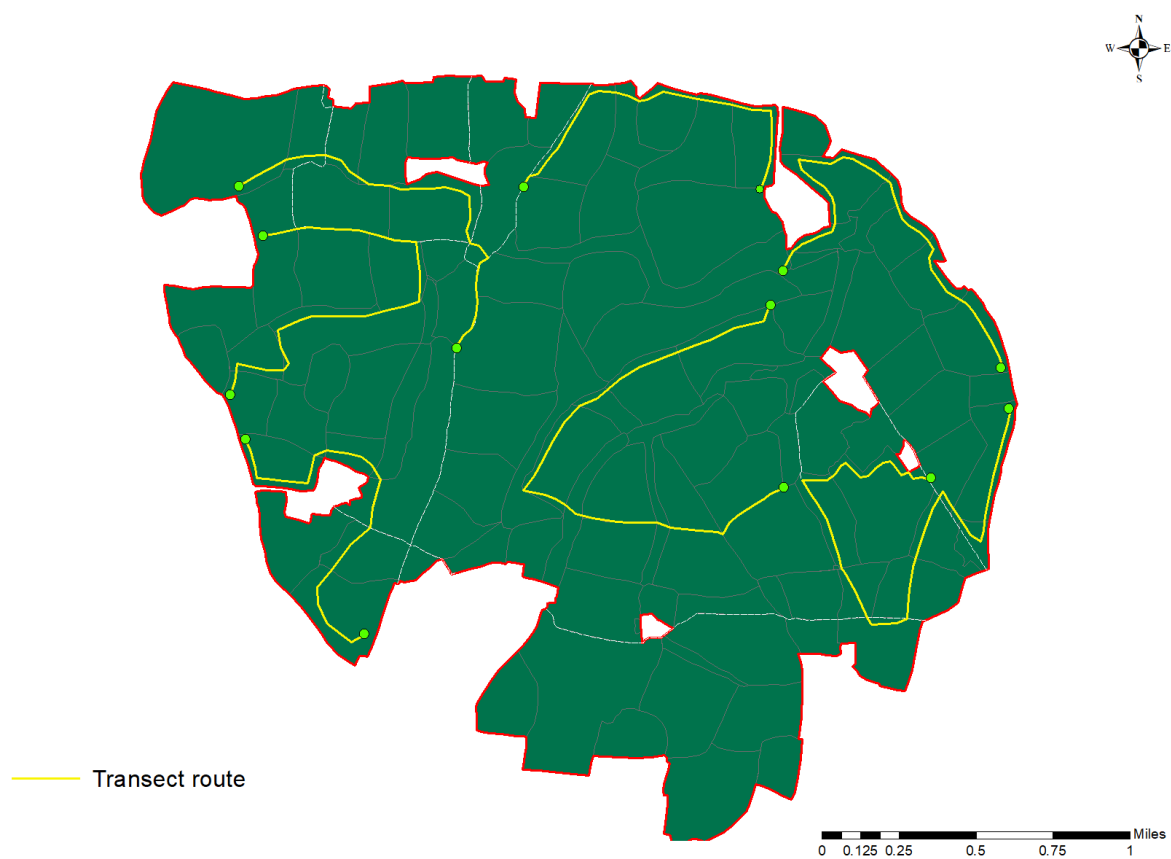
Appendix Figure 2: Map of transect routes undertaken in the southern block of Knepp