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How vegetational succession in relation to rewilding influences small mammal communities at Knepp Castle Estate.

By Betsy Gorman

Candidate number: 177335

Supervisor: Dr Christopher Sandom

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Abstract

Small mammals represent a useful biological indicator regarding vegetation development and succession due to their responses to both micro and macro changes in the environment. Such changes include shelter availability as plant communities develop from short grasses to scrub or closed canopy. This can affect small mammal diversity and abundance, as different species find niches within these habitats, going on to effect predator numbers and further vegetation development. As such, rewilding, the passive or active restoration of previous landscapes, represents an untested area for the effects of vegetation change on these organisms, with small mammals acting as indicators into the functionality of emerging ecosystems. Whilst time since vegetation disturbance has been explored, the effect of agricultural cessation on plant development and small mammal occurrence remains un-investigated in a UK setting, prior to this study.

Small mammal abundance and diversity was assessed in relation to vegetational changes and time since rewilding within the Southern block of Knepp Castle Estate, Horsham, UK. Fifteen fields, taken out of agricultural development between the years 2002 and 2005, in addition to a control (permanent pasture), were surveyed for vegetational height, structural diversity, and habitat type, alongside small mammal surveying. Analysis of small mammal abundance against the standard deviation of vegetational height i.e. within field habitat heterogeneity, showed a significant association between small mammals and the level of scrub/ tall vegetation present. This concurs with previous findings that structural complexity is a large predictor of patterns of small mammal occurrence compared to temporal factors. In contrast, no significant association was found between small mammal abundance or diversity and year of agricultural abandonment. This is again consistent with previous research into European and Australian habitats, where time since disturbance had limited influence on small mammal colonisation.

Comparison between this data and previous years showed a difference between small mammal diversity, with 2016 showing a significantly higher bank vole population at 55 individuals, compared to 2005 (27) and 2016 (0). These results, taken together, highlight a potential emergence of typical multi-annual fluctuations, with habitat heterogeneity predicting small mammal occurrence at field levels. The exact influences of the small mammal population changes remains unknown, however Knepp provides the opportunity for longer-term analysis into these factors, accounting for the changing landscape typical of a rewilding site.

Key words: small mammal, rewilding, vegetation, succession, passive, trophic, predator-prey, agriculture

1. Introduction

Future challenges in conservation such as a growing population and global climate change (Dickinson., *et al*. 2015) require reassessment of historic tactics in biodiversity conservation. In the past decade, analysis of global biodiversity trends indicates steady declines whilst threats such as resource consumption and reduction in wild habitats are increasing (Butchart., *et al*. 2010). This highlights a challenge in addressing global food shortages and overpopulation whilst reducing biodiversity loss; however, it also presents opportunities for novel conservation tactics that integrate human welfare and ecosystem restoration. One such method for biodiversity conservation lies in rewilding, a process which aims to restore degraded landscapes to self-sustaining, functional ecosystems that require minimal to no human management, either through land abandonment or animal reintroductions (Rewilding Europe. no date; Sandom., *et al*. 2013). Rewilding schemes, whilst non-goal oriented and so potentially less predictable, aim to reinstate processes that allow ecosystems to thrive. Classically, this would involve reintroduction of ecosystem engineers or apex predators in order to influence lower trophic levels, so called trophic rewilding (Beschta., & Ripple. 2008; Arts., *et al*. 2016; Svenning., *et al*. 2016;Wolf., & Ripple. 2018). Examples include wolf (*Canis lupus*) reintroductions in Yellowstone National Park (Beschta., & Ripple. 2008) and natural recolonizations of lynx (*Lynx lynx*) and wolves (*C.lupus*) between Scandinavian countries and Germany, Denmark and the Netherlands in Europe (Louvrier., *et al*. 2017). This has been attributed to an array of protective legislation that has enabled co-existence of humans and predators, as well as shifts in attitudes regarding their perceived dangers and ecological worth (Chapron., *et al*. 2014). For example, the largest lynx population currently recorded resides in the Carpathians where protective legislation is enforced (Deinet., *et al*. 2013). Influences of these top predators include trophic cascades (indirect interactions of predators on prey that can enhance survival of species at lower trophic levels through prey control; Silliman., & Angelini. 2012) or predator-prey oscillations that change vegetational development by reducing herbivore numbers. However, another avenue for restoring ecologically damaged landscapes lies in passive rewilding: the cessation of human management or intervention to allow natural processes such as vegetational succession and disturbance to take place.

Natural passive rewilding experiments are becoming commonplace in mainland Europe, with agricultural abandonment giving way to revegetation and habitat change (Van der Zanden, *et al*. 2017). The response of organisms to these vegetational changes has shown to be influenced by both temporal and spatial factors largely associated with the process of succession. Models proposed by Connell and Slatyer (1977) detail the varying interactions of primary and later stage colonising plants in the form of facilitation, enhancement, and inhibition and their roles in shaping these new habitats. As agricultural abandonment and passive rewilding is, by definition, devoid of human intervention, the successional stages and final community is unpredictable as certain succession driving plants are not encouraged or removed (Connell., & Slatyer. 1977). For this reason, agricultural abandonment can be both beneficial and detrimental to faunal species which rely on habitats at varying transitional stages or vegetational densities, being largely dependent on factors driving habitat formation and vegetational heterogeneity (Plieninger., *et al*. 2014). For example, species will colonise areas at different times based on habitat preference and inter-specific interactions. It is therefore important to study emerging rewilding projects and areas of agricultural cessation to monitor changing vegetation and animal diversity/abundance.

Knepp Castle Estate represents a UK equivalent to the rewilding projects that are occurring in mainland European countries, as it employs both passive and active rewilding techniques to restore the landscape. Originally an arable farm, the estate has reintroduced several large herbivore species including long-horn cattle (*Bos tauros*), Exmoor ponies (*Equus ferus caballus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), and Tamworth pigs (*Sus scrofa domesticus*) - the aim being to reinstate ecological processes and create a biodiverse self-sustaining ecosystem (Knepp.co.uk. no date). The estate was split into three ‘blocks’; Northern, Middle, and Southern. Each of these represent different habitats due to their varying baselines. For example, the Northern block was previously used as permanent pasture and as such thorny scrub was slow to establish, whereas the focus of the Middle block is regeneration of riparian tree species alongside the River Adur in order to encourage fish species (Kneppestate.co.uk/woodland/. no date). The Southern block, due to the cessation of agriculture at varying times across the site has field level variation in scrub level, which, alongside the aforementioned reintroduction of herbivores, has led to unique habitats. Due to this variation and the changing nature of the site, a baseline study of multiple taxa within Knepp was conducted in 2005 (Greenaway. 2006) including; Mollusca, Odonata, Lepidoptera, amphibians, reptiles, birds, and mammals. This was followed by several monitoring efforts looking at the changing biodiversity and vegetation as the habitat develops.

One such line of study included in the baseline data is the small mammal population within the Southern block of the estate, looking at how varying habitats influence small mammal abundance and diversity (Greenaway. 2006; Briggs. 2016). Small mammals, including mice (*Mus* spp.), shrews (*Soricidae* spp.), and voles (*Microtus* spp.) can act as an indicator species to both the ecosystem health and changes experienced in a habitat due to their responses to vegetation disturbance (Bowland., & Perrin. 1989; Hoffman. 1999; Avenant. 2011). The presence of herbaceous habitats, characteristic of more developed vegetation, is associated with higher small mammal abundance (Stephens., & Anderson. 2014), with heavy grazing being associated with small mammal diversity reduction (Hoffman., & Zeller. 2005). Crucially, for understanding the processes of rewilding, small mammal community composition is influenced by succession. Theories of recolonization patterns of small mammals into a disturbed habitat were described in Fox's (1982) "habitat accommodation model", which suggests that time since disturbance in association with developing successional traits influences species presence due to niche separation (Fox. 1982; Monamy., & Fox. 2010). Habitats at varying successional stages can then potentially provide for a greater diversity of species (Panzacchi., *et al*. 2010). Vegetational changes can therefore have a large impact on small mammal populations, the importance of which lies dually in their role as biological indicators as well as intrinsic influencers of future vegetational development; small mammals have been known to influence vegetational growth through selected seed dispersal, in some cases increasing diversity of plant species by 33% (Howe., & Brown. 2000). The effect of temporal influences on vegetational development and small mammal communities within rewilding sites should therefore be investigated in order to determine ecosystem functionality and justify this conservation approach.

This study details the previously un-investigated effect that year since agricultural cessation has on small mammal communities at Knepp Castle Estate. This was done by vegetational analysis in the form of drone mapping and National Vegetation Classification (NVCs) system alongside a three-week mark-recapture small mammal survey within fields taken out of production between the years 2002 and 2005. This was done in addition to permanent pasture fields which are regularly mown and therefore act as a control against the rewilding process. Alongside this, data provided by Knepp allowed for a longer-term investigation into small mammal community changes.

The study was conducted under the following hypotheses:

H_{a1}: There will be a significant difference between year of agricultural cessation and vegetational structural diversity, with fields taken out of agricultural production in earlier years showing later stages of succession.

H_{a2}: There will be a significant difference between year of agricultural cessation and small mammal abundance and diversity, with spatial heterogeneity influencing small mammal species composition.

H_{a3}: There will be a significant difference between small mammal diversity & small mammal abundance and years of study.

2. Methodology

2.1. Study area

Vegetation and small mammal surveys were conducted within the Southern block of Knepp Castle Estate, a 14.164km^2 rewilding site located south of Horsham, East Sussex, UK. The Southern block of the estate is comprised of fields taken out of agricultural production between the years 2000 and 2006. This is accompanied by fields that were left as permanent pasture, undergoing periodic mowing. Three fields from four time periods (2002-2005) were randomly selected, alongside three permanent pasture fields which acted as a control. Overall 15 fields were surveyed, with 5 fields surveyed each week (figure 1; appendix 1). In total, 75 small mammal trap stations were placed, five for each field.

Fig.1. Study site: the Southern bock of Knepp Castle Estate, Horsham, West Sussex, UK. Studied fields were comprised of 4 fields taken out of agricultural production between the years 2002 and 2005, in addition to a permanent pasture field which acted as a control. These fields were then separated out into 'zones' which were surveyed a week at a time. Central points of each field were determined and used as the centre of the 20m surveying grid. PP; permanent pasture. Exact GPS coordinates and names of the fields are located in appendix 1. Image created in ArcGIS version 10.5.1.

2.2. Small mammal trapping procedure

Longworth traps (nest chamber with shrew hole, 14 X 6.5 X 8.5cm; total length, 25cm) were placed in a 10 X 10m grid, 10m from each other, within the centre of the study field with a 10m buffer zone to account for edge effects (formation shown in figure 2). After 24 hours habituation all traps were baited with a mixture of peanut butter, rolled oats, standard hay bedding, apples and casters. These were then set and left overnight to be checked at 08:00 and 18:00 the following day. This procedure was observed for 6 days, at which point traps were removed and relocated to the proceeding five study sites. In total, the surveying period lasted three weeks split over three zones. Small mammals were marked with a unique fur clipping to allow for identification upon recapture. This prevented re-counting the same individuals for a more accurate analysis of abundance levels. In addition, mass, species, sex, age, length of back foot, length of body, and length of tail were recorded in order to assist in identification. The small mammals were then released at the site of capture, and the traps re-baited.

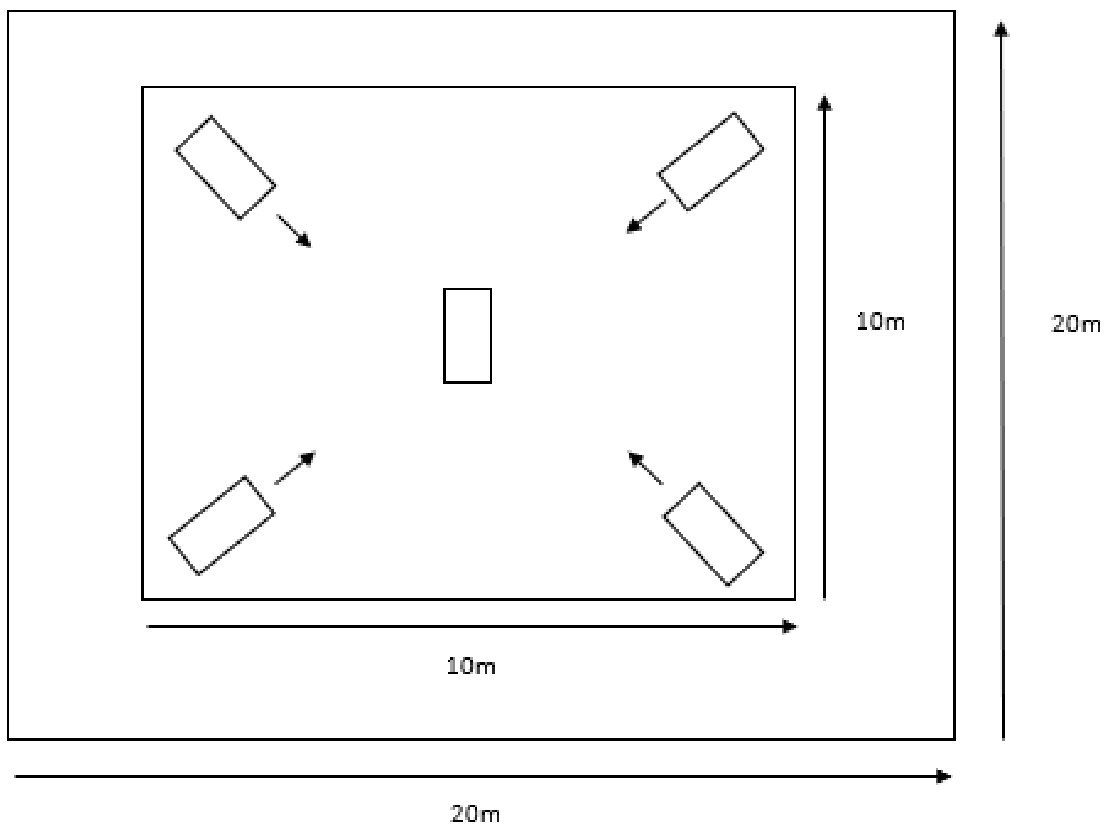

Fig.2. Small mammal trap configuration. Five longworth traps were placed in a central point of each study field, 10m apart, with a 10m buffer zone to reduce edge effects. The entire study area covered 20m which was then mapped using a drone. In total 75 traps were used over the study period, with 5 traps per field.

2.3. Vegetation surveys

Field level NVCs were conducted in each of the study fields during times when small mammal trapping was not occurring to reduce disturbance. Ground layer habitat type was quantified by recording plant richness and abundance using the Domin scale within the 20 X 20m surveying grid where small mammal trapping would take place, using five 1 X 1m quadrats. These were distributed randomly. This was done in association with a 5 X 5m survey of the scrub layer, again within the 20m surveying grid and a 20 X 20m survey of the canopy where trees occurred within the study area. Opportunistic sightings of plants not found in the quadrat grids were also recorded, in order to account for rarer species. NVC data were then analysed using *Modular Analysis of Vegetational Information system* (MAVIS; Centre for Ecology and Hydrology, 2018) to determine most likely habitat classification (table 1).

To determine overall vegetation structure, height, and density, drone analysis was conducted alongside the surveys. A central point of each field corresponding to the small mammal surveying site was taken, with an application of a 20m buffer zone to select the area for mapping. A DJI Mavic Pro drone was flown at 78m, producing an image at 2cm per pixel resolution. Using DroneDeploy software a structure from motion image was generated, which was used to calculate the standard deviation of vegetational height of the study area (table 1).

2.4. Statistical analysis

Statistical analysis was conducted in R studio, version 3.4.4. NVC habitat classification was analysed using *Modular Analysis of Vegetational Information system* (MAVIS; Centre for Ecology and Hydrology. 2018). Data were checked for normality using the Shapiro-Wilk test. Differences in small mammal frequency as well as the diversity of small mammals against year that fields were taken out of agricultural production were analysed using a Kruskal-Wallis test, separately. A two-way ANOVA was used to test the difference in frequency of small mammals between years of study and a non-parametric Kruskal-Wallis test was used to determine difference in diversity of small mammals between years of study. For heterogeneity of vegetation against small mammal frequency, a Lillie test was used to determine normality followed by a parametric linear regression.

3. Results

3.1. Vegetation

In order to analyse the relationship between small mammal communities and vegetation changes post-rewilding, vegetational community structure, standard deviation of vegetational height, and NVC habitat classification were analysed. Determination of habitat type within each field found that the dominant habitat within the Southern block across years was *Lolium perenne repens leys* (table 1) at 60% of surveyed sites. This is a typical lowland grassland and heathland habitat dominated by perennial ryegrass. There was found to be no significant association between the standard deviation of vegetation height and the year of agricultural abandonment ($X^2(4) = 4.8$, $P = 0.31$), suggesting that time allowed for vegetational growth is not the defining factor in successional rate. This is shown by the structural difference between fields of the same year (figure 3A-C).

Table 1. Habitat type of study fields at the ground layer and mean vegetational height.

Year removed from agricultural production	Field name	NVC	Habitat type	Standard deviation of vegetational height (m)
2005	Newbarn 1	OV26	*Epilobium hirsutum* community	0.1743
	Newbarn 3	MG7A	*Lolium perenne repens* leys	0.1079
	Hampshire buildings big	MG7A	*Lolium perenne repens* leys	0.7425
2004	Pound corner	MG7A	*Lolium perenne repens* leys	0.2444
	Brookhouse 6	MG7B	*Lolium perenne-Poa* trivialis leys	0.2557
	Oaklands 3	MG7A	*Lolium perenne repens* leys	0.5884
2003	Hammer	MG7A	*Lolium perenne repens* leys	0.3527
	Brookhouse 11	MG7A	*Lolium perenne repens* leys	2.4907 2.9873
	Honeypools house	MG7A	*Lolium perenne repens* leys	
2002	Keens field	MG11a	*Lolium perenne* subcommunity	0.2142
	Benton's place	OV21	Poa annua-Plantago major community	0.1785 2.2858
	Oaklands 5	MG7A	*Lolium perenne repens* leys	
Permanent pasture	PP	OV21	Poa annua-Plantago major community (Lolium perenne dominate)	0.2698
	Pond field	MG7A	*Lolium perenne repens* leys	0.2090
	Wildflower field	MG9	Holcus lanatus-Deschampsia cespitosa grassland	0.6506

A

B

C

Fig 3. Fields taken out of production in 2002. Analysis found no significant association between year and standard deviation of mean vegetational height. The varied successional stage of the fields suggests multiple factors in determining rate of vegetational growth and therefore suitability for small mammal habitation. A) Keens field; B) Benton’s place, C) Oaklands 5.

3.2. Small mammals

Over the course of the study a total of 23 individual small mammals were captured, spanning three species; Yellow-necked mouse (*Apodemus flavicollis*), wood mouse (*Apodemus sylvaticus*), and field vole (*Microtus agrestis*). In contrast to previous years no bank voles (*Myodes glareolus*) were captured. During the 2018 study period, wood mice were the most abundant species at 14 individuals (table 2), however, where field voles occurred, wood mice numbers reduced in favour of higher species diversity (figure 4B).

Table 2. Numbers of small mammals caught in 75 Longworth traps over a period of 3 weeks, May-June, 2018 in Knepp Castle Estate, West Sussex; Total amount captured is separated by year of agricultural abandonment. Wood mice show the highest occurrence, however where field voles were present, mice numbers decreased.

Latin name	**Common name**	**2002**	**2003**	**2004**	**2005**	**Permanent pasture** [a]	**Total**	
							Capture	**Recapture**
Apodemus flavicollis	Wood mouse	2	7	0	5	0	14	9
Apodemus sylvaticus	Yellow-necked mouse	1	3	0	3	0	7	0
Microtus agrestis	Field vole	2	0	0	0	0	2	3
							23	12

[a] Control – fields which are periodically mown.

3.2.1. Small mammal abundance and diversity against year

A non-parametric Kruskal-Wallis rank Sum test found no significant difference between the frequency of small mammal captured and the year that fields were taken out of production ($X^2(4) = 7.271$, $N = 23$, $P = 0.12$; figure 4A). Nor was there a significant difference between small mammal species diversity and the year that fields were taken out of production ($X^2(4) = 6.449$, $N = 23$, $P = 0.17$; figure 4B). Despite this, higher species richness was recorded in fields taken out of production in 2002, where wood mice, yellow-necked mice, and field voles were all recorded. In comparison, all other years only exhibited the two mice species.

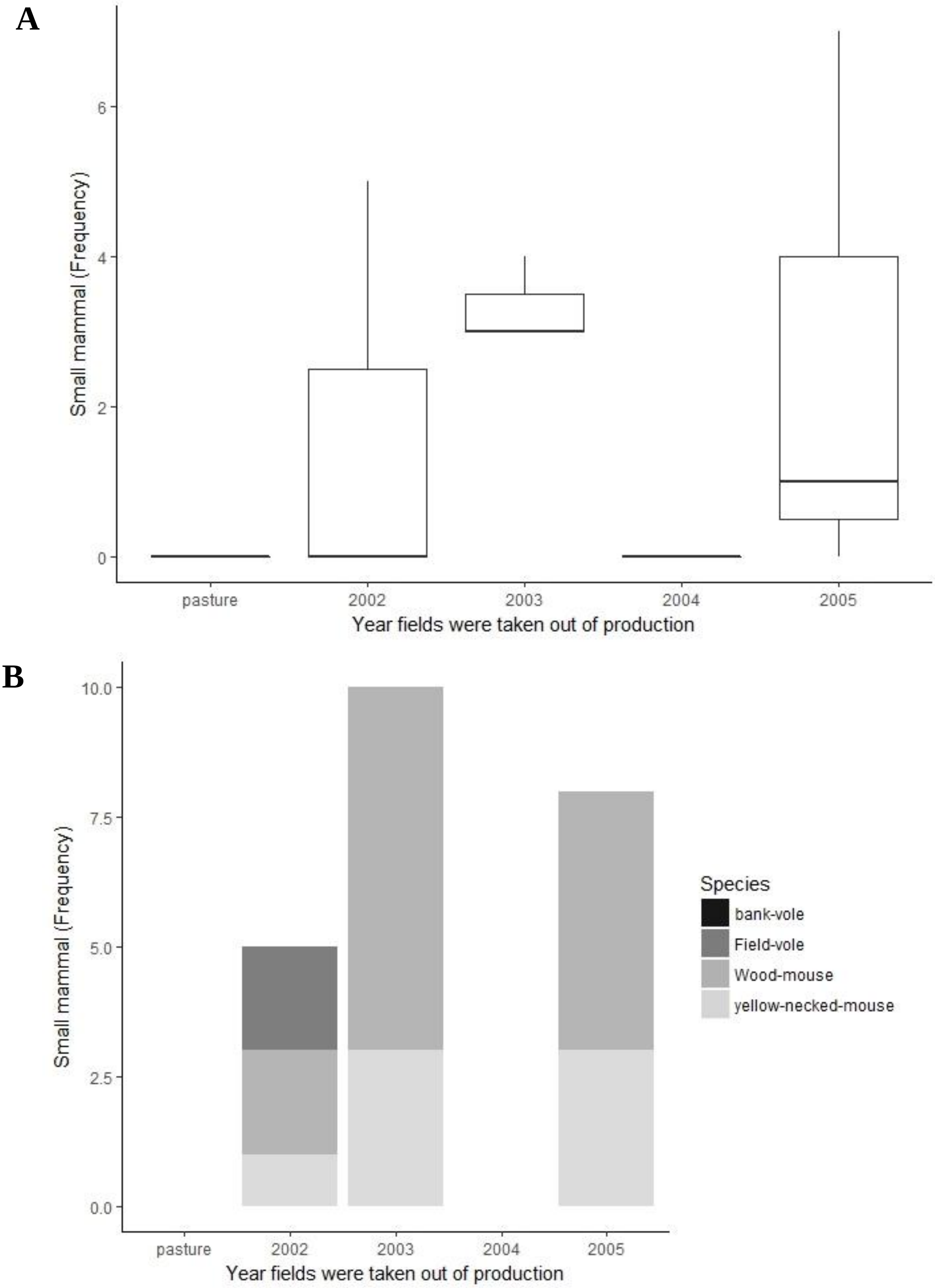

Fig. 4 A) Small mammal capture frequency in different fields taken out of agricultural production at different times, excluding recaptures. There was no significant difference between fields in terms of small mammal abundance ($X^2(4) = 7.271$, N= 23, P = 0.12) Error bars; SD. B) Small mammal species diversity in fields taken out of agricultural production at different times. There was found to be no significant difference between years in terms of small mammal diversity ($X^2(4) = 6.445$, $P = 0.168$). There was however a higher species richness in 2002 compared to the other fields, being the only study site to exhibit field vole activity.

3.2.2. *Small mammal abundance against vegetation*

The response of small mammal abundance to vegetational heterogeneity was determined using the standard deviation of vertical vegetational height within the 20m study site in each field. A linear regression showed a significant correlation between small mammal frequency and vegetation height standard deviation (R^2 = 0.34, F = 8.13, df = 13, P = 0.014; figure 5).

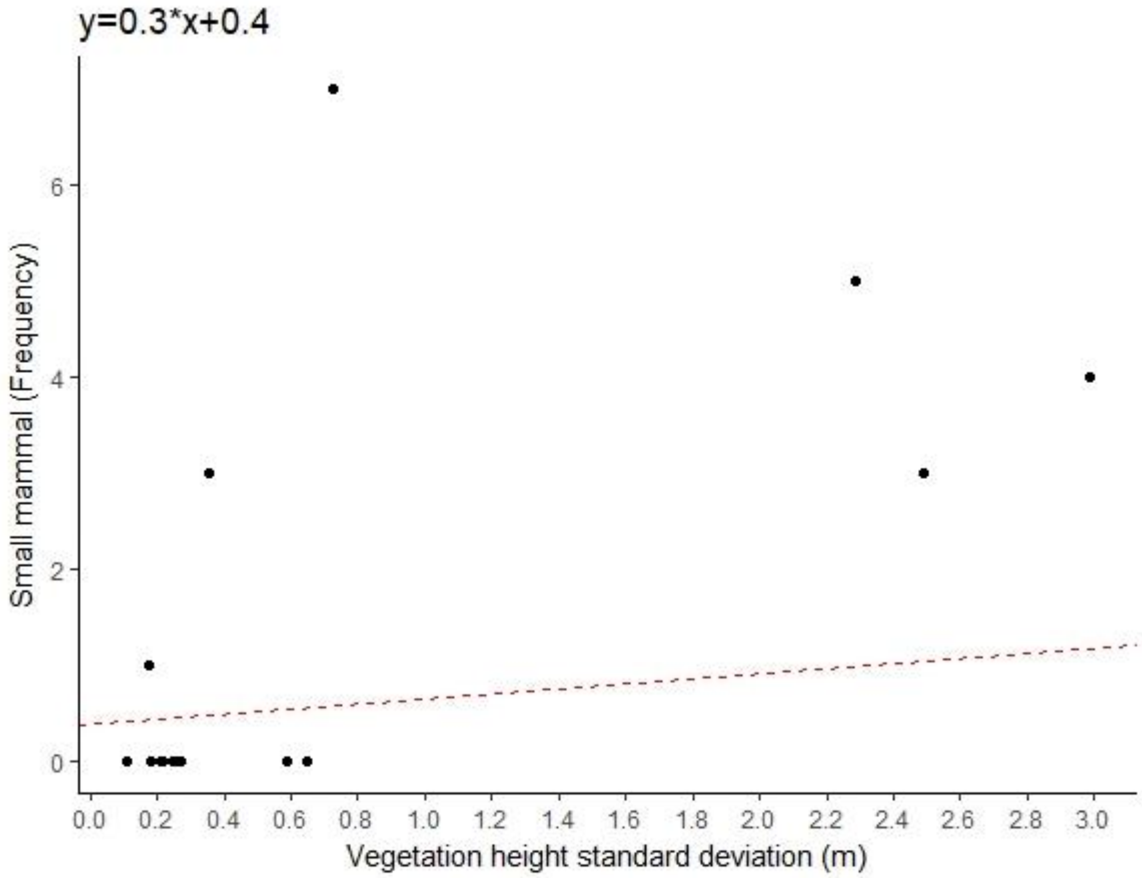

Fig.5. Small mammal abundance against the standard deviation of vegetation height (m). Increases in vegetational height deviation saw a significant increase in small mammal abundance, suggesting vegetational heterogeneity promotes small mammal occupation (R^2 = 0.34, F = 8.13, df = 13, P = 0.014).

3.3. *Long-term small mammal community dynamics*

To understand the long-term trends in small mammal abundance within the southern block, data collected in 2018 was compared to data collected in two previous study years; 2016 and 2005.

3.3.1. *Small mammal abundance and diversity*

A non-parametric Kruskal-Wallis showed no significant difference between the mean abundance of small mammals caught within each year of study ($X^2(2)$ = 2.42, P = 0.29; figure 6A), with 2016 showing the highest mean population (mean = 27, SD = 6.23, N= 4), compared to 2005 (mean = 19.5, SD = 17.40, N = 4), and 2018 (mean = 5.75, SD = 6.23, N = 4). Analysis of the small mammal diversity did, however, show variation, with a two-way ANOVA highlighting a significant difference between species found and year (F = 3.57, df = 6, *P* <0.005; figure 6B). Specifically, there was a significant difference in population diversity between 2005 and other years (t =3.843, *P* <0.001) and the 2016 bank vole population and other years (t = 3.22, *P* <0.005). 2016 showed the highest frequency of bank voles at 55 individuals, compared to 2005, which saw 28, and 2018, which showed zero captures.

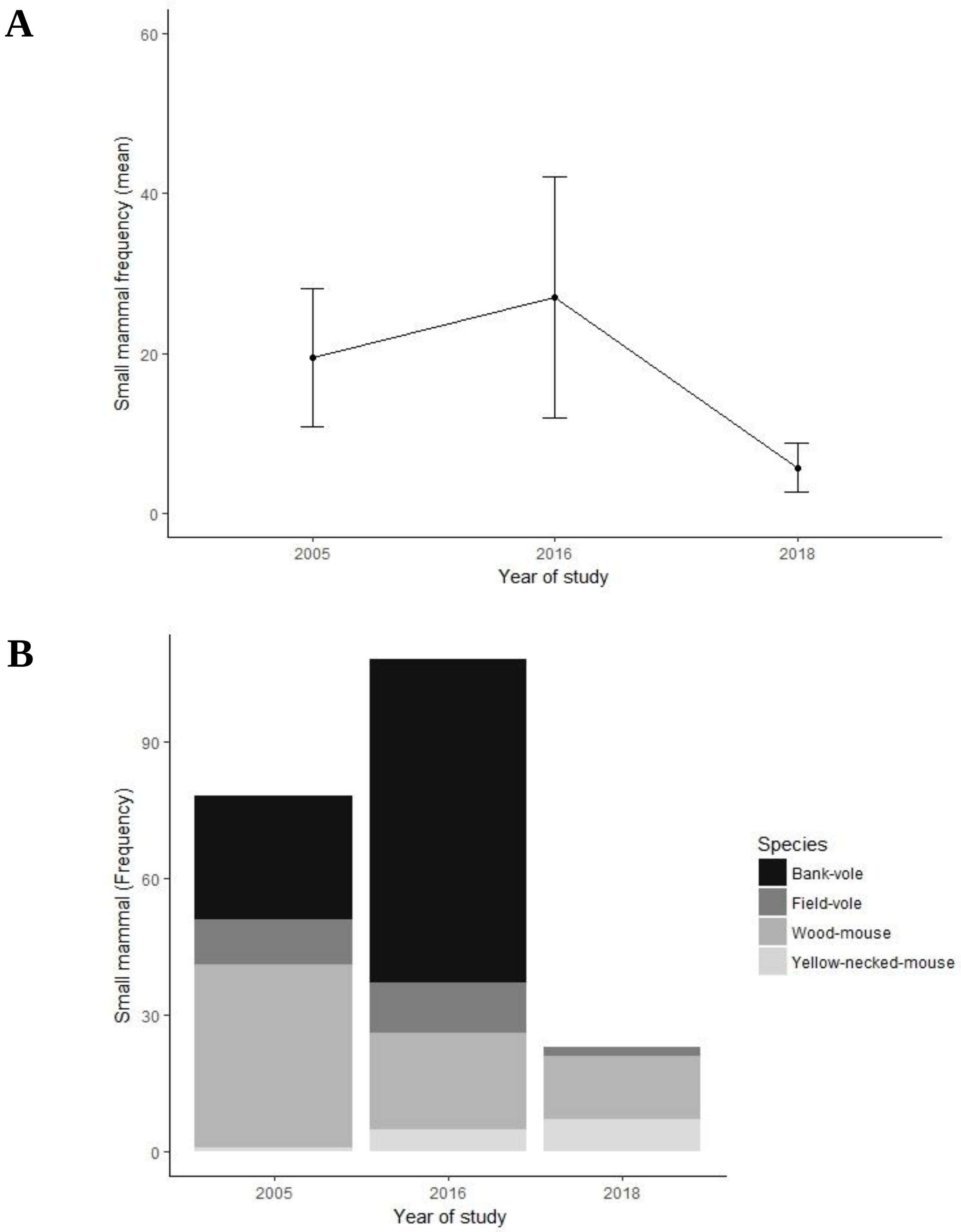

Fig.6. (A) Mean small mammal abundance over 3 years, 2005, 2016, and 2018. (B) Total small mammal diversity over three years, 2005, 2016, and 2018. There was found to be no significant difference between small mammal frequency ($X^2(2) = 2.423$, P = 0.29) Error bars: S.E; whilst diversity did show variation with bank voles being significantly more abundant in 2016, compared to 2005 and 2008 (2016 mean = 55, t =3.216, *P* < 0.005).

4. Discussion

The methodology employed in this study allowed for analysis of small mammal communities in response to structural and temporal changes in vegetation within a previous agricultural setting. The deviations in small mammal frequency between years are discussed and attributed to multi-annual fluctuations, climate, or predation. This is consistent with previous literature, and whilst capture rates were low within this study, it provides an opportunity to understand the ecosystem functionality within Knepp Estate and inform further projects in understanding changing landscapes at a rewilding site.

4.1. Vegetation in response to time since agricultural abandonment

Statistically there was no significant difference between fields of different years and the standard deviation of vegetation. In addition, there was no association between fields of the same year in terms of standard deviation of vegetation, suggesting that time since abandonment has a limited effect on succession and other factors heavily involved in vegetational development. Hypothesis Ha1 can therefore be rejected. Despite this, there was clear physical variation between the permanent pasture fields and other fields, which were allowed to develop naturally, with the control showing limited to no scrub or vertical heterogeneity. In contrast, all other fields had an element of scrub and taller vegetation.

These observations indicate that ceasing management does influence vegetational growth rate as a whole, but not necessarily as a result of time under natural processes. It may be the case that a year is not long enough to impact field level vegetation in a significant way. Results from studies in agricultural abandonment have indicated that the typical stages of vegetational succession; herbaceous, shrub, and woodland, are largely influenced by previous land management and the subsequent effect on soil nutrients and erosion (Nunes., *et al*. 2012). As fields within the Southern block were farmed in the same way prior to rewilding, it may not be possible at this point to identify significant differences between field sites this soon after agricultural cessation. Fertilizer and pesticide use prior to rewilding may be another crucial factor in vegetation growth, however this was not investigated within this study. Other factors such as large herbivore movement dynamics and grazing may also have an effect on succession at Knepp (Persson., *et al*. 2000). For example, preferential herbivore grazing within different sites prevents shorter perennial establishment and influences succession from grasses and shrubs to forest communities (Persson, *et al*. 2000). As such, conducting long-term investigations into these processes at Knepp, particularly regarding site selection by the longhorn cattle and deer species, is important. These impacts can also influence small mammal communities; heavily browsed understory vegetation by herbivores can have direct and indirect effects on small mammal occupancy at local scales due to removal of plants and reduction in habitat quality (Smit., *et al*. 2001). As the herbivores at Knepp have been shown to display preferences for fields/sites within the Southern block (Dando. unpublished) further research into the successional development of each field within this study, in association with large herbivore movements is suggested to investigate unidentified factors influencing vegetational changes at Knepp.

4.2. Small mammal abundance and diversity in response to year since abandonment and vegetational structure

The hypothesis that time since agricultural abandonment would have an effect on small mammal communities was rejected in this study. Rather, fields of higher vegetational structural complexity were the best predictor of small mammal occurrence, regardless of year of rewilding. Such outcomes are consistent with previous literature. Studies in Australia found that small mammal colonisation post-wildfire outbreak is concordant with vegetation regeneration, rather than time since disturbance (Monamy., & Fox. 2000). Such examples are also consistent across European landscapes, with mid-level succession and ground layer structural complexity being the best predictor of small mammal presence (Panzacchi., *et al*. 2010, Balčiauskas., *et al*. 2017).

As stated, vegetational structural complexity is considered the largest predictor of small mammal occurrence, which was found to be the case in this study. There was a significant association of small mammal abundance and vertical height heterogeneity with 34% of small mammal presence explained by this vegetational factor, suggesting that variation in habitat type within fields promotes small mammal occurrence to some extent. Such heterogeneity was often associated with dense vegetation or scrub, which would explain the preference for these kinds of habitats; within this study, consistency was found between managed fields and the rate of small mammal capture, with no small mammals being found within the permanent pasture fields. These trends can be explained by the reliance on tall vegetation for protection from predators (Jensen., & Honess. 1995) – most captures occurred when traps were placed in thick vegetation or tall grass.

The presence of grassland within Knepp should not be overlooked as a potential benefit to overall ecological stability within the southern block. Alongside providing benefits for other species within the site, such as moths and butterflies (Wallace. unpublished), studies have suggested that there is seasonal variation in species-specific small mammal occupation over two types of landscape; grassland and scrubland (Pita., *et al*. 2003). This means that over the course of the year small mammals may separate into these different habitats based on food availability and associated inter-specific competition. This suggests that whilst habitats at an earlier successional stage are potentially less diverse, a mix of habitats of varying vegetational density is desirable in agro-ecosystems to provide habitat for different small mammal species. Such evidence was found within this study; whilst all small mammal captures occurred in habitats showing a degree of cover, voles were primarily caught in dense woodland/scrubland whilst mice were caught in a wider range of habitats. This may be the case due to vole species' tendency to avoid predation using shelter, whilst mice rely on speed to avoid predation in addition to vegetational cover (Jensen., & Honess. 1995).

4.3. Small mammal community diversity against vegetational structure

No significant difference was recorded between community composition of small mammals between fields sites. The most abundant species within the study was the wood mouse, followed by the yellow-necked mouse and finally field voles, whose presence was only recorded in one field. Our findings are consistent with early phase vegetational development, where there has found to be limited variation in both temporal and spatial variance of species composition (Schweiger., *et al*. 2000). Due to the low number of individuals and species trapped, it was not possible to determine the diversity index for specific fields.

Despite this, field voles and in fact the highest species variation occurred within a field of high variation in vegetational height (2m, 2002, Oaklands 5; table 1). This particular field had a high degree of scrub and dense vegetation. Whilst not significantly different, the variation in wood mice and vole numbers in relation to habitat type is consistent with theories on niche separation and long-term community dynamics. Wood mice have been reported to be more abundant in cultivated fields and meadows, but with high association of forest edge (Panzacchi., *et al*. 2010), suggesting that a mixture of farmland, scrubland and forest is beneficial to a variety of small mammal species. This was seen to be the case with the current study, with wood mice being present in fields of less dense scrub whilst also appearing in the edges of forested areas. The deviation in mice and field vole occurrence could be a result of inter-specific competition where field voles occur. However, previous research has rejected this as a possibility (Lambin., & Bauchau. 1989), meaning that species coexistence may be occurring through niche separation within these heterogeneous habitats, but total abundance is low due to carrying capacity being reached (Golley., *et al*. 2009). This highlights the need for landscape-scale habitat heterogeneity to provide for different small mammal species as it reduces fragmentation and provides opportunities for niche separation and emigration – important factors in supporting a functionally diverse small mammal community.

4.4. Small mammal community structure over the years

Long-term analysis of the species composition within the southern block showed that, despite no significant difference in total small mammal abundance, there was a significant shift towards bank vole dominance in 2016. This came at the apparent expense of mice species, specifically wood mice, which halved from 40 to 21 individuals. A potential explanation for this is inter-specific competition for food and breeding space (Hansen.., *et al*. 1999), which is typical for habitats going through varying successional stages. Despite this, as stated, research indicates that competition between the two species of Rodentia is limited due to species-specific diets and habitat selection (Galindo., & Krebs. 1985; Lambin., & Bauchau. 1989). Rather, it may be vegetational structure that influences species dominance; factors such as perennial grass depth and tree density (M'Closkey., & Fieldwick. 1975), as well as seasonal fluctuations in species-specific food availability can better explain changes in species diversity as vegetation develops (Abt., & Bock. 1998; Schweiger., *et al*. 2000; Eccard., & Ylonen. 2003).

This does not, however, explain the variation in recorded individuals with no bank voles and only 2 field voles being caught in 2018 (table 2). Potential explanations could lie in weather conditions earlier in the year and during the study period. Capture rates in relation to weather tend to be species-specific in Rodentia (Stokes., & colleagues. 2001), with bank voles responding negatively to increased rainfall and decreased temperatures due to their high body surface-to-volume ratio (Wrobel., & Bogdziewicz. 2015). Within the first and second week of the 2018 study there was severe rain over a couple of the study days. This can have a significant influence on bank voles capture and therefore reduce the reliability of the population analysis during 2018 i.e. fluctuations seen over the three study period years may be artificial and not represent the changing dynamics within the rewilding site.

4.5. Predator-prey interactions

Alternatively, the fluctuations in total small mammal numbers and in individual species could be a result of predator-prey interactions. Within the literature, variations in cyclical patterns of small mammal communities are highly documented, with the main factor influencing fluctuations accounted for by predator numbers (Lambin., *et al*. 2006; Henttonen., *et al*. 2017). Such a relationship would be common in a functioning ecosystem, with multi-species assemblages of small mammal undergoing density-dependent oscillations with predator numbers (Hanski., & Henttonen. 1996; Hanski., *et al.* 2001). Typically, voles are shown to follow multi-annual fluctuations over 3 years in the south of Europe and 4-5 years in the north (Henttonen., *et al*. 2017). These occur as part of a natural cycle (Hein., & Jacob. 2015), with yearly fluctuations being driven by specialist and generalist predators respectively (Lambin., *et al*. 2006). Such a relationship can potentially explain the community structure changes seen in figure 6, however, long-term analysis is required in order to confirm this dynamic. Other factors such as habitat heterogeneity also convey a degree of resilience to vole populations in the face of stressors such as climate and weather, which would negatively impact their ability to avoid predation and maintain cohesive social groups (Andreassen., *et al*. 2013; Dalkvist., *et al*. 2013).

Such complex interactions are difficult to determine using the limited data available in this study. The three years of data collected on small mammals is too small a sample size to accurately compare to barn owl (*Tyto alba*) data to investigate such an interaction. Additionally, these interactions do not occur in isolation (other predator parameters such as fox numbers, as well as intrinsic cyclical oscillations in small mammal numbers will also likely have an effect on the results seen in this study). The importance of understanding the trophic interactions occurring at Knepp in efforts to establish a functioning ecosystem requires further investigation and it is likely small mammal community drivers will be a combination of all the aforementioned factors. It would therefore be beneficial to conduct further yearly monitoring to investigate predator and small mammal population interactions occurring within the Southern block of the estate. If one is not found, other primary causes of small mammal abundance fluctuations can then be established so as to better understand the ecosystem processes at Knepp.

5. Limitations and further research

Heavy rain impacted the ability to collect data on certain days, as well as potentially reducing the reliability of abundance estimates due to the decreased activity of vole species during this time. Repeating this study during the same time of year, over a longer period to account for fluctuations in weather would correct for this. In addition, changes to small mammal populations based on field-level habitats was not possible for cross year analysis due to placement of traps in different sites. Pooling of this data into a total Southern-block analysis was then required to account for this, however it meant that historic changes in small mammal abundance in fields separated by year of abandonment was not possible. Again, a suggestion would be to repeat this study yearly, in the fields detailed in this report, so that consistent data can be produced and analysed accordingly.

In terms of further research, the results of this study present the opportunity for a more in-depth predator-prey interaction study. This is possible with the ongoing barn owl data collection occurring at Knepp but can be supplemented with small mammal monitoring in consistent sites.

In addition, other factors such as changing vegetation, weather, climate, and inter-specific competition between small mammals can be incorporated to investigate more complex ecosystem processes. This will create a more accurate representation of the functionality of Knepp Estate as a rewilding site. This would be done in addition to a woodland habitat which can act as an additional control. Whilst this was not possible during this study due to time and resource constraints it would provide further understanding of the habitat preferences displayed by small mammals.

6. Conclusion

Whilst there was no association between small mammals and year since agricultural cessation, there was a significant correlation between vegetational height standard deviation and small mammal abundance. This is consistent with previous research that suggests that within-field and between-field heterogeneity promotes long-term functionality in ecosystems due to provision of multiple niches for different species. Long-term analysis of small mammal data suggests fluctuating patterns in total small mammal abundance but also individual species, specifically the bank vole population. Again, this concurs with small mammal multi-annual cycles. As other factors are likely to influence these changes in a complex food web, consistent, yearly monitoring is advised to investigate these trends fully.

References

Abt, K F., & Bock, W F. (1998) Seasonal variations of diet in farmland field mice *Apodemus* spp. and bank voles *Clethrionomys glareolus*. *Acta Theriologica*, **43**, 379-389.

Andreassen, H P., Glorvigen, P., Remy, A., & Ims, R A. (2013) New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. *Oikos*, **122**, DOI.org/10.1111/j.1600-0706.2012.00238.x.

Arts, K., Fischer, A., Van der Wal, R. (2016) Boundaries of the wolf and the wild: a conceptual examination of the relationship between rewilding and animal reintroductions. *Restoration Ecology*, **24**, 27-34.

Avenant, N. (2011) The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South African grasslands, *Wildlife Research*, **38**, 626-639.

Balčiauskas, L., Čepukienė, A., & Balčiauskienė, L. (2017) Small mammal community response to early meadow-forest succession. *Forest Ecosystems*, **4**, https://doi.org/10.1186/s40663-017-0099-6.

Beschta, R L., & Ripple, W J. (2008) Wolves, trophic cascades, and rivers in the Olympic National Park, USA. *Ecohydrology*, **1**, 118-130.

Briggs, A A. (2016) *A report of small mammal trapping surveys at Knepp castle estate, West Grinstead, West Sussex*. Unpublished BSc (Hons.) report. University of Cumbria.

Bowland, A E., & Perrin, M R. (1989) The effect of overgrazing on small mammals in Umfolozi Game reserve. *Zeitschrift für Säugetierkunde*, **54**, 251-260.

Butchart, S H M., Walpole, M., Collen, B., Strien, A V., Scharlemann, J P W., *et al*. (2010) Global biodiversity: indicators of recent decline. *Science*, **328**, 1164-1168.

CEH. (2018) Centre for Ecology and Hydrology: Modular Analysis of Vegetational Information System (MAVIS). Available: https://www.ceh.ac.uk/services/modular-analysis-vegetation-information-system-mavis. [Accessed: 26/06/2018].

Chapron, G., Kaczensky, P., Linnell, J D C., Von Arx, M., Huber, D., *et al*. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517-1519.

Connell, J., & Slatyer, R O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Society of Naturalists*, **111**, 1119-1144.

Dando, T. (2018) *The role of large herbivore foraging in shaping a rewilded landscape*. Unpublished MRes thesis. University of Sussex.

Dalkvist, T., Sibly, R M., Topping, C J. (2013) Landscape structure mediates the effects of a stressor on field vole populations. *Landscape Ecology*, **28**, 1961-1974.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R., Collen, B. & Böhm, M. (2013) Wildlife comeback in Europe: The recovery of selected mammal and bird species. *Zoological Society of London*.

Dickinson, M., Prentice, I C., & Mace, G M. (2015) Climate change and challenges for conservation. *Grantham institute – Imperial College London,* **Briefing paper No 13**, 1-20.

Eccard, J A., & Ylonen, H. (2003) Interspecific competition in small rodents: from populations to individuals. *Evolutionary Ecology*, **17**, 423-440.

Fox, B J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*, **63**, 1332-1341.

Galindo, C., & Krebs, C J. (1985) Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. *Canadian Journal of Zoology*, **63**, 1870-1879.

Golley, F B., Petrusewicz, K., Ryszowski, L. (2009) Small mammals: Their productivity and population dynamics. Cambridge university Press, ed:1.

Greenaway, T E. (2006) Knepp castle estate baseline ecological survey. *English Nature Research Reports*, **693**, 1-194.

Hansen, T F, Stenseth, N C, Henttonen, H, & Tast J. (1999) Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. *PNAS*, **96**, 986-991.

Hanski, I., & Henttonen, H. (1996) Predation on competing rodent species: a simple explanation of complex patterns. *British Ecological Society*, **65**, 220-232.

Hanski, I., Henttonen, H., Korpimaki, E., Oksanen, L., & Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology*, **82**, 1505-1520.

Hein, S., & Jacob, J. (2015) Recovery of small rodent populations after population collapse. *Wildlife Research*, **42**, 108-118.

Henttonen, H., Gilg, O., Ims, R A., Korpimaki, E., & Yoccoz, N G. (2017) Ilkka Hanski and small mammals: from shrew metapopulations to vole and lemming cycles. *Annales Zoologici Fennici*, **54**, 153-162.

Hoffman, M T., Cousins, B., Meyer, T., Petersen, A., & Hendriks, H. (1999) Historical and contemporary agricultural land use and the desertification of the Karoo. In: Dean, W R J., & Milton, S J (eds), *The Karoo. Ecological patterns and processes*, Cambridge University Press, Cambridge: 257-273

Hoffman, A., & Zeller, U. (2005) Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belgian Journal of Zoology*, **135**, 91-96.

Howe, H F., & Brown, J S. (2000) Early effects of rodent granivory on experimental forb communities. *Ecological Applications*, **10**, 917-924.

Jensen, S P., & Honess, P. (1995) The influence of moonlight on vegetation height preference and trappability of small mammals. *Mammalia*, **59**, 35-42.

Knepp.co.uk (no date) Knepp Wildland, rewilding in West Sussex: Background. Available at: https://knepp.co.uk/background/. [Date Accessed: 16/08/2018].

Knepp.co.uk (no date) Knepp Wildland, rewilding in West Sussex: what we do: woods & Trees. Available at: https://www.kneppestate.co.uk/woodland/. [Accessed: 20/08/2018].

Lambin, X., & Bauchau, V. (1989) Contest competition between wood mice and bank voles: is there a winner? *Acta Theriologica*, **34**, 385-390.

Lambin, X., Bretagnolle, V., & Yoccoz, N G. (2006) Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? *Journal of Animal Ecology*, **75**, 340-349.

Louvrier, J., Duchamp, C., Lauret, V., Marboutin, E., Cubaynes, S., *et al*. (2017) Mapping and explaining wolf recolonization in France using dynamic occupancy models and opportunistic data. *Ecography*, **41**, 647-660.

M'Closkey, R T, Fieldwick, B. (1975) Ecological separation of sympatric rodents (Peromyscus and Microtus). *Journal of Mammalogy*, **56**, 119-129.

Monamy, V., & Fox, B J. (2000) Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. *Austral Ecology*, **25**, 580-587.

Monamy, V., & Fox, B j. (2010) Responses of two species of heathland rodents to habitat manipulation: vegetation density threshold and the habitat accommodation model. *Austral Ecology*, **35**, 334-347.

Nunes, A., Figueiredo, A., & Almeida, A. (2012) The effects of farmland abandonment and plant succession on soil properties and erosion processes: a study in central of Portugal. *Revista de Geografia e Ordenamento do Território*, **2**, 165-190.

Panzacchi, M., Linnell, J D C., Melis, C., Odden, J., & Odden, M., et al. (2010) Effect of land-use on small mammal abundance and diversity in a forest-farmland mosaic landscape in southern-eastern Norway. *Forest Ecology and Management*, **259**, 1536-1545.

Persson, I L., Danell, K., Bergstrom, R. (2000) Disturbance by large herbivores in boreal forests with special reference to moose. *Annales Zoologici Fennici*, **37**, 251-263.

Pita, R., Mira, A., & Mathias, M L. (2003) Small mammal community structure in two successional stages of a Mediterranean ecosystem. *Centre for Applied Ecology*, **15**, 67-79.

Plieninger, T., Hui, C., Gaertner, M., & Huntsinger, L. (2014) The impact of land abandonment on species richness and abundance in the Mediterranean basin: A meta-analysis. *Plos One*, **9**, DOI: 10.1371/journal.pone.0098355.

Rewilding Europe. (no date) What is rewilding. Available at: https://rewildingeurope.com/what-is-rewilding/. [Accessed: 02/07/2018].

Sandom, C., Donlan, C J., Svennig, J-C., & Hansen, D. (2013) Rewilding. *Key Topics in Conservation: Biology 2*, https://doi.org/10.1002/9781118520178.ch23.

Schweiger, E W., Differndorfer, J E., Holt, R D., Pierotti, R., & Gaines, M S. (2000) The interaction of habitat fragmentation, plant, and small mammal succession in an old field. *Ecological Monographs*, **70**, 382-400.

Silliman, B R., & Angelini, C. (2012) Trophic cascades across diverse plant ecosystem. *Nature Education Knowledge*, **3**, 44.

Smit, R., Bokdam, J., Ouden, J D., Olff, H., Schot-Opschoor., & Schrijvers, M. (2001) Effects of introduction and exclusion of large herbivores on small rodent communities. *Plant Ecology*, **155**, 119-127.

Stephens, R B., & Anderson, E M. (2014) Habitat associations and assemblages of small mammals in natural plant communities of Wisconsin. *Journal of Mammalogy*, **95**. 404-420.

Stokes, M K., Slade, N A., & Blair, S M. (2001) Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. *Canadian Journal of Zoology*, **79**, 966-972.

Svenning, J-C., Pedersen, P B M., Donlan, C J., Ernes, R., Faurby, S., *et al*. (2016) Science for a wider Anthropocene: Synthesis and future directions for trophic rewilding research. *PNAS*, **113**, 898-906.

Van der Zanden, E H., Verburg, P H., Schulp, C J E., & Verkerk, P J. (2017) Trade-offs of European agricultural abandonment. *Land Use Policy*, **62**, 290-301.

Wallace, C. (2018) *The impact of a rewilding project on pollinator abundance and diversity at a local scale*. Unpublished MRes thesis. University of Sussex.

Wolf, C., & Ripple, W J. (2018) Rewilding the world's large carnivores. *Royal Society Open Science*,**5**, DOI: 10.1098/rsos.172235.

Wrobel, A., & Bogdziewicz, M. (2015) It is raining mice and voles: which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus*? *Eur J Wildl Res*, **61**, 475-478.

Appendix

Appendix table 1. *Study sites within the Southern block of Knepp castle estate. Each week represents a repeat, with four fields taken out of agricultural production at different times (2002-2005). In addition, a permanent pasture field was included to act as a control.*

Week	Field name	Year removed from agricultural production	GPS coordinates of central point
1	Permanent pasture	-	N 50º58.477' W000º21.877'
	Keens	2002	N 50º58.249' W000º22.467'
	Hammer	2003	N 50º58.689' W000º22.067'
	Pound corner	2004	N 50º58.722' W000º21.924'
	New barn 1	2005	N 50º58.070' W000º21.699'
2	Pond Field	-	N50º57.887' W000º22.452'
	Benton's place	2002	N50º58.007' W000º22.700'
	Brookhouse 11	2003	N50º58.019' W000º22.897'
	Brookhouse 6	2004	N50º58.092' W000º23.049'
	Newbarn 3	2005	N50º57.968' W000º22.201'
3	Wildflower field	-	N50º58.507' W000º22.949'
	Oaklands 5	2002	N50º58.362' W000º23.356'
	Honeypools house	2003	N50º58.745' W000º22.272'
	Oaklands 3	2004	N50º58.511' W000º23.225'
	Hampshire buildings big	2005	N50º58.756' W000º22.748'