



Short communication

Trade-offs between passive and trophic rewilding for biodiversity and ecosystem functioning

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ABSTRACT

Trophic rewilding that reintroduces large animals into landscapes to re-establish food web interactions and restore biodiverse ecosystems has gained widespread attention. Despite this attention, few empirical studies have assessed the effectiveness of trophic rewilding for promoting biodiversity and its wider ecological benefits. Here we tested if trophic rewilding that introduced functional analogues for extinct large herbivores into former farmland of lowland England delivered additional benefits to biodiversity and ecosystems functioning. We predicted that these benefits would exceed those achieved through passive rewilding, that is, unassisted habitat succession after the cessation of agricultural activity. Using a 9-year enclosure experiment, we found trophic rewilding reduced woody plant diversity and total carbon storage by 73% and 23%, respectively, compared to passive rewilding plots that excluded mammalian herbivores. However, trophic rewilding likely increased plant diversity and carbon storage compared to if land was left under continued agricultural production, e.g. artificial pastures associated with intensive livestock production. The vegetation changes accompanying trophic rewilding were further linked to a greater diversity and biomass of ground-dwelling arthropods by 21% and 167%, respectively, relative to passive rewilding, partly by creating more structurally complex vegetation. Given the trade-offs in biodiversity and ecosystem functions between trophic and passive rewilding, our study highlights that trophic rewilding will need to be applied alongside other interventions to tackle biodiversity loss while combatting climate change. Ultimately, the utility of trophic rewilding as a restoration tool will depend on the conservation outcomes valued by society.

1. Introduction

Trophic rewilding is receiving widespread attention as an approach to tackle jointly the crises of biodiversity loss and climate change by reversing anthropogenic impacts on nature (Bakker and Svenning, 2018; Perino et al., 2019; Svenning, 2020). However, its potential to do so has rarely been assessed empirically (Tanentzap and Smith, 2018). Trophic rewilding involves adding species into ecosystems to restore extinct top-down interactions in food webs so that they can be sustained without continuous human intervention (Svenning et al., 2016). Added species are those that have been locally extirpated or, more controversially, act as functional substitutes for species that have gone extinct (Seddon et al.,

2014). This strategy contrasts with that of passive rewilding, that is, the unassisted and natural succession of habitat after the cessation of human activities like agricultural production (Perino et al., 2019). It is well established that agricultural abandonment benefits overall biodiversity and carbon sequestration via woodland expansion if given enough time (Isbell et al., 2019; Plieninger et al., 2014). This knowledge inspired set-aside programmes that removed land from production as a cornerstone of global agri-environment policy (Van Buskirk and Willi, 2004). However, an open question is if trophic rewilding delivers added benefits to biodiversity and ecosystem functioning as compared with passive rewilding.

Most trophic rewilding focuses on re-establishing large herbivores

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(>45 kg body mass) because they are often important for sustaining biodiversity (Svenning et al., 2019) but have been disproportionately extirpated (Svenning et al., 2016). At the scale of local food patches in woodland-grassland mosaics (e.g. $\leq 100 \text{ m}^2$; Cromsigt and Olff, 2006), removal of preferred forage that is dominant alleviates competition for light, nutrients, and water, and promotes plant diversity (Borer et al., 2014; Boulanger et al., 2018; Koerner et al., 2018). If less dominant and competitive forage is preferred by browsing or grazing animals, local plant diversity is reduced (Koerner et al., 2018). However, the intensity of herbivory and its coevolutionary history with local vegetation will influence these outcomes (Bernes et al., 2018; Hegland et al., 2013). Herbivores can also change the structure of vegetation patches by physical disturbance (Howison et al., 2017) and transporting nutrients (Wolf et al., 2013) and seeds (Galetti et al., 2018). As food patches are spatially non-random, the impacts of herbivores can altogether create a mosaic of differently structured vegetation (Bakker et al., 2016; Olff et al., 1999). The resulting landscape heterogeneity may subsequently enhance invertebrate biodiversity and that of other animals by providing more niches for species to occupy (Stein et al., 2014). These outcomes may contrast those of passive rewilding. With passive rewilding, the landscape may become less heterogeneous and less biodiverse because vegetation patches develop in a more directional and predictable way towards a late-successional community, especially without repeat disturbance by large herbivores (Olff et al., 1999).

Ecosystem functions, such as carbon storage and pollination, and the services they deliver to people may also respond differently to large herbivores because they are often maximized by a specific vegetation state (Lamy et al., 2016; van der Plas et al., 2019). For example, large herbivores reintroduced to the Oostvaardersplassen, the Netherlands – one of Europe's oldest large-scale rewilding projects – created heterogeneity in wet grasslands that promoted plant diversity (van Klink et al., 2016). However, herbivores also prevented woody plant regeneration (Smit et al., 2015), limiting above- and below-ground carbon storage (Tanentzap and Coomes, 2012). Reintroduction of feral horses (*Equus ferus caballus*) to Swedish semi-natural grasslands similarly enhanced plant diversity and promoted habitat use by pollinators, which lacked habitat in the forest monocultures that otherwise dominated this landscape (Garrido et al., 2019). Thus, trophic rewilding may impact ecosystem functioning differently than biodiversity, even in the same habitat type. Passive rewilding has similarly been found to have both positive and negative effects on ecosystem functions in meta-analyses of restoration outcomes (Jones et al., 2018). To our knowledge, there has been no formal experimental test of how trophic rewilding with large herbivores alters these potential synergies and trade-offs and how these may differ from outcomes under passive rewilding.

Here we asked how trophic rewilding changed biodiversity and ecosystem functioning in semi-natural wood-pasture relative to passive rewilding. We addressed this question using a 9-year enclosure experiment in southern England. We predicted large herbivores would promote the biodiversity of plants and ground-dwelling arthropods more than passive rewilding by removing competitively dominant vegetation and increasing structural heterogeneity (van Klink et al., 2015). Arthropod biomass production may also benefit from more structurally diverse habitat (Lind et al., 2017; Schuldt et al., 2019), and so should be greater under trophic than passive rewilding. By contrast, we predicted large herbivores would reduce above-ground carbon stocks relative to passive rewilding by consuming vegetation (Bakker et al., 2016), though their effects on below-ground carbon would be less predictable and depend on soil compaction and organic content (Forbes et al., 2019; Tanentzap and Coomes, 2012). Although our main objective was to compare the added benefit of trophic versus passive rewilding and the trade-offs between these two strategies, we also used an existing geospatial data product to compare vegetation structure between rewilding and non-rewilding areas across a larger spatial scale.

2. Methods

2.1. Experimental design

We studied the Southern Block of Knepp Wildland, England (50°58'32.81"N, 0°20'41.35"W), consisting of 450 ha of former arable farmland that has undergone trophic rewilding (Tree, 2018). Soils are poorly drained, heavy clay historically covered by oak woodlands (*Quercus robur*) with regenerating scrub, e.g. *Prunus spinosa*, *Crataegus* spp., and *Rubus* spp. In 2009, the entire site was stock-fenced and Old English longhorn cattle (*Bos primigenius primigenius*), Exmoor ponies (*E. ferus caballus*), and Tamworth pigs (*Sus scrofa domestica*) were introduced. These are all older domesticated breeds intended to act as functional analogues for extinct auroch (*B. primigenius taurus*), tarpan (*E. ferus ferus*), and wild boar (*Sus scrofa scrofa*), respectively (Bunzel-Drüke, 2001; Tree, 2018). Non-native fallow deer (*Dama dama*) and native red deer (*Cervus elaphus*) were also introduced respectively in 2009 and 2013. The animals roam freely alongside native roe (*Capreolus capreolus*) deer, as their home ranges in open habitats of southern England are typically smaller than that of our study site (Gates, 1979; Langbein, 1998). There were no other management interventions aside from some annual removals aimed at maintaining herd structure similar to 2010 levels (Tree, 2018; Fig. 1).

In 2009, before herbivores were introduced, we established paired open-fenced monitoring sites in each of 10 fallow fields (Fig. 2). The fields were randomly stratified within the four quadrants of the Southern Block in habitats of similar and vegetation composition. All the fields had been removed from agricultural production between 2003 and 2006 and were never used for intensive grazing. Within each field, we randomly positioned a 7.2 m \times 7.2 m fenced plot enclosed by a 1.9 m-high stock fence (0.15 m \times 0.15 m panels) with rabbit wire (0.03 m \times 0.03 m panels, 0.9 m tall) to exclude primarily rabbits (*Oryctolagus cuniculus*). These fenced plots represented passive rewilding and were compared to similarly sized trophic rewilding plots that were accessible to large herbivores and situated 10 m away.

We also compared the impacts on field-scale vegetation structure from trophic rewilding with those from maintaining pastures for livestock production, i.e. the absence of explicit rewilding. In the Southern Block of Knepp Wildland, four permanent pasture fields (area: 1.6 to 5.7 ha) associated with livestock production were retained once large herbivores were introduced (Fig. 2). We compared these with 71 neighbouring fallow fields (area: 1.4 to 163.3 ha) that were subjected to trophic rewilding (Fig. 2). Vegetation was mapped in 2001 and 2009 across all fields at 3 m resolution, and its maximum height was estimated in each field using airborne light detection and ranging (LiDAR) surveys processed through an existing geospatial data product (Henshaw et al., 2021).

2.2. Biodiversity and ecosystem functions

We measured 11 indicators of biodiversity and ecosystem functioning within passive and trophic rewilding plots.

Woody species richness was calculated by identifying all woody stems in each plot after Fitter and Peat (1994).

In 2018, we measured above-ground carbon content. Carbon in woody stems was determined from plant height and diameter using allometric equations. We followed UK Forestry Commission guidance to calculate the carbon content of woody stems (Jenkins et al., 2018). Oak (*Quercus* spp.), blackthorn (*Prunus spinosa*), and willow (*Salix* spp.) stems that were <7 cm in diameter at breast height (DBH) were grouped together based on Table 5.2.6 in Jenkins et al. (2018). Carbon content was then estimated directly from stem height based on Table 6.1.3 in Jenkins et al. (2018). For stems of the three species that were ≥ 7 cm in DBH, we input DBH, height, and species-specific woody density into species-specific allometric equations in Jenkins et al. (2018) and summed stem, crown, and root biomass. For dog-rose (*Rosa canina*), we

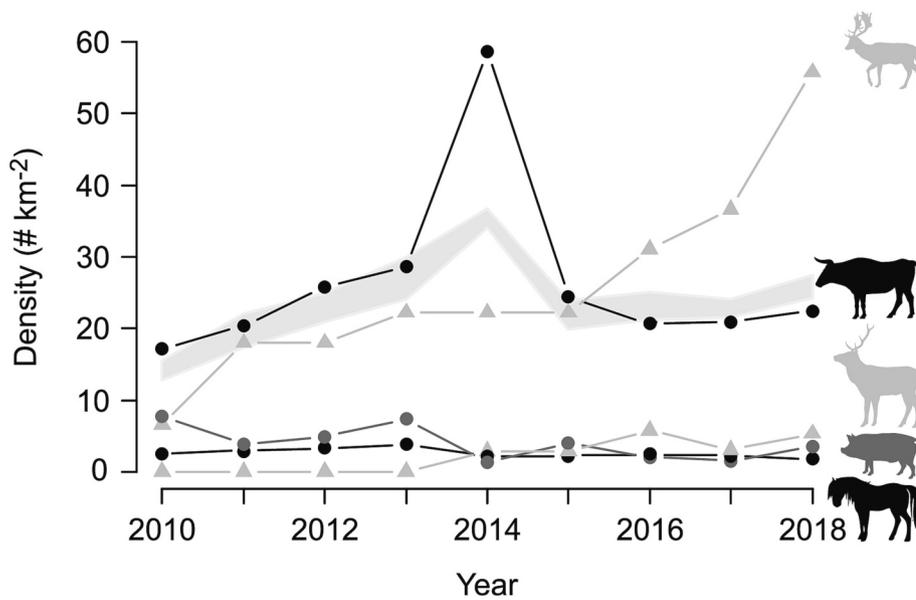


Fig. 1. Densities of introduced herbivores in the Southern Block, Knepp Estate. Animals were censused annually on 31 March and included Old English longhorn cattle (*Bos primigenius primigenius*, black circles), Exmoor ponies (*E. ferus caballus*, black circles), Tamworth pigs (*Sus scrofa domesticus*, grey circles), red (*Cervus elaphus*, light grey triangles) and fallow (*Dama dama*, dark grey triangles) deer. Grey polygon is range of total livestock units (LSU; 0.13 to 0.37 LSU ha⁻¹) calculated annually across the Southern Block from two different sets of species-specific LSUs defined in Table A2. During our resurvey, that is, from 2018 and 2019, between 0.18 and 0.19 LSU ha⁻¹ were removed from the Southern Block based on the two calculation methods in Table A2.



Fig. 2. Study plots within Knepp Estate, England. Grey line denotes boundary of the Southern Block with interior orange and blue lines outlining fallow fields that underwent trophic rewilding or were retained as permanent pasture, respectively. Circles denote location of paired rewilding plots. Aerial imagery from March 2022. Inset shows location of Knepp in orange within western Europe. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

calculated a cylindrical volume of clearly defined stems from their diameter and height and converted values to biomass with a stem density of 0.20 g cm⁻³ (Castro-Díez et al., 1998), assuming that any crown or root biomass was negligible. Finally, we used biomass-volume

associations to estimate biomass for dense blackthorn and dog-rose thickets. We measured the width, height, and length of blackthorn patches and derived biomass from the regression equation in Riedel et al. (2013). For dog-rose, we subsampled three thickets that varied in

volume from 0.08 to 0.19 m³ and calculated a conversion factor of 0.83 kg m⁻³ after oven drying stems and crowns.

Carbon in herbaceous vegetation was estimated from cover-biomass regressions in four 1 m × 1 m quadrats positioned 1 m from plot corners and one identical quadrat in the plot centre. To avoid destructive sampling of herbaceous vegetation within the long-term enclosure experiment, we developed a biomass-volume regression using fifteen 1 m × 1 m quadrats in the surrounding landscape. In each quadrat, we estimated the percent cover of all vegetation and sward height using a standard disc (30 cm diameter, 200 g mass) dropped from a 1-m height. The drop disc method has been widely used for measuring productivity and herbivore impacts of grassland and agricultural landscapes (Stewart et al., 2001). We then harvested and oven-dried all above-ground vegetation in each quadrat and fitted 11 different linear models to predict log-transformed vegetation dry mass (Table A1). The model with the lowest value of the Akaike Information Criterion corrected for small sample sizes (AICc) was then used to estimate biomass in each of the five 1 m × 1 m quadrats recorded in the larger 7.2 m × 7.2 m experimental plots. All biomass was assumed to be 50% carbon (Matthews, 1993). We also compared vegetation composition only at the onset of our experiment in 2009 by summing the percent cover of all species in five identically positioned and sized quadrats (i.e., four corners and plot centre) and destructively sampling biomass in the plot centres.

In 2018, we measured below-ground carbon content to 10 cm depth by pooling duplicate soil samples in each plot. After measuring mass loss-on-ignition after 8 h at 550 °C and correcting for bulk density measured volumetrically by displacement, we multiplied values by 0.58 to convert them to total organic carbon (De Vos et al., 2005). Carbon in herbaceous vegetation and below-ground were normalised to the area of the 7.2 m × 7.2 m plot – the true unit of replication – for statistical analyses and direct comparison with carbon in woody stems. The area of the entire plot was divided by the total area encompassed by quadrats or bulked soil cores and then multiplied by the sum of measurements in the corresponding subsamples. We assumed this normalisation was representative because soil carbon stocks have been shown to vary negligibly in lowland England over the spatial scale of our plots (Lark and Marchant, 2018). We also compared soil chemistry at the onset of our experiment. Three 0.15 m deep soil cores were bulked from each passive rewilding enclosure and the two corresponding trophic rewilding plots in July 2009 with a 5 cm Dutch auger. Samples were frozen at -20 °C and measured for pH, soil available P and K, and total nitrogen and total carbon by a commercial laboratory following standard methods (NRM Laboratories, Bracknell, UK). Briefly, pH was measured in a 1:2.5 water extract, available P (Olsen's) was measured by colourimetry after sodium bicarbonate extraction, and K was measured by atomic absorption spectroscopy after ammonium-acetate extraction. Total nitrogen and carbon were measured using Dumas combustion.

Maximum vegetation height was measured at 20 and 5 random locations per plot in 2009 and 2018, respectively. We also extracted the maximum height of vegetation present in 2019 but not 2001 across all fields from the LiDAR surveys (Henshaw et al., 2021).

To estimate structural diversity in 2018, we used a point-height intercept method at the same locations in the paired plots that were used for measuring vegetation height (Scott, 1965). At each of the five sampling points, we recorded the number of times that an individual plant contacted each of sixteen 20-cm-tall intervals between 0 and 320 cm height along a 1-cm diameter pole. The pole was positioned vertically into the plot so as not to disturb the vegetation by sideways displacement. We then used the Inverse Simpson Index to estimate structural diversity by summing the total number of hits in a plot n_{ij} in each height tier i across each sampling point j (Simpson, 1949):

$$\left[\sum_{i=1}^{16} \sum_{j=1}^5 n_{ij} \times \left(\sum_{i=1}^{16} \sum_{j=1}^5 n_{ij} - 1 \right) \right] / \left[\sum_{j=1}^5 n_{ij} \times \left(\sum_{j=1}^5 n_{ij} - 1 \right) \right].$$

This metric effectively quantifies the number of height tiers occupied by vegetation (Ehbrecht et al., 2016).

Finally, in 2018, we measured family-level diversity, structure, total biomass, and three indices of trophic functioning of ground-dwelling arthropods in 5 paired plots. In each plot, we assessed the community composition of ground-dwelling arthropods with two pitfall traps at least 1 m from plot edges and at least 4 m apart. Plots were sampled on two consecutive nights except for one plot that was sampled only on the second day. Pitfall traps consisted of plastic containers (8 cm diameter) filled with soapy water that were buried flush to the ground with a gap of 1.5 cm between their lid and soil. After 24 h, trap contents were rinsed into specimen jars with 70% ethanol and we identified all individuals to family level. We also classified each family as herbivores (including fungivores), predators (including parasitoids), and/or decomposers (including detritivores, saprophytes, and scavengers), allowing for multiple groupings, after Evans et al. (1961); Barnard (2011); Tilling (2014). Using these data, we calculated the number of unique families (i.e. family-level diversity) and numbers of individual herbivores to predators, herbivores to decomposers, and decomposers to predators found in each plot on each sampling night. We then oven dried the contents of each trap to record dry biomass. Duplicate pitfall traps were aggregated nightly for statistical analyses to avoid pseudo-replication of the same 7.2 m × 7.2 m plot.

2.3. Statistical analyses

We compared trophic and passive rewilding treatments in four ways depending on the response and predicted effects. We used paired *t*-tests to compare impacts on above- and below-ground carbon, vegetation structural diversity, and indices of arthropod trophic structure between treatments in 2018. Second, linear mixed effects models were used to compare treatments at the two time periods (2009 vs 2018) for woody species richness (with a Poisson error structure) and maximum vegetation height (Gaussian errors). We accounted for repeat sampling of the same plot pair by including pair identity as a random effect and weighted the mean maximum height in each plot by the inverse of its corresponding variance. We also used linear mixed effects models to compare baseline (2009) soil chemistry between treatments accounting for random variation due to repeated measurement of the same site (i.e. trophic and passive pairs). Third, for vegetation and ground-dwelling arthropod community data in 2009 and 2018, respectively, we used permutational analysis of variance (PERMANOVA) with the *adonis2* function in the R package *vegan* to compare composition between treatments. We estimated dissimilarity between co-occurring species using the Raup-Crick metric, which compares composition independent of differences in species richness (Chase et al., 2011). We accounted for repeat measurements of arthropods both on the same day and in the same plot pair by including these factors as predictors in our PERMANOVA alongside rewilding (exclosure) treatment. We calculated the marginal effects of each term with 999 random permutations. Finally, we expected that the difference in ground-dwelling arthropod species richness and biomass between paired plots would vary with vegetation structure besides rewilding treatment, so we fitted linear models that accounted for these predictors along with sampling night. We considered only treatment and night in models of trophic structure. We summarised treatment effects from *t*-tests and linear models by presenting means and 95% confidence intervals (CIs). These measures are more informative about true effect sizes and their associated uncertainty than *p*-values (Amrhein et al., 2019). We also simplified arthropod linear models by removing sampling night where 95% CIs for its effect overlapped zero, i.e. was not statistically significant.

To test the effect of rewilding versus a business-as-usual scenario of continued agricultural production (i.e., no rewilding), we compared maximum height between fields exposed to trophic rewilding and permanent pastures used for more intensive grazing. LiDAR returns only the maximum vegetation height at a given point measurement, so we averaged values to derive the mean maximum height per field. We then compared values between trophic rewilding and a control of permanent

pastures using a linear model that weighted observations by the inverse of the variance in maximum heights for each field. For all analyses, data were log-transformed where not normally distributed. All analyses were performed in R v3.6, and code and data to reproduce the analyses are available at <https://github.com/atanzap/experimental-rewilding>.

3. Results

Biodiversity and ecosystem functioning showed contrasting responses between the two rewilding strategies. Woody species diversity was nearly 4-times higher by 2018 within passive rewilding exclosures than in trophic rewilding plots: estimated mean of 1.1 (95% CI: 0.5–2.4) vs 0.3 (0.1–0.9) species respectively (Fig. 3; Table 1). By contrast, ground-dwelling arthropod diversity was 1.2-times greater in the trophic rewilding plots with an estimated mean of 11.1 (95% CI: 5.6–17.4) vs 9.2 (4.4–13.6) families per pitfall trap day within passive rewilding exclosures (Fig. 3). This difference arose because large herbivores made vegetation more structurally complex, i.e. a positive effect of structural diversity on arthropod richness rather than trophic rewilding directly ($t_7 = 2.71, p = 0.030$; Table 1). The vertical distribution of vegetation was estimated to span a mean of 8 (95% CI: 3–13) different 20-cm height tiers in the trophic rewilding plots vs 2 (1–3) tiers in the passive rewilding exclosures, with the less pronounced canopies reaching one-fifth the height: mean of 26 (95% CI: 19–37) vs 138 (87–216) cm, respectively (Fig. 3). Ground-dwelling arthropod biomass was also 2.5-times higher in trophic rewilding plots than in the passive rewilding exclosures: mean of 0.08 (95% CI: 0.02–0.16) vs 0.03 (0.02–0.05) g per pitfall trap day, respectively (Fig. 3). As arthropod biomass varied directly with trophic rewilding, it was likely promoted by large herbivores because of other factors than vegetation structural diversity (Table 1). Trophic structure also shifted outside of the exclosures with herbivorous and predatory arthropods more common relative to decomposers (Figs. 3, 4), and, consequently, the family-level composition of ground-dwelling arthropods changed with trophic rewilding (Table 1).

Carbon stocks also showed contrasting responses between the two rewilding strategies. Total carbon storage was higher within the passive

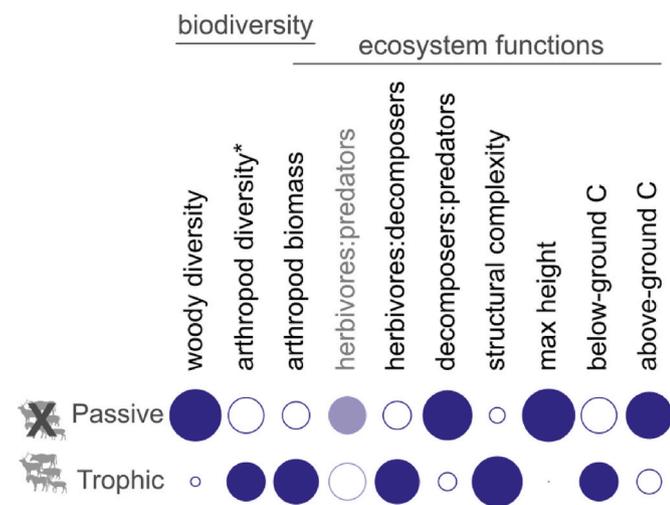


Fig. 3. Introduced herbivores created trade-offs between biodiversity and ecosystem functioning. Circles show mean effect size of ten indicators within passive rewilding and trophic rewilding plots after 9-years of herbivore exclusion. Indicators were normalised to z-scores so they were directly comparable. Filled symbols denote larger values. Differences in ground-dwelling arthropod species composition were omitted because they are multivariate and cannot be summarised by a single value. Grey indicator was the only one without a statistically significant difference between treatments ($p > 0.05$, Table 1). * denotes indirect difference mediated by structural complexity. $N = 10$ plots per treatment, except for arthropod data where $N = 5$ plots.

Table 1

Effects of herbivore presence on biodiversity and ecosystem functioning. Bolded values indicate statistically significant effects. Test statistics show direction of effects, e.g. negative values indicate a reduction in a response with herbivore exclusions, and are either t (paired t -tests, linear models), z (generalised linear mixed models), or F (permutational analysis of variance) values depending on the analysis.

Response	Predictor	Test statistic	p
Woody species richness	Herbivore presence	$z = 0.83$	0.409
	2018 vs 2009	$z = -1.17$	0.243
	2018 vs 2009 for presence	$z = -2.52$	0.012
Arthropod family richness	Herbivore presence	$t_7 = 1.88$	0.102
	Structural diversity	$t_7 = 2.71$	0.030
Vegetation structural diversity	Herbivore presence	$t_9 = 10.4$	<0.001
Maximum height	Herbivore presence	$t_{46} = -0.24$	0.812
	2018 vs 2009	$t_{46} = 3.17$	0.003
	2018 vs 2009 for herbivore presence	$t_{46} = -4.40$	<0.001
Arthropod community composition	Herbivore presence	$F_{1,17} = 3.26$	0.049
Arthropod biomass	Herbivore presence	$t_7 = 2.49$	0.042
	Structural diversity	$t_7 = 0.22$	0.833
Herbivores:predators	Herbivore presence	$t_8 = -0.01$	0.993
Herbivores:decomposers ^a	Herbivore presence	$t_7 = 3.05$	0.019
Decomposers:predators	Herbivore presence	$t_8 = -2.56$	0.034
Below-ground carbon	Herbivore presence	$t_9 = 2.46$	0.036
Above-ground carbon	Herbivore presence	$t_9 = -3.17$	0.011
Total carbon	Herbivore presence	$t_9 = -2.47$	0.036
Soil bulk density	Herbivore presence	$t_9 = 0.70$	0.503
<i>Measured only in 2009</i>			
Above-ground vegetation biomass	Herbivore presence	$t_{19} = 1.57$	0.133
Plant community composition	Herbivore presence	$F_{1,28} = 1.10$	0.439
Soil pH	Herbivore presence	$t_{17} = -1.13$	0.275
Soil total nitrogen	Herbivore presence	$t_{17} = 0.52$	0.612
Soil phosphorus	Herbivore presence	$t_{17} = 0.65$	0.526
Soil potassium	Herbivore presence	$t_{17} = 0.94$	0.361
Soil total carbon	Herbivore presence	$t_{17} = 0.66$	0.520

^a Ratio undefined in one case.

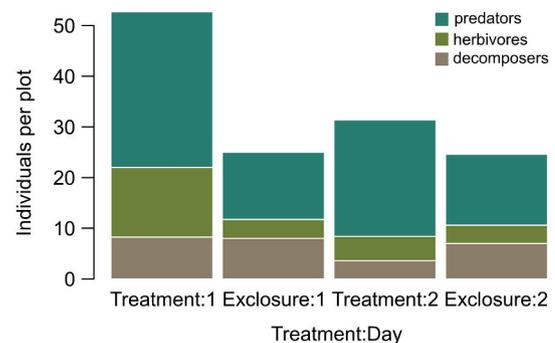


Fig. 4. Predatory and herbivorous ground-dwelling arthropods are more abundant relative to decomposers with introduced herbivores. Bars are the mean number of individuals per plot after two separate sampling nights denoted by number after colon (i.e., nights 1 and 2). Plot-level values were calculated from summing data from two pitfall traps per plot. Indices of trophic structure were calculated from ratios of trophic guilds and were statistically significant between treatments (Table 1).

rewilding exclosures with a mean of 7.8 (95% CI: 5.6–11.4) vs 6.0 (3.8–8.7) kg C m⁻² in the trophic rewilding plots (Fig. 3). While below-ground carbon (C) in the top 10 cm of soil (corrected for bulk density) was marginally lower within the passive rewilding exclosures, with a mean of 3.8 (95% CI: 2.7–5.4) vs 4.1 (2.9–6.4) kg C m⁻² in trophic rewilding plots, C in above-ground vegetation was double within the passive rewilding exclosures with a mean 4.0 (95% CI: 2.0–7.6) vs 2.0 (0.5–3.6) kg C m⁻² in the trophic rewilding plots (Fig. 3; Table 1).

Although several indicators were measured only in 2018, baseline data showed that trophic rewilding plots were not originally different from the passive rewilding exclosures in vegetation or soils. Woody species diversity was similar between rewilding treatments at the start of our experiment and only changed in the trophic rewilding plots by decreasing when exposed to herbivory (Table 1). Likewise, above-ground biomass, vegetation height, and plant community structure were initially indistinguishable between rewilding treatments (Table 1; Fig. A1). Soil nutrients and pH also did not vary between rewilding treatments in 2009 (Table 1).

Trophic rewilding did increase the height of vegetation as compared to maintaining fields under conventional agricultural production. Vegetation that regenerated in fallow fields after trophic rewilding was estimated to average (95% CI) 9 (5–17) cm height vs 1 (<1 to 3) cm in controls under permanent pasture, but was still one-third the height of the passive rewilding exclosures (Fig. 5).

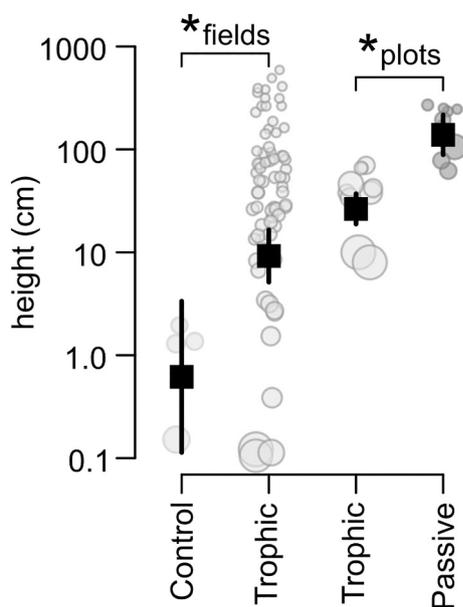


Fig. 5. Shift from intensive to extensive browsing and grazing promotes regeneration more slowly than if herbivores are entirely excluded. The maximum height of vegetation present in 2019 but not 2001 was mapped at 3 m resolution using airborne light detection and ranging surveys (Henshaw et al., 2021). We then averaged values in each of 4 permanent pastures (Control) and 71 formerly fallow fields that had been exposed to trophic rewilding (Trophic) at Knepp Estate. Log-transformed maximum height was compared between field types, and we similarly averaged the maximum height among 2018 point-height intercept surveys in each paired open-fenced monitoring plot to compare trophic and passive rewilding. Circles are the average of maximum height measurements within each field and plot scaled by their inverse variance. Squares are estimated marginal means \pm 95% confidence intervals. * = statistically significant differences in estimated marginal means generated with the R package emmeans: $t_{73} = 3.01$, $p = 0.004$ and $t_{46} = 5.95$, $p < 0.001$ for LiDAR (fields) and point-height (plot) datasets, respectively.

4. Discussion

4.1. Trophic and passive rewilding differentially tackle biodiversity loss and climate change

Trophic rewilding by introducing large herbivores created habitat heterogeneity that benefited ground-dwelling arthropods but reduced total carbon storage when compared to herbivore-free exclosures that represented passive rewilding. Increased habitat heterogeneity can enhance arthropod diversity by providing more niches for species (Joern and Laws, 2013; Woodcock et al., 2009). Arthropod biomass, particularly herbivorous taxa, may also benefit from large herbivores that make higher quality food plants more available (Farrell et al., 2015). Reductions in plant litter production associated with browsing and grazing by large herbivores will further shift arthropod trophic structure away from decomposers (Lind et al., 2017). By contrast, browsing pressure likely remains strong enough to suppress woody plant diversity (Jia et al., 2018). Woody plants are rare in former farmland (Smit et al., 2015), as studied here, and so can experience strong browse pressure, especially outside of the growing season (Hosey, 1981). Consequently, herbivore introductions will still reduce above-ground carbon storage where closed-canopy forest is the natural, late-successional vegetation state (Tanentzap and Coomes, 2012). Even if carbon storage increases with a shift from intensive to extensive animal stocking densities, above-ground carbon storage requires decades of woody plant regeneration to approach its potential in the presence of even limited herbivory (Tanentzap and Coomes, 2012). Increases in below-ground carbon storage, which we attributed in our study to changes in nutrient inputs rather than soil compaction (Table 1), were too small to offset the reduction in total carbon from the prevention of woody regeneration. Belowground carbon may take decades to accumulate after abandonment of agricultural activity and this rate can depend on historical cultivation practices as natural vegetation re-establishes (Schierhorn et al., 2013; Vuichard et al., 2008). Together, our study indicates that trophic rewilding can help managers to deliver some aspects of biodiversity and ecosystem functioning beyond those attained from passive rewilding.

An outstanding question in rewilding is how carbon storage translates into an ecosystem service, i.e., climate change mitigation (Cromsigt et al., 2018; Malhi et al., 2022). Assuming uniform carbon accumulation over time, which may be appropriate over the relatively short duration of our study (Cook-Patton et al., 2020), we estimated trophic rewilding sequestered 7333 kg CO₂e ha⁻¹ yr⁻¹ less than passive rewilding by dividing the difference in total carbon accumulated in vegetation and soils between treatments by the 9-year duration of our study. Other fluxes, like enteric methane emissions associated with ruminants (Sandom et al., 2020), can further exacerbate these differences. For example, we multiplied annual densities of each introduced herbivore species (Fig. 1) by species-specific, per-animal rates of annual CH₄ emissions (Crutzen et al., 1986; Dansen et al., 2015). After summing the values across species in each year, and assuming CH₄ had a global warming potential of 25 over a 100-year period, we estimated introduced herbivores emitted 268 to 905 kg CO₂e ha⁻¹ yr⁻¹ at Knepp solely because of enteric fermentation, further reducing the climate change mitigation potential of trophic rewilding. Rewilding with smaller herbivores (taxa <1000 kg in body size) or without ruminants may help reduce potential methane emissions (Sandom et al., 2020). A large uncertainty is how these differences will change over time periods that are relevant for climate change mitigation (e.g. decades to centuries; Kristensen et al., 2022) and consider interactions with disturbances that control carbon accumulation, such as wildfire. Nonetheless, our coarse estimate emphasises that different types of rewilding can deliver very different benefits to people.

4.2. Implications for conservation policy and practice

Our results suggest that, while rewilding should not be viewed as a panacea for land management, it can be useful alongside other interventions to tackle both biodiversity loss and climate change. By undertaking one of the first experimental tests of trophic rewilding (Tanentzap and Smith, 2018), we found clear trade-offs in its ability to deliver different aspects of biodiversity and ecosystem functioning relative to leaving land to recover on its own, i.e., passive rewilding. These results suggest managers and policymakers will face challenges when choosing what outcomes to optimise, as we found that the added benefits of trophic rewilding may improve some ecological properties (e.g. biodiversity) but not others (e.g. carbon stocks). The different outcomes between trophic and passive rewilding may pose a further challenge for managers if species of conservation concern are associated with different vegetation structure, which we found were favoured by these two strategies. Spatially-explicit, planning frameworks that optimise often competing conservation goals into multifunctional landscapes can start to inform managers and policymakers of how best to reverse both biodiversity loss and climate (Chan et al., 2006). For example, by maximising carbon stocks with passive rewilding or high-yielding tree plantations in small habitat patches, other land could be left for biodiversity conservation through trophic rewilding (Betts et al., 2021). As a mixture of strategies is likely to reduce trade-offs among competing management goals (Butsic and Kuemmerle, 2015), identifying the combinations of trophic and passive rewilding that minimise trade-offs between biodiversity and ecosystem functioning should be a priority of future research efforts. Such varied, multi-scale management may ultimately offer the best way to deliver local- and broader-scale goals.

Managers face additional challenges given the time scales associated with restoration, particularly if the trade-offs between trophic and passive rewilding change over time. For example, we found short-term biodiversity benefits of trophic rewilding, but, over centuries, passive rewilding may lead to old-growth forests. In England, old-growth forests are rare. They are estimated to cover 1.5% of total land area (Natural England, 2023), despite evidence that forests covered 90% of the pre-historic landscape (Kaplan et al., 2009). These ancient woodlands are uniquely associated with species found nowhere else (Kimberley et al., 2013), and will eventually store more total carbon than forests where woodland regeneration is less dense because of higher herbivore densities (Tanentzap and Coomes, 2012). Therefore, the trade-off between trophic and passive rewilding may disappear after centuries, with the latter strategy being best for both biodiversity and carbon storage. Managers need to be aware of these temporal effects when setting their goals, and simulation modelling can play an important role in forecasting landscape change.

Identifying conservation targets is necessary to for managers and policymakers to measure progress towards restoration and our study illustrates the challenges in defining these for a human-modified world (Corlett, 2016). We compared the impacts of trophic rewilding to passive rewilding that excluded large herbivores, assuming the latter represented the natural vegetation succession at our study site before the onset of widespread human impact (Birks, 2005). While restoration of woody biodiversity and carbon stocks was incomplete based on this baseline of passive rewilding, relative to artificial pasture associated with conventional dairying and beef production systems, we found trophic rewilding increased vegetation structure and evidence suggests it will benefit biodiversity by promoting open woodland species (Garrido et al., 2019). Trophic rewilding that reintroduces even some natural

processes into ecosystems can therefore benefit conservation compared to sustained human impacts (Corlett, 2016). However, managers and policymakers need to think carefully about the roles of functional analogues where these are introduced. Although some species introductions can improve the protection of wildlife populations that are threatened elsewhere, this benefit must be balanced with the risk of creating undesirable interactions and invasive species problems, which would reduce the effectiveness of trophic rewilding (Tanentzap and Smith, 2018). Ecological context, such as predator control and landscape connectivity, is another important consideration for any species introductions (Lundgren et al., 2018). Finally, the perceived success of rewilding will depend largely on conservation goals. For example, in 2020, Knepp reintroduced the first wild breeding storks (*Ciconia ciconia*) in Britain for >500 years. Knepp has also recruited large populations of other protected and threatened, charismatic species like the turtle dove (*Streptopelia turtur*) and purple emperor butterfly (*Apatura iris*) (Tree, 2018; Balfour et al., 2021). Yet there remains no objective way to compare these benefits to changes in total carbon storage or woody species diversity. Thus, while rewilding may have predictable ecological outcomes given the traits of both (re)introduced animals (e.g. body mass, feeding strategy, density) and habitats (e.g. climate, productivity, plant community composition) (Cromsigt et al., 2018; Forbes et al., 2019), its success as a restoration strategy ultimately depends on the priorities of local communities rather than historical baselines.

CRediT authorship contribution statement

Andrew J. Tanentzap: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Georgia Daykin:** Investigation, Writing – review & editing. **Thea Fennell:** Investigation, Writing – review & editing. **Ella Hearne:** Investigation, Writing – review & editing. **Matthew Wilkinson:** Investigation, Writing – review & editing. **Peter D. Carey:** Conceptualization, Investigation, Writing – review & editing. **Ben A. Woodcock:** Conceptualization, Investigation, Writing – review & editing. **Matthew S. Heard:** Conceptualization, Investigation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility

All new data that support the findings of this paper (including Figs. 1, 3, 4, Table 1, Table A1, and Fig. A1) are deposited in <https://github.com/atanzap/experimental-rewilding>. Remaining data used for analyses of livestock units in Fig. 1 are given in Table A2. Data presented in Fig. 5 are available at doi:<https://doi.org/10.5281/zenodo.5556944>.

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Appendix A. Supplementary Results

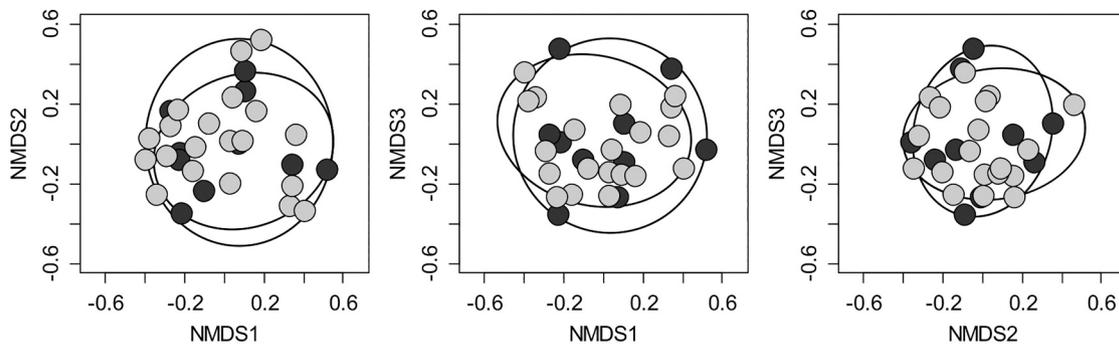


Fig. A1. Initial plant community structure in 2009 did not differ between rewilding and control plots. Plotted points are coordinates from non-metric multidimensional scaling ordination of the Raup-Crick dissimilarity matrix of percent cover for each of 88 vascular plant species in 10 passive rewilding exclosures (dark grey) and 20 paired trophic rewilding (light grey) plots (stress = 0.15). In each plot, we summed percent cover across five 1 m × 1 m quadrats to derive plot-level percent cover. Ellipses enclose all points in each group, which were not statistically significant based on a permutational analysis of variance (Table 1). The number of axes used in the ordination was selected so that further increases in dimensionality did not appear to reduce stress, a measure of the fit between the percent cover of species and distances between sites in the ordination.

Table A1

Model comparison to estimate dry mass of ground vegetation non-destructively. We used AICc to calculate model weights, which estimate the relative likelihood of a model being the best fitting out of the candidate set.

Predictors	AICc	Weight	R ²
log(cover × height)	19.42	0.51	0.71
cover + log(height)	22.41	0.11	0.69
log(cover × height) + (log[cover × height]) ²	22.58	0.10	0.68
log(cover) + log(height)	22.60	0.10	0.68
cover × height	23.70	0.06	0.61
cover + log(height) + cover × log(height)	25.48	0.02	0.67
log(cover) + log(height) + log(cover) × log(height)	25.50	0.02	0.67
cover + height	26.53	0.01	0.59
log(cover) + height	26.86	0.01	0.58
cover + height + cover × height	30.17	<0.01	0.55
log(cover) + height + log(cover) × height	30.42	<0.01	0.55

Table A2

Livestock units per animal calculated according to age and sex. Infants and yearlings were defined as animals <1 and 1 to 2 years old, respectively. Not all classes were recorded for all animals, denoted by NA.

Class	Cattle	Pony	Pig	Red deer	Fallow deer
<i>Method 1</i>					
Breeding female	0.80	0.40	0.20	0.20	0.20
Infant	0.30	0.15	0.05	0.05	0.05
Yearling	0.60	0.30	0.15	0.15	0.15
All others	0.80	0.40	0.15	0.20	0.20
<i>Method 2</i>					
Breeding male	0.65	0.80	0.80	0.50	0.20
Immature female	0.80	NA	NA	0.30	0.15
Infant	0.20	NA	0.10	NA	NA
Yearling	0.65	0.80	NA	NA	0.15
Breeding female	0.90	0.80	0.70	0.35	0.20

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