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ORIGINAL ARTICLE

A critical investigation into the effects and implications of pig (*Sus scrofa domesticus*) rootling on invertebrate biodiversity at a naturalistic grazing site in lowland Britain

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SUMMARY

As more studies catalogue the ongoing decline of invertebrate taxa, the search for solutions to this situation, become more urgent. Knepp Wildland, UK, with its free-ranging herds of ancient herbivore-analogues, has seen enviable increases in invertebrate, bird and mammal numbers. This study investigated the aftermath of rooting by Tamworth pigs and the impact on invertebrate and plant diversity for upto two years after disturbance. Four sites had combinations of grazing and/or rootling pressures (including a control). Plants and invertebrates were surveyed (by sweep net and pitfall trapping) to species level where possible. Abundance, Simpson's Diversity Index and species richness analyses were performed, along with nMDS multivariate plotting of community dissimilarities.

Pig-rootling reduced biodiversity measures in pitfall traps, but this reversed as the disturbance aged. Coleoptera and particularly carabidae abundance was substantially negatively correlated to time since rootling. Sweep net fauna, including pollinators were more abundant with reduced grazing pressure, but moreover with a greater variation in sward structure and height. Feeding guild analysis indicated that pig disturbance decreased omnivores, that were dominant in undisturbed, grazed systems. Total abundance and guild distribution was optimal in ungrazed, post disturbed plots. Multivariate analysis indicated clear communities in all surveys and suggested distinct separation due to both grazing and rootling.

Pig rootling initially reduced overall invertebrate abundance, impacting most on omnivores, especially ants, yet increased the beetle, (particularly carabidae), populations. Once grazing was halted for a year or two, invertebrates increased, rapidly overtaking grazed and control populations. (Grazing alone was found to be less beneficial to invertebrates than control, however, this may be stocking-level dependent).

This study recommends further investigation, but also advocates more widespread use of pigs in conservation. Whether naturalistic grazing can achieve the very light, pulsed grazing required for optimal results, (or curtailment), will depend on site and management factors.

KEYWORDS

Disturbance, invertebrate biodiversity, pigs, rewilding, succession, wild herbivore analogues

1 | INTRODUCTION

Invertebrates are an essential component of our continued survival on earth, (Wilson, 1992). They are an integral element of food production, via pollination and pest control, fundamental to aquatic and terrestrial nutrient recycling, and therefore soil creation, hence in turn supporting habitat development, carbon storage and oxygen production (Catherine, 2010). They are also enmeshed, through both production and consumption, in the survival and control of most other species that we value and depend upon, (Kellert, 1993).

In recent years however, there has been increasing evidence of steep declines in invertebrate populations (Brooks *et al.*, 2012; Conrad *et al.*, 2006; Hallmann *et al.,* 2017) and according to Sanchez-Bayo and Wyckhuys (2019), even possible classwide collapse within decades. (Although, this study is strongly criticised for poor design, (Komonen *et al.,* 2019; Simmons *et al.,* 2019)). Thomas *et al.* (2004), suggest that insect biomass has fallen significantly more quickly than the known losses in birds or plants, and while challenged, (Hambler and Speight, 2004; Shaw, 2005), the paper is convincingly defended by Thomas and Clarke (2004). Moreover, the loss itself of invertebrates, could lead to an extinction vortex encompassing both plant and animal kingdoms.

Thomas and Morris (1994) clarified the reasons for these losses, finding the majority of

British endangered invertebrates associate with very early or late successional stages - bare earth, grassland within two years of disturbance, early wood coppice, early heathland and deadwood. In the opinion of Stewart and New (2007), many of these habitats provide warmer microhabitats to invertebrates near the northern limit of their range; an idea supported by Kirby (2001). Until very recent times, all these habitats have become increasingly rare as land management has evolved away from traditional practices; bare and disturbed earth is often left to succession, coppicing is no longer practiced at scale, heathland is built or forested over and unsightly deadwood is cleared.

Another highly influential factor is habitat integrity. Many invertebrates are poor dispersers with short life-cycles; they often need varied habitat components each year, for shelter, feeding (as adults and larvae) and finding mates, within close proximity. Deviation from this, even for a few months, that could be survived by many plants or vertebrates, can wipe out a local invertebrate population, (Kirby, 2001). However, the European landscape, dominated by agriculture, has become both increasingly monocultural and uniform in structure, where fields of wheat or maize can abut pine plantations, and viable habitats are increasingly isolated beyond the dispersal range of most invertebrates.

Additionally, pesticides, herbicides and ivermectins, inherent to intensive farming, cause further losses. For example, a widely respected, UK-government sponsored study, into the effects of neonic seed treatments on oil seed rape, found despite significant increases in bees from the increased availability of pollen and nectar, on balance, 40% of bee species showed losses of over 10%, purely from this one agricultural scenario, (Heatherington, 2016).

Due to the lack of wide-scale, standardized monitoring, it is undoubtedly difficult to clearly estimate invertebrate abundance far back into the twentieth century, let alone before. However, since many of the known triggers of invertebrate decline can be ascribed to a particular decade or century, it is logical to assume that conditions before those changes would have been party to potentially greater invertebrate, (and hence general), biodiversity. Were it possible to remove artificial fertilizers, pesticides, herbicides and antibiotics from the soil, to more selectively hand manage our woods and deintensify our fields, greater invertebrate biomass would be expected. In the Atlantic period, before widespread domestication, wild herbivores roamed at will, moved on by predators, varying succession and disturbance. Of the elk, deer, auroch, and boar, only deer have survived undomesticated in the landscape of the UK, whilst none of their natural predators (wolf, bear or lynx), now exist to control their populations.

Vera (2000), has theorised that these grazers would have manifold effects on habitat succession, resulting in a cyclic mosaic of grasslands, scrub, open trees and woodland groves, known as wood pasture. This is strongly at odds with Tansley's (1939) accepted norm of primordial forest, and has polarised opinion, (Hodder *et al.,* 2005), but, if correct, would appear as a heterogeneity of substantially varied landscape, at all scales; inherently favourable for vertebrates and invertebrates. The evidence is inconclusive (Rackham, 2006), but most strongly suggests a gradient between wood pasture and closed canopy forest that varied spatially and temporally with soils, topography, climate and herbivore densities.

Due to boundaries, urbanisation and culture, it would be thought inconceivable to return to either scenario in the modern day British Isles. However, over the last twenty years, projects in the field of rewilding have returned large tracts of land (in Britain and Europe) to natural processes, including naturalistic grazing of large herbivores. Rewilding, coined in 1990 by Dave Foreman, a founder of the Wildlands Network in the US, is a hands-off system of allowing large areas of (preferably interconnected) land, broadly self govern, often augmented by the reintroduction of keystone species. Worldwide, rewilding has been implicated in profound trophic cascades that have interested a wider public audience through books like Feral (Monbiot, 2013), but such schemes can conflict with cultural norms and landscapes (Lorimer, 2015). In Europe, notable successes have been the Oder Delta, Poland and Oostvaardersplassen, in the Netherlands; although the model purity of the latter's naturalistic grazing has caused controversy among dutch animal-rights campaigners and even politicians, due to large winter die-offs of herbivores, (Barkham, 2018).

One such venture, at Knepp Castle, West Sussex, has enjoyed significant increases in biodiversity and equally intense scientific observation. Of key importance, is the possibility that Knepp could provide a realistic, successful, financially viable model to regenerate biodiversity, that could be rolled out at a variety of scales by interested land owners, individuals or communities, to provide stepping stones between SSSIs and nature reserves, (Burrell, 2017); fulfilling the mantra, "more, bigger, better and joined", (Lawton *et al.*, 2010, p.viii). Knepp uses modern analogues for extinct native herbivores, under various grazing regimes to achieve a mosaic of varied habitat, the succession of which is being studied.

One of the most interesting of Knepp's assemblage of herbivores, are Tamworth pigs, in place of having wild boar (*Sus scrofa*) active in the landscape. Boar rootling disturbs large areas of moist grassland and woodland, preventing botanical dominance, affecting the grazing of other herbivores through redistribution of unpalatable weeds and driving the development of scrub, (Massei and Genov, 2004). Natural England have yet to recognise this omnivore as native, despite thousands of years of coexistence with our flora and fauna, which dictates that boar were not merely environmentally neutral, but likely to perform essential services for some biota; indeed they are only present at all from farm escapes and illegal reintroductions. Naturally, they have been absent in significant quantities from the UK landscape for nearly a millennium; ecosystems have changed, their predators are extinct, and their future management will require comparative population control. However, observations at Knepp implicate Tamworth pigs in the creation of patches of sallow (willow (*Salix sp.*)), which in turn are instrumental for UK-leading purple emperor butterfly (*Apatura iris*) and turtle dove (*Streptopelia turtur*) numbers (Tree, 2018). UK research into the effect of boar on woodlands, (including bluebells and interestingly, invertebrates), concluded in their role being of negligible impact, except their proclivity for bluebells, although admittedly they are at low population densities (Department for the Environment, Food and Rural Affairs and the Forestry Commission, 2011) . Contrastingly, there are a wealth of unfavourable boar studies worldwide from the non-native perspective, implicating them in predation, farmland and habitat destruction, (Bankovich *et al.*, 2016; Bengsen *et al.*, 2014; Bruland and Eversen, 2010; Meyer and Brisbin, 2009; Sweitzer and Van Vuren, 2002). There is also disparity in popular consciousness between pigs as pork and boar as unhealthy pests, in contrast to condemnation for lethal control of wild swine appropriately targeting piglets and young females (Nahlik *et al.,* 2017). Most hunts and even organised culls, favour older individuals, generating a younger population, but unusually boar can drop the lower age and condition thresholds for primiparity - thereby counteracting the effect of hunting pressure, (Gamelon *et al.*, 2011). Therefore, despite huge human take, and continued urban expansion, suidae populations have risen greatly in Europe since the 1980s, (Massei *et al*., 2015). Additionally, synurbanization is occurring as boar and human populations are driven closer together, (Cahill *et al.*, 2012). There is little balancing positive research into the uses and place of pigs in the landscape.

However there are some naturalistic examples. In the UK, traditional breeds (in lieu of boar), have been used for woodland scarification and rhododendron clearance (CALU, 2006), and are still used for pannage in the New Forest (Verderers, 2019), removing acorns and beech mast. They are effective in removing brambles, weeds and bracken (Conservation Pigs, n.d.;

Randall, 2006). They have been successfully used at Rahoy Hills Reserve, Scotland, to remove bracken and purple moor grass to create seed beds for reforestation (Kennedy, 1998).

Herbivore disturbed soils and mosaic habitats, will undoubtedly play a role in invertebrate abundance and diversity, (Knepp has considerably richer invertebrate biodiversity than arable farmland, (Lyons, 2016)), and their significantly increased bird populations and diversity support this. Therefore, it is reasonable to assume that to fully appreciate whether this kind of rewilding is a route to reversing national (and international) invertebrate declines, it is vital that the individual contribution to the model from each herbivore clade should be understood.

There is not yet enough data on exact pig rootled locations at Knepp to relate to significant time frames of vegetative succession. However, an opportunity arose where a designated area of the estate was solely occupied by pigs in 2017 and 2018, along with unrootled and herbivore-grazed controls, that allowed the analysis of early pig rootling effects on invertebrate biodiversity. This project aimed to investigate the relative abundance, diversity and community structure in key invertebrate and plant orders, between areas subject to pig rootling, areas subject to other herbivore disturbance, and controls. The study's prime objective was to determine the contribution pig rootling has on invertebrate biodiversity, individually and in relation to other herbivores at Knepp, and the wider implications for the field of rewilding.

2 | METHODS AND MATERIALS

2.1 | Sites

The study was completed during May and July 2019 in the middle and southern blocks of the Knepp Castle Estate, near Horsham, West Sussex, UK. The site in the southern block, Lucas (LU), was closely grazed by all herbivores: free-roaming English longhorn cattle (*Bos primigenius)*; Exmoor ponies (*Equus ferus caballus*); fallow deer (*Dama dama*); red deer (*Cervus elaphus*) and Tamworth pigs (*Sus scrofa domesticus*). The field had extensive, fresh, winter 2018 pig rootled areas, (turfs turned over creating bare earth depressions and raised grassy / earthen mounds) over its western third. Grazing in LU was supplemented, particularly around the fringes, by rabbits (*Oryctolagus cuniculus*). Of the three sites that abutted one another in the middle block, the largest, Charlwoods (CW), was again evenly grazed and contained all herbivores, bar pigs. Charlwoods Barn (CB), a large paddock reserved for pigs that needed segregation, had been markedly rootled and grazed by pigs in 2017 and 2018, but, unlike LU, not overwinter 2018. By April 2019, CB had a substantially varied sward that covered any signs of rootling. The smallest site, Trollards Barn (TB), included as an ungrazed control, bordered the other two fields and had a high sward around a mowed lawn; it was later discovered to have been grazed by sheep and ponies in 2017 (figure S1 - supporting information).

A late revelation concerning LU, was that under the Injurious Weeds Act 1959, Common Ragwort (*Senecio Jacobaea*) is pulled before flowering, and 100m bordering the northern boundary, is then mowed. It was not considered that this topping would substantially affect results (supported in Ausden, 2006). Unlike the other plots CW was seeded with a county-specific wildflower mix in 2004. TB and CB were traditionally pony paddocks, and only agricultural or wildflower seed dispersal from other fields would have influenced their botanical diversity.

2.2 | Surveys

The study required three different survey types to be undertaken on each site: a vegetation survey in the manner of the National Vegetation Classification (NVC) methodology; pitfall trapping for ground-dwelling invertebrates and light sweep-netting for flying invertebrates, or those that prefer more three dimensional micro-habitat. The surveys aimed to identify carabidae and aculeates to species level, useful due to their bioindication of the health of grassland and bare earth communities, (Burgio *et al.*, 2014; Koivula, 2011; Kotze *et al.*, 2011; Rainio and Niemela, 2003). Sweep netting was found to be an accurate method for hymenoptera bioindication (Tscharntke, Gathmann & Steffan-Dewenter, 2018), although caution is urged in interpretation of pitfall results due to the presence of migrant carabidae, especially on disturbed soils (Matalin and Marakov, 2007).

The invertebrate surveys closely followed the guidance in Drake, Lott, Alexander &

Webb (2007), with the difference, that to interrelate sites, rather than transect methods, surveys were performed across a large, representative area of each site. Each area maximised microhabitat features (e.g. anthills; past/present rootled areas; non-rootled areas), whilst avoiding areas within ten metres of hedges to maintain the predominantly grassland nature of the investigation. To achieve thirty spatially independent replicates for each survey, a 50m by 60m area was dissected into 10m^2 units in CB. In TB, to avoid a mown area of garden, two 50m by 30m rectangles forming an “L” shape were segregated in the same manner. In each of the two grazed fields, a 50m by 80m grid was constructed, giving forty units, to allow for herbivore interference. Some pitfall disturbance did occur, (one trap in LU, and ten in CW), either through lid removal by birds or curious herbivores, allowing rain dilution of the preservative and thence potential escape of some taxa, or through herbivores treading on and destroying traps, resulting in no recoverable sample. In both fields the first thirty, intact, viable, samples, collected in numeric order were included in the survey and the same sample squares used for sweep-net surveys to maintain relativity. Each grid was marked out from a starting position in the NW corner determined from a Garmin Etrex GPS device, (table 1), then a 50m tape, compass and stakes were used to create the grid. Samples were numbered from one to thirty or forty at each site, starting at the NW origin, then alternating five grid squares east then five west, in a southerly manner.

TABLE 1 | Grid location and design for the invertebrate surveys by site.

SITE	TROLLARDS BARN (TB)	CHARLWOODS BARN (CB)	CHARLWOODS (CW)	Lucas (LU)
NW grid coordinate	TQ15438 21175 / TQ15490 21140*	TQ15352 21194	TQ15408 21390	TQ15258 20822**
10m grid squares East	3 / 5*	5	5	5
10m grid squares South	5 / 3*	6	8	8

* TB had two 15 square grids to fit the small field shape; the first figures in each couplet describe the first grid, and the second figure describe the second grid, which are approximately at right angles to each other.
** The 40 square grid in LU pivoted to fit in the field, from the NW coordinate, it went 5 squares on a bearing of 145° and 8 squares on a bearing of 235°.

Unfortunately, the invertebrate surveys predated and spatially differed from the vegetation survey, undertaken in July 2019, which followed an existing methodology, and therefore compromised analytical comparison. The vegetation survey comprised of just twenty randomly distributed 1m^2 quadrats, on each of the four sites. Each site was sectioned into 10m^2 grid-referenced squares, these were numbered, then twenty picked randomly, and the NE corner used for the quadrat coordinate. Whereas invertebrate surveys were concentrated in a representative area, in CW and CB, vegetation was surveyed randomly across the entire field, up to the boundaries. In TB, the vegetation survey overlay a similar “L”-shaped fringe to the invertebrate surveys, although again over a wider area. In LU, both survey types covered the western third of the field, but again at a comparable scale ratio to TB.

2.2.1 | Pitfall Traps

Traps were placed at the centre of the 10m^2 grid-squares, plotted as the origin of two strings crossing diagonally from the grid-square corners and avoiding preferentially taking advantage of features. This ensured each sample was 10m in any direction from any other trap for sample independence and to ensure a balance of sufficient data with animal welfare. Each trap consisted of two stacked, 75mm diameter vending machine cups, placed in an auger-dug hole, levelled with the surrounding earth, (the innermost cup could be emptied of excess earth after levelling, then replaced), covered by pinned 25mm mesh to protect small vertebrates, and finally a raised, pegged aluminium rain cover (figure S1). Traps were laid from 05/05/19 to 10/05/19 and all emptied, then set with 50ml ethylene glycol, to kill and preserve captured invertebrates, on 14/05/2019. Although, due to the presence of a pet dog, this prevented the inclusion of TB in this survey. A pseudo-control of six long-term, ungrazed exclosures, from across Knepp’s southern section were surveyed by pitfall, although their scrub-prevalent vegetation precluded sweep net and NVC survey. All traps were collected 14 days later on 28/05/19 and the contents maintained in solution during identification throughout June and July. The weather during the two week survey was warm, and partially wet.

2.2.2 | Sweep-netting

As for pitfall traps, the sweep-netting methodology closely followed Drake *et al.* (2007). However, two minutes per sample, rather than ten, was deemed sufficient for robust sample returns, whilst allowing thorough coverage of a $10m^2$ grid-square without the need for in-sample, time consuming, net emptying. This enabled the 120 samples to be collected over two days, between 09:00 and 19:00 on 22/05/19 and 24/05/19 thereby minimizing effects of weather, temperature, dispersal and shifting invertebrate population demographics. Along with staggering the order of site visit on each day (half the samples at each site were taken each day), to allow for diurnal variation in emergent animals, this maintained temporal sweep-net sample independence, whilst only requiring two surveyors. One surveyor swept evenly across the entire $10m^2$ for two minutes, emptying samples into plastic, slide-lock bags, whilst the second surveyor managed resources and survey time (figure S1). The weather on both days was warm and sunny, with occasional cloud. Vegetation was removed from the sample bags within 24h to reduce condensation and hence freeze-thaw damage, and the samples transferred to a freezer throughout May to September whilst identification was undertaken.

2.2.3 | Vegetation Survey

The twenty $1m^2$ quadrats surveyed per site, equalled in area the five $2m^2$ quadrats used in an NVC survey, and the methodology employed was similar. Plants were identified using Sterry (2008) or Streeter (2010), to species level, an estimation made of their percentage cover (or number of plants if below 10%) and the average quadrat sward height estimated. The survey was carried out between 09:00 and 19:00 from 02/07/19 to 12/07/2019 by the author, Knepp and volunteer ecologists. The weather throughout was warm and mostly sunny, with no rain.

A floristic index (FI) was applied to each field in the manner of Lyons (2015), as a measure of the floristic and micro-habitat quality of the vegetation (table 2).

2.3 | Identification

Whereas plants were mostly identified in the field, invertebrates were manually identified *ex situ* by sortation, then by a combination of eye, hand lens and binocular microscope to the lowest taxonomic level possible using appropriate keys (Benson, 1952; Broad, 2011; Brock, 2014; Chinnery, 1986; Hackston, 2019; Lindroth, 2012; Morgan, 1984; Tottenham, 1954; Telfer, 2012). Whilst most pitfall samples were well preserved in ethylene glycol, the quality of preservation, (and therefore identification), was more variable in the sweep-net samples. Whether this was due to freezing, damage from netting or net-bag transfer is unknown. Where an individual was not reliably identifiable they were eliminated from the investigation. Quantities of each invertebrate and plant were input into spreadsheets in readiness for statistical analysis.

2.4 | Analysis

Both plant and invertebrate data were analysed with the Vegan library and R software (R Core Team, 2013) for abundance, species richness, evenness and Simpson's Diversity Index (1-D), (preferred by Drake *et al.*, 2007 and Magurran, 2004). Data sets were analysed using non-metric multidimensional scaling [nMDS] multivariate analysis, both by site and species/taxonomic identity to look for community and site associations. Linear regressions could not be performed on plants versus invertebrate measures, (e.g. species richness), due to the difference in sample quantities between the surveys, (i.e. n=20 versus n=30). Therefore, despite the reduction in power, regressions were performed on means of site metrics, (n=3 or n=4), as although unreliable in terms of significance, relating results could still reveal trends. Basic means and standard deviations were performed on the exclosure pitfalls, as lacking samples they had little power for statistical analysis. Invertebrates were assigned to guilds by their main feeding mechanism as an alternative to species level identification (Buschke and Seaman, 2011) and abundance calculated at each site. The complete data set was split into carabidae and pollinator daughter sets to allow abundance analyses to be performed separately.

3 | RESULTS

In all, 13364 identified invertebrates were collected, 5682 by pitfall surveys and 7682 by sweep net surveys. All invertebrate surveys had a sample size of thirty at each primary site, and the vegetation survey had twenty. Six secondary exclosure sites were surveyed by pitfall as pseudo-controls but caution was exercised in the interpretation of this data.

Table 2 shows that the FI is lowest where least grazing occurs, (the control), and highest where grazing is heavy and continual. There are two distinct tiers of mean sward height [MSH], with TB and CB over three times the length of CW and nearly five times that of LU. The variation (standard deviation) in MSH is far greater in TB than any other site.

TABLE 2 | A table of the floristic index designation of each site at Knepp and mean sward height from NVC quadrat data. FI scoring ranges from -2 for ungrazed, reverting to shrub, -1 under grazed with a high sward, 0 grazed with a variable sward, +1 over grazed with a primarily short sward to +2 heavily grazed with a very short sward or bare earth.

	Trollards Barn (TB)	Charlwoods Barn (CB)	Charlwoods (CW)	Lucas (LU)
Floristic Index	-1	0	+2	+2
Mean Sward Height (cm)	38.90±24.71	39.00±14.38	12.65±4.80	8.55±3.19

Figure 1 shows that vegetation richness and diversity decrease in order from LU, CW, CB to TB. Equally, there is a very marked separation in diversity and evenness between LU and CW on the one hand, and CB and TB on the other. There is considerable variation in richness, diversity and evenness within CB quadrats, which corresponds to the low mean evenness.

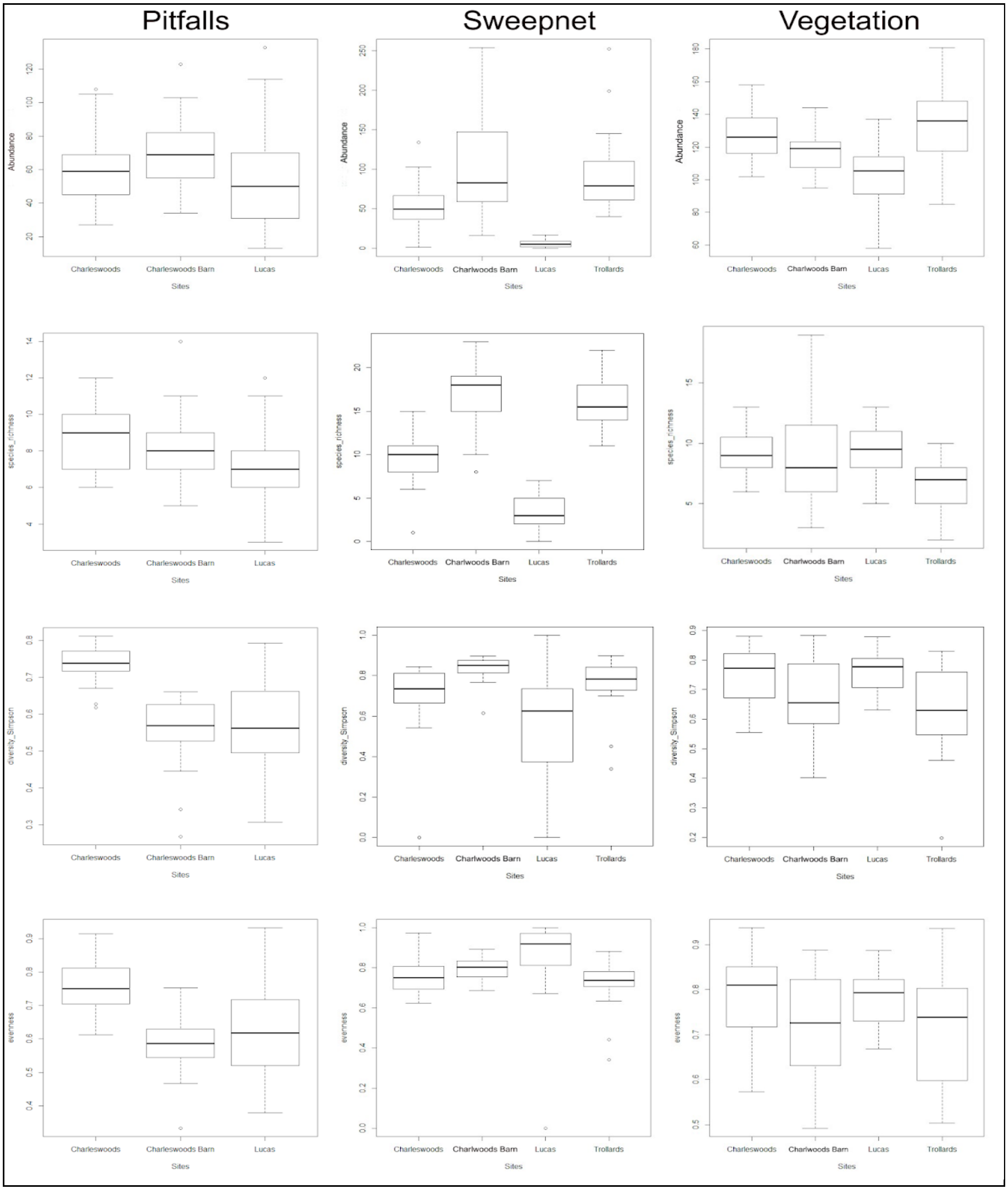

FIGURE 1 | Boxplots of abundance, richness, Simpson's Diversity Index (1-D) and evenness across all surveys. Plots are derived from R (R Core Team, 2013), using the Vegan library. Note, variation in the y-axis in some instances requires care with interpretation.

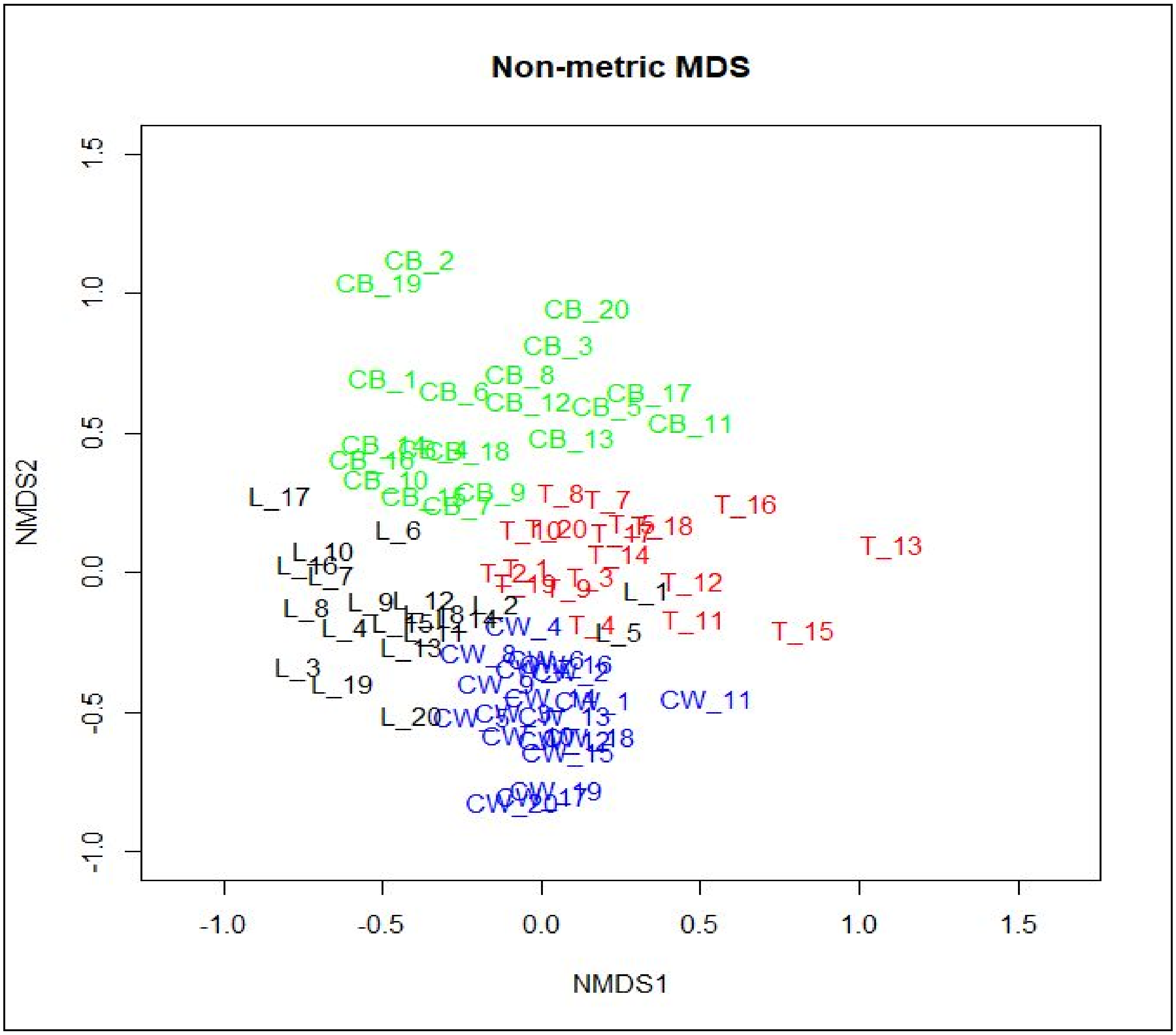

FIGURE 2 | Non-metric multidimensional scaling plot of vegetation surveys, derived from R, using the Vegan library, where CB is Charlwoods Barn, CW is Charlwoods, L is Lucas and T is Trollards Barn. Note, number suffixes apply to quadrat numbers. The stress of this plot = 0.209 which is satisfactory.

The Bray-Curtis distances of community dissimilarity between vegetation quadrats on the multivariate, non-metric, multidimensional scaling plot (figure 2) show considerable separation of plant communities in all four sites. However, there is a clear axis separating LU and CW, from CB and TB, and CB shows greatest variation in communities. Interestingly, there is a slightly less marked axis dividing LU and CB communities from CW and TB communities.

Pitfall richness, diversity and evenness are greatest in CW, whereas abundance is highest in CB (figure 1). Samples in LU are low but very variable for all measures. If results from exclosures are then investigated, the mean exclosure diversity, (0.83±0.09), is greater than CW, (0.75±0.05), whilst the mean exclosure richness, (8.50±3.59), is closer to CW, (8.83±1.93), than CB (8.07±1.96), (although attention is drawn to the high standard deviations in exclosure means).

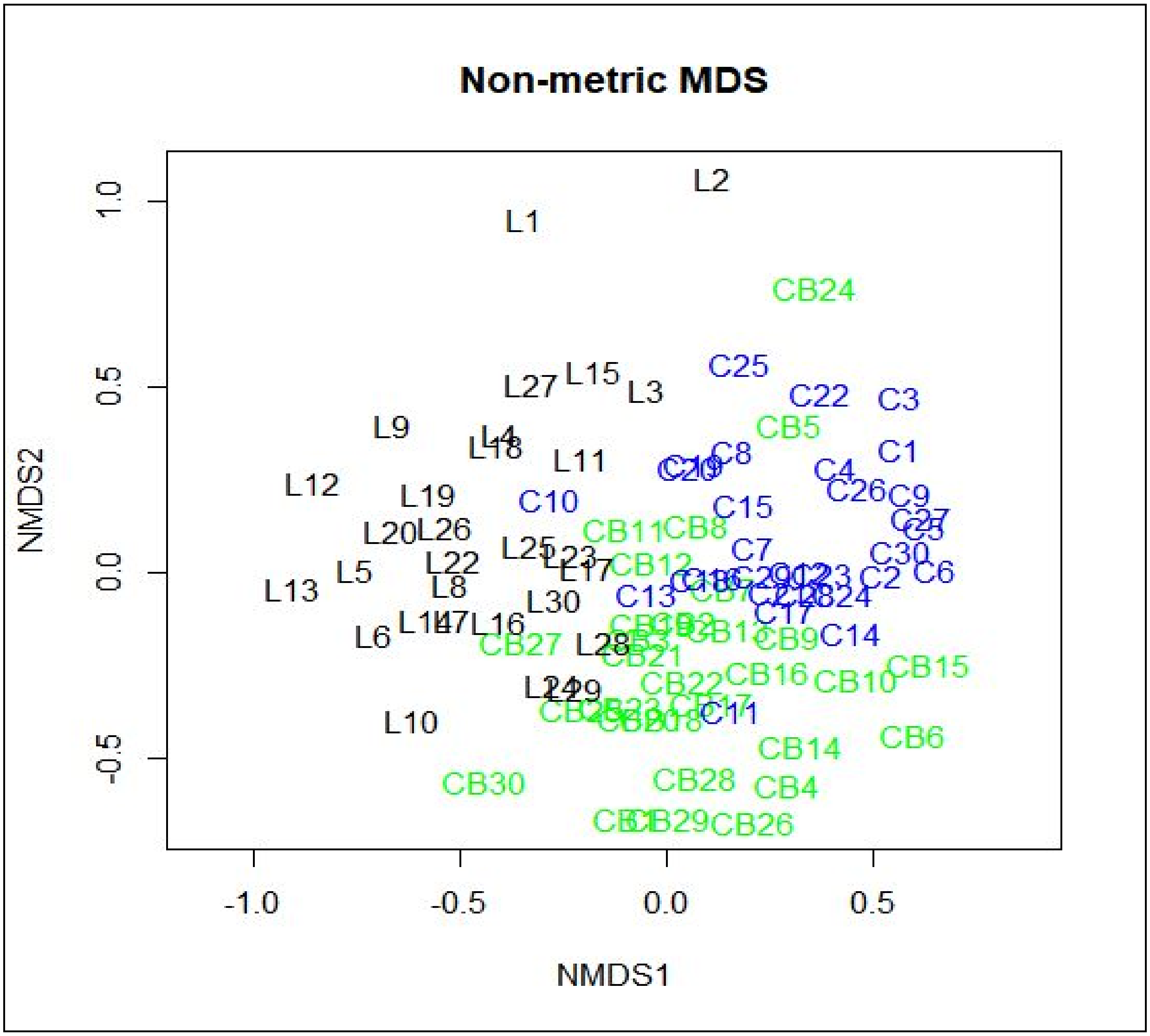

FIGURE 3 | Non-metric multidimensional scaling plot of pitfall surveys, derived from R, using the Vegan library, where C is Charlwoods, CB is Charlwoods Barn and L is Lucas. Note, number suffixes apply to grid square/pitfall sample number. The stress of this plot = 0.273 which is acceptable.

The nMDS plot for pitfall traps, (figure 3), shows clear aggregation of samples within each site, indicating marked between-site community dissimilarities, and there is visibly more intrasite variation at LU and CB, than at CW. However, there is a larger degree of overlap, (community similarity) between CW and CB, than with LU.

Sweep net metrics (figure 1) are high in CB and TB, whilst much lower in CW and LU, although the abundance in CW is 60-65% of that in CB. There is great variation seen in sweep net abundance in CB, and extremely low and uniform abundance seen in LU. CB's measures are greater than in TB, apart from evenness.

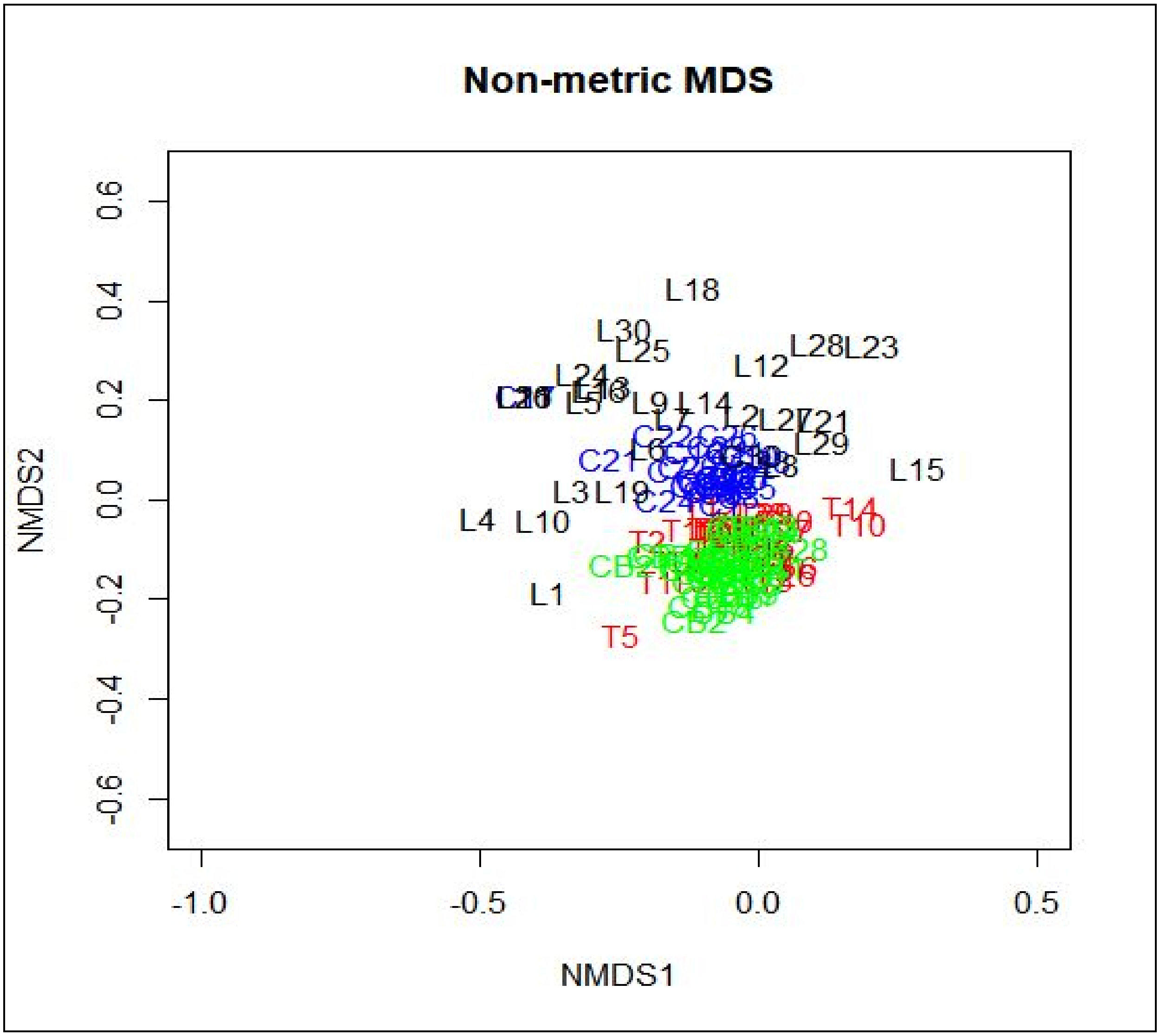

FIGURE 4 | Non-metric multidimensional scaling plot of sweep net surveys, derived from R, using the Vegan library, where C is Charlwoods, CB is Charlwoods Barn, L is Lucas and T is Trollards Barn. Note, number suffixes apply to grid square/sweep net sample number. The stress of this plot is acceptable at 0.156.

Figure 4 shows a great similarity in sweep net communities between TB and CB and to a lesser degree between LU and CW, but very little overlap between these pairs, with a clear axis dividing them. All sites apart from LU show very little intrasite variation.

TABLE 3 | Trends in basic linear regressions between key metrics using R-derived data. (Due to the different sample sizes on plant and invertebrate surveys, only mean site figures could be plotted, giving sample sizes of three for pitfall surveys and four for sweep net surveys. Hence, the degrees of freedom are very low, the models are considerably lacking in power, and therefore, the adjusted R^2 and p-values are purely for reference. However, comparison of p-values from regressions with a common variable can still show trends in the data between the non-constant variables, and provide valuable insights).

Variable	F-statistic	DF	Adjusted R^2	p-value	trend
Mean plant abundance vs. mean pitfall abundance	0.561	1 and 1	-0.281	0.591	Plant abundance explains more of sweep net invertebrate abundance than pitfall invertebrate abundance
Mean plant abundance vs. mean sweep net abundance	1.445	1 and 2	0.129	0.352	
Mean plant diversity vs. mean pitfall diversity	0.162	1 and 1	-0.721	0.756	Plant diversity explains more of sweep net invertebrate diversity than pitfall invertebrate diversity
Mean plant diversity vs. mean sweep net diversity	1.992	1 and 2	0.249	0.294	
Mean plant diversity vs. mean sward height	11.070	1 and 2	0.770	0.080	Plant diversity is more correlated with floristic index than sward height
Mean plant diversity vs. floristic index	60.31	1 and 2	0.952	0.016	
Mean sward height vs. mean pitfall diversity	0.300	1 and 1	-0.539	0.681	Sward height explains more of sweep net invertebrate diversity than pitfall invertebrate diversity
Mean sward height vs. mean sweep net diversity	7.137	1 and 2	0.672	0.116	
Floristic index vs. mean pitfall diversity	0.521	1 and 1	-0.315	0.602	Floristic index explains more of sweep net invertebrate diversity than pitfall invertebrate diversity
Floristic index vs. mean sweep net diversity	2.237	1 and 2	0.292	0.273	

Considering linear regression analysis (table 3), plant abundance and diversity correlate more with sweep net metrics than pitfall metrics. Regression analysis suggests a greater influence on vegetative diversity is explained by FI than MSH. Both floristic index and MSH identify more closely to sweep net diversity than pitfall diversity.

CB has high pitfall abundance, (figure 1), but low overall pitfall carabidae abundance, although high numbers of specific carabidae, *Amara aenea* and *Pterostichus madidus*, (table 4). Also, despite many anthills, and swarms of ants being seen in the field in CB, pitfall numbers are moderate. By contrast, LU has low overall pitfall abundance, (figure 1), but high carabidae abundance, (table 4).

TABLE 4 | Notable species abundances by site and survey, where "g" is grasses and "f" is forbs. Note, relative richness in vegetation surveys gives the number of species per site, (within grasses and forbs separately), as a fraction of all species surveyed at Knepp.

SURVEY	CLASS ABUNDANCE	TROLLARDS BARN (TB)	CHARLWOODS BARN (CB)	CHARLWOODS (CW)	Lucas (LU)
PITFALL	HIGH		Arachnida (spiders); Gastropoda (slugs); *Amara aenea* (ground beetles); *Pterostichus madidus* (ground beetle);	Diptera (true flies); Staphylinidae (rove beetles); Formicidae (ants)	*Tasgius morsitans* (rove beetle); Elateridae (Click beetle); Carabidae (ground beetles); *Poecilus cupreus* (ground Beetle); *Nebria brevicollis* (ground beetle);
	MEDIUM		Formicidae (ants); Elateridae (click beetle);	Arachnida (spiders); *Pterostichus madidus* (ground beetle);	Arachnida (spiders);
	LOW		Diptera (true flies); Staphylinidae (rove beetles); Carabidae (ground beetles);	Elateridae (click beetles); Carabidae (ground beetles);	Formicidae (ants); Diptera (true flies); Staphylinidae(rove beetles);
SWEEP	HIGH	Parasitica (parasitic wasps); Diptera (true flies); Curculionidae (weevils); Coccinellidae (lady bird beetles); Malachiidae (soft winged flower beetles); Chrysomelidae (leaf beetles);	Formicidae (ants); Arachnida (spiders); Bombus (bumble bees); Homoptera (true bugs); Heteroptera (true bugs); Tipulomorpha (crane flies); Chrysomelidae (leaf beetles); Curculionidae (weevils); Oedemeridae (false blister beetles);	Cantharidae (soldier beetles); Orthoptera (crickets/ grasshoppers);	-
	MEDIUM	Arachnida (spiders); Orthoptera (crickets/ grasshoppers); Homoptera (true bugs);	Parasitica (parasitic wasps); Diptera (true flies); Coccinellidae (weevils); Orthoptera (crickets/ grasshoppers);	Diptera (true flies); Coccinellidae (weevils); Homoptera (true bugs);	-
	LOW	Heteroptera (true bugs); Cantharidae (soldier beetles); Oedemeridae (false blister beetles);	Malachiidae (soft winged flower beetles); Cantharidae (soldier beetles);	Arachnida (spiders); Formicidae (ants); Hymenoptera (bees, wasps and ants); Heteroptera (true bugs); Tipulomorpha (crane flies); Oedemeridae (false blister beetles); Curculionidae (weevils); Malachiidae (soft winged flower beetles);	-

				Chrysomelidae (leaf beetles);	
PLANT	UNIQUE SPECIES	4 (1g + 3f)	7 (1g + 6f)	6 (2g +4f)	11 (1g + 10f)
	TOTAL SITE RICHNESS	10/17g + 14/41f	11/17g + 20/41f	12/17g + 15/41f	10/17g + 24/41f
	PLANTS OF NOTABLE ABUNDANCE (Common bent, *Agrostis capillaris* and Yorkshire fog, *Holcus lanatus* abundant in all)	*Dactylis glomerata* (Cocks foot); *Urtica dioica* (Common nettle); *Ranunculus repens* (Creeping buttercup); *Lolium perenne* (Perennial ryegrass); *Festuca ovina* (Sheep fescue);	*Agrostis stolonifera* (Creeping bent); *Ranunculus repens* (Creeping buttercup); *Cirsium arvense* (Creeping thistle); *Veronica chamaedrys* (Germander speedwell); *Poa trivialis* (Rough meadow grass); *Festuca ovina* (Sheep fescue);	*Dactylis glomerata* (Cock's foot); *Lolium perenne* (Perennial ryegrass); *Festuca ovina* (Sheep fescue); *Phleum bertolonii* (Smaller cat's tail); *Poa pratensis* (Smooth meadow grass); *Trifolium repens* (White clover);	*Ranunculus repens* (Creeping buttercup); *Poa pratensis* (Smooth meadow grass); *Trifolium repens* (White clover).

Figure 5 clarifies the details of coleoptera presence in pitfall traps, showing a far greater abundance of beetles in LU compared to the other two sites. Additionally, in LU, and to a lesser degree, CB, carabidae form a far greater proportion of coleoptera than in CW.

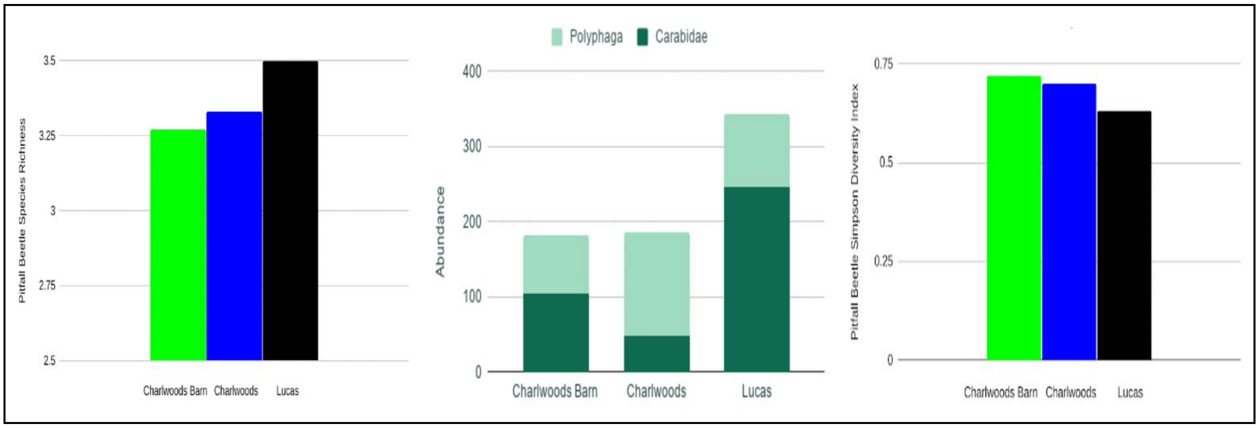

FIGURE 5 | Charts of coleoptera species richness, abundance and Simpson's Diversity Index (1-D) from pitfall data by site. Abundance data is divided between carabidae and non-carabidae (polyphaga) beetles.

There are significantly large amounts of arachnida and formicidae in CB, (figure 6). Arrestingly, arachnida, formicidae, diptera and gastropoda form 85% of pitfall abundance in CW, 86% in CB and just 75% in LU. Also of note, is that despite similar arachnida abundance, TB has far lower formicidae abundance than CB.

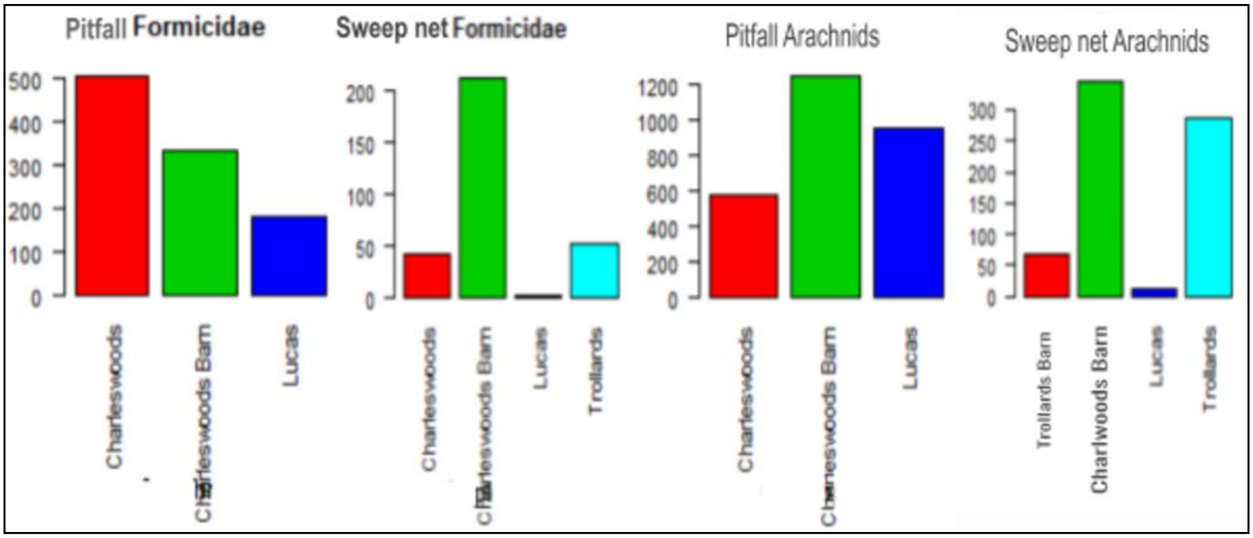

FIGURE 6 | Charts of arachnid and formicidae abundance by site for sweep net and pitfall surveys.

Table 4 shows the variety of sweep net taxa that are highly abundant in CB, is greater than the combined total of all the other sites. Arachnida are again conspicuous, as are many types of plant-borne beetles, tipulomorpha and hemiptera. High and moderately high abundance of taxa are conspicuously absent in CW and LU. Parasitica however, are considerably more prevalent in TB, than CB. Studying diptera in more detail, they form 42% of sweep net abundance in TB, 43% in LU, 44% in CW, however, they form just 23% in CB.

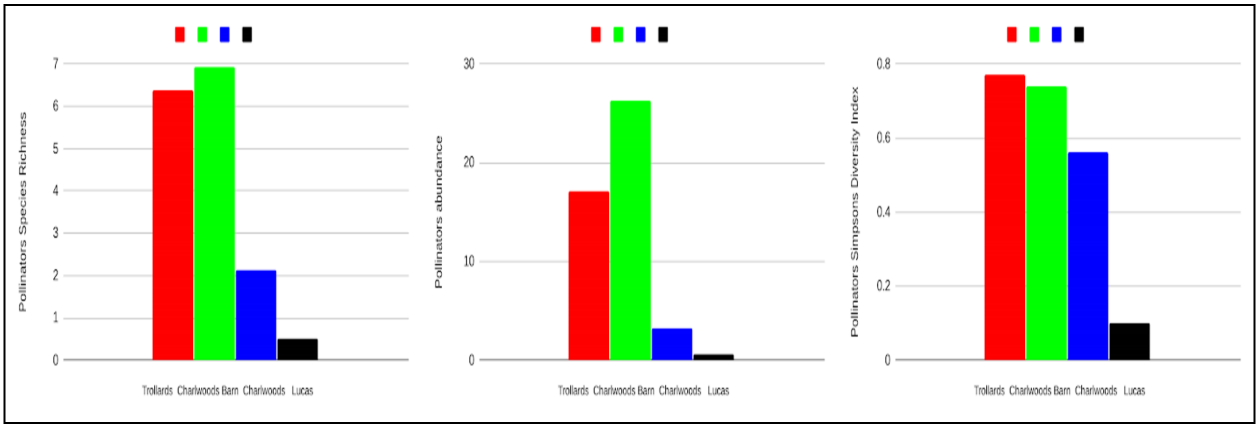

FIGURE 7 | Charts of pollinator species richness, abundance and Simpson's Diversity Index (1-D) from sweep net data by site. Note, diptera and arachnida are absent due to the in-taxa variation in pollination combined with large sample sizes, and hence the likelihood of results being skewed.

When pollinators are studied in more detail, (figure 7), TB and CB significantly out-perform the other two sites, as with the total sweep net statistics, (figure 1). As noted in table 4, CB and TB have high numbers of pollinating coleoptera, and while the former has greater tipulomorpha populations, the trend is reversed for hymenoptera, (apart from species of bombus).

Table 4 demonstrates that LU has far greater richness in vegetation than any other site, and many more unique species, not found in other areas. LU has the least number of dominant species, (table 4), and high evenness with low standard deviation, (figure 1). The intersite variation across the study area in grasses is negligible, whereas relative richness is driven by forb assemblages. The vegetation richness in table 4 is total site richness rather than individual quadrat richness, (figure 1), and it shows that CB has greater forb richness than TB or CW.

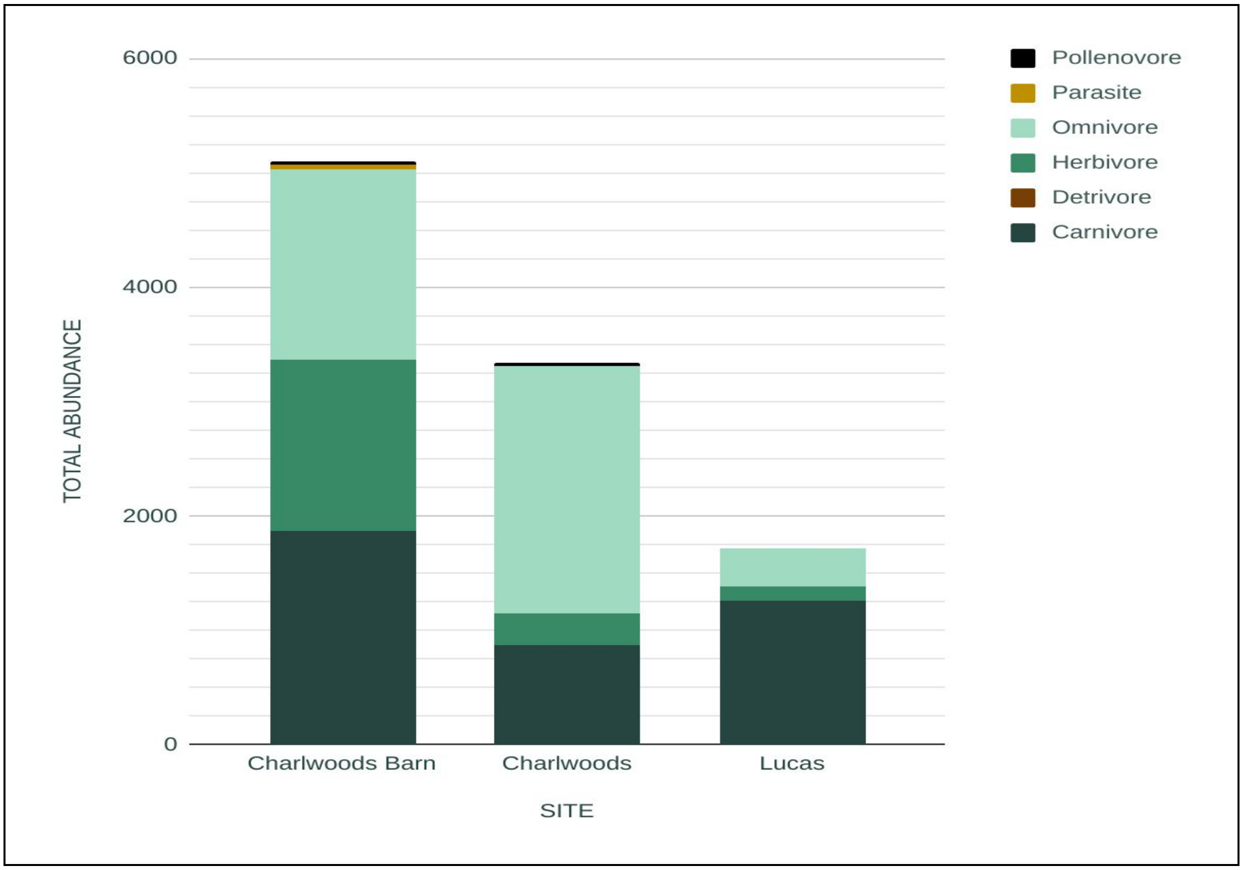

FIGURE 8 | Cumulative abundance of pitfall and sweep net surveys by site, indicating the relative abundance of invertebrates by feeding guild

By combining sweep net and pitfall survey populations and dividing amongst feeding guilds, clear patterns emerge, (figure 8). CB's invertebrates are roughly evenly divided between carnivores, herbivores and omnivores. CW is dominated by omnivores, with carnivores making up about a quarter of the total, and very few herbivores. By contrast, LU has >70% carnivores, (the highest dominance of a guild in any site); omnivores make up most of the rest of the samples. Pollenovores, detritivores and parasites are very underrepresented; although the highest parasite figures were in TB, which is excluded from this part of the study due to the lack of pitfall results.

Figure 8 also demonstrates the total invertebrate abundance between the three sites, with CB clearly more densely populated than either of the other sites. Although tenuous, were the exclosure pitfall results weighted to thirty samples, and added to TB sweep net abundance, the control result would be about 80% that of CB.

4 | DISCUSSION

The data shows some very clear associations for vegetation, pitfall invertebrates and sweep net invertebrates between sites at Knepp.

The multivariate analysis (figure 2) shows a clear division between plant communities in LU and CW, and those in CB and TB, whilst following quadrat diversity and richness (figure 1), paralleling FI (as supported by the regression trends - table 3) and being inversely related to MSH (table 2). These sites do not experience mutual geography, seeding history or pig presence, whereas they do share similarities in grazing pressure. With heavy grazing (thence lower FI), plant communities favour low, creeping forbs or grasses with intercalary meristems. These plants gain dominance as increased grazing reduces sward height both physically, and through selection, reducing competition and shading effects from taller forbs or grass (Andrews and Rebane, 1994). Conflictingly, Bottone (2016) found heavy grazing reduced species richness past a certain threshold at Knepp. However, this is weakened by methodology utilising few replicates and a grazing intensity index generalised across thirds of the estate.

Parallel to this, the multivariate analysis demonstrates that the differences in biodiversity measures (figure 1) are driven by distinct differences in plant community assemblages. This in turn manifests as the second axis on figure 2, between LU and CB communities and those in CW and TB; a separation visible in total richness at site, rather than at quadrat level. Total site richness is most described by variation of forbs, with grasses being fairly consistent across the project (table 4). LU is richest again, with the highest proportion of unique species and consequently least dominants. However, using total site richness, CB is next richest in forbs, separating it from CW and TB, (although not as clearly as LU separates (figure 2)). The level of unique plants in the former pair, juxtaposed to the lack of dominants, is typical of primary succession from bare earth, that reduces as time following disturbance, (primarily pig rootling), increases, (i.e. CB). This agrees with studies that found pig rootling provides opportunities for field weeds and poorly competitive species (Welander, 2014; Wahlgren, 2015).

Therefore vegetative richness and diversity are greatest in LU with its mosaic of heavy grazing, (some of the heaviest in the southern section (Knepp Wildland, 2017)), and levels of primary disturbance. In CB, where the grazing pressure is lacking, and succession is allowed to proceed for one or two years, the quadrat richness and diversity have dropped to less than the steadily grazed CW. Pulsed or seasonal grazing (a scenario between CW and CB) is often optimal for vegetative diversity (Ausden, 2007). However, CB still has greater site richness than CW, and the broadest variation in community structure (figure 2), quadrat richness, diversity and evenness (figure 1) of any site. These results are partially supported by Kotanen (1995), although in an ungrazed prairie, where species richness dropped following pig rootling, but could be richer than control by the next year. In the field, CB's grids had a tussocky, greatly heterogenous sward, whereas TB had a high, even sward (figure S1), but these differences are largely masked by the mismatch between random vegetation quadrats and the sweep net grids. Most significantly, CB had far greater total invertebrate abundance than other sites. TB, left for two years following light grazing, scores lowest in all vegetation measures.

Pitfall trap results again demonstrate clear intersite community differences (figure 3), and show significantly uniform, higher, diversity, richness and evenness in CW than the other two sites (figure 1). Yet CW shares strong grazing, and therefore sward and FI, with LU. Furthermore, it is next door to CB, so geography is nullified, (although there is a small degree of community overlap not shared by LU, which may be due to invertebrate dispersal or migration - figure 3). Once it is considered that exclosure richness and diversity align closest to CW, (although caution is recommended with this data as the exclosure sample number drives high standard deviations and their pitfall locations at the edge of exclusions are within 2m of potentially pig-influenced communities), lack of pig disturbance is the only linking factor, and hence the only parameter, bar seed history, that separate it from LU or CB. However, due to similarities in LU and CW plant communities, this discrepancy is more likely due to pig disturbance than seed mix. This is further supported by the greater variation seen in the LU and CB pitfall communities on the nMDS plot (figure 3), which is likely due to fresh or post-pig disturbance causing a more varied microhabitat.

As described above, the only visible commonality between LU and CB is a history of pig rootling. It appears that bare earth following pig disturbance is likely to be increasing the coleoptera, and particularly the carabidae populations in LU (figure 5; table 4), and that this may explain the higher proportion of pitfall abundance remaining in LU, compared to the other sites, if gastropoda, diptera, arachnida and formicidae are discounted. Results found in boar studies in English woodlands are similar, although explained by boar targeting areas preferred by carabidae (DEFRA and the Forestry Commission, 2011). Such conclusions are discounted here as these grassland sites share similar topography, geography, and in winter, vegetation. Whilst CB is not particularly notable habitat for beetles, having similar coleoptera levels to the heavy grazing regime in CW, its carabidae numbers are significantly higher, although they are assumed to have fallen during the one or two years since disturbance (when compared to LU). Possibly the carabidae abundance is due to the variation in sward height (and therefore favourable microhabitat seen in CB in the field, although a study by Murphy (2018) at Knepp, which used potentially, low-resolution UAV-analysis of habitat, found little correlation). Again caution must be exercised, as these comparisons are partially driven by different invertebrates, whose population sizes, despite every effort to minimise temporal sampling bias, may be dependent on their relative adult emergence schedules. However, enough degree of species overlap exists in the authors opinion, to support the pig disturbance theory.

The data suggests that pig rootling effects eventually improves overall pitfall abundance. Not initially, as LU has the lowest abundance, aligning with Vtorov (1993), but by disturbing, then removing grazing pressure for a year or two, as in CB. Ants and spiders are strongly believed to be responsible for this. It seems probable that spiders drive the higher overall pitfall abundance in CB (figure 1; figure 6). When comparing the similarity in total ant figures between CW and CB, alongside the far greater spider biomass in CB, than CW, it is likely that CB has a much greater ant population than surveyed. This aligns the far higher frequency that ants and anthills were seen in CB, with ants being under represented in pitfalls, due to prior, or *in situ*, spider predation. However, If the predation did occur *in situ*, then this may positively skew the spider figures in CB pitfalls. It is clear that spiders and ants are disguising the abundance of many other taxa, even in LU, where lowest pitfall abundance overall, is masking the highest coleoptera figures. Findings in steep oak forests found spiders dropped in pig rootled sites, but these disturbances were simulated, and the results at odds with lowland studies (Mohr *et al.*, 2005).

Sweep net results show very defined communities again in each field, with great similarities between CW and LU, and between CB and TB, but not between either couplet (figure 4). LU shows the greatest sample variation (figure 4) - possibly from grid squares with, and without pig disturbance. There is a marked higher level of sweep net abundance in CB and TB (figure 1), that is highly suggestive of light grazing history (FI) and higher sward and unsurprisingly, this is supported by the linear regressions (table 3). However, were this hypothesis to be applied fully, TB having experienced the longest time since grazing, should have greater sweep net abundance than CB. As it does not, it appears other pressures need to be accounted for. Along with high mean abundance, CB has wide variation in sweep net abundance, which may be explained by the parallel variation in plant abundance, richness and diversity (figure 1), a result of the varied sward, providing a structurally-complex, mosaic of microhabitats. Moreover, this site has many, highly-abundant, sweep net, invertebrate taxa (table 4), to the point where there may be a saturation of available niches, producing an equilibrium that drives down dominants (and along with high spider levels, possibly explaining the far lower diptera percentage in CB). This hypothesis, originating from pig-disturbed soils, appears to be the most legitimate interpretation for the greatest overall invertebrate abundance occurring in CB. However, proof would be challenging as niche saturation and population equilibrium is a hypothesis that not only suffers underlying conceptual difficulties (Olivares *et al.*, 2018), but would entail high modelling complexity introduced by the sheer number of species, and hence niches, present.

When pollinators are considered, again CB and TB are richest and most abundant (figure 7), which naturally correlates highly with FI. TB is particularly rich in parasitic wasps, whilst CB has many crane flies, ants and bugs. What sets CB apart, are again its' microhabitat options, which favour greater pollinator richness and supports other surveys at Knepp (Goulson and Wood, 2016; Wallace, 2018).

Feeding guild partition relates to habitat succession. In LU, there was little nutrition in May for herbivores, and what there was, formed a rich assembly of pioneer species (table 4), which in turn were likely to support specialist herbivores, and remanent generalist omnivores from the predisturbed phase. These were predated on by a wealth of both specialist and generalist carnivores, including ground beetles and spiders, possibly also capitalising on less fit species remaining from before rootling. This differs from a German study (Mohr *et al.*, 2005) where predator numbers drop after rootling; however this was in a steep woodland system. In contrast, CB has less unique species, and the sward has grown up considerably; herbivores and omnivores have far more opportunity, and the guilds appear to balance out, rather like the niche saturation inference above. It is logical to theorise that the greater microhabitat opportunities available in CB benefits most guilds. It is likely that most species will exist near top-down driven carrying capacity as resources are not limited (Maciej Gliwicz,2002), and were they to decline, enough species are competing for the niche, that to a point, dominance is regulated out of the system. Of course, redisturbance would cause entropy in this system, albeit it contains sufficient quantities of generalist omnivores to survive the new phase shift. In CW, vegetation is dominated by several common species that favour mainly generalist invertebrates, with a few species specialists. With grazing, herbivory is naturally resource limited, so omnivores predominate, as they can switch feeding mechanism to maximise the fewer opportunities available in this less diverse system. These results differ from Cagnolo *et al,* (2002), partly from the distribution of guild partition, but also in the relative abundance within the different grazing regimes. For example, this study found very few pollenovores, detritivores or parasites, but that is probably due to assignment of most of these classes to the overarching omnivore guild, demonstrating the importance of methodological standardisation.

A caveat to the guild apportionment is again that adult invertebrate emergence may result in some species appearing at different times to optimise grazing or feeding. Whilst pitfalls were surveyed at the optimal time for coleoptera, sweep netting in May was less desirable; June being the best compromise for the various taxa under investigation. Therefore, this guild investigation, and equally the entire study, may not fully show all taxa. For premium results, the study would benefit from replication through the year.

In overall invertebrate abundance, as mentioned previously, disturbance from pig rootling, initially results in a large deficit (Scandurra *et al.*, 2016), as shown when comparing LU to CW (figure 8). Most of this difference can be explained by low sweep net abundance, which is due to the low sward, and potentially from physical sweep net difficulties created by differing post-rootled ground levels. In turn the low sward in LU is partly the result of heavier grazing than CW (particularly cattle, but including more visible rabbit encroachment) and possibly delayed sward development in winter rootled areas. Grazing itself, without pig disturbance seems to negatively impact on invertebrate abundance. To clarify, if the tentative control (two years ungrazed) estimate of overall invertebrate abundance of 3972 is used, (a reasonable figure given the total sweep net field abundance of 2712 in TB), grazing in CW has reduced abundance by 14%. In CB, where pig-rootling is left ungrazed, the abundance is 32% greater than control, (even adding CB pitfall results to TB sweep net results, as a more cautious control, CW has 10% greater abundance than control).

This study provides confirmatory evidence of both reduced plant dominance, and accession of pioneering species, following pig-initiated disturbance. Moreover, the bare earth disturbance is highly supportive to both ground beetles and coleoptera in general, and although the initial disturbance reduces overall invertebrate abundance, this may be exaggerated by grazing. Equally it demonstrates the reduction in botanical diversity, (and the increase in structural diversity), that occurs as succession proceeds after pig rootling, and that this is paralleled by a surge in invertebrate richness and numbers, filling up the newly evolving microhabitat niches; ants and spiders appear to particularly benefit. The impact seems to be greatest on omnivore species, when a generalist-friendly, grazed field is rootled, but as succession progresses, their recovery is in line with similar increases in herbivores, resulting in a far more balanced system of specialists and generalists

Therefore, the evidence strongly supports winter pig rootling as a mechanism for improving general invertebrate biodiversity and hence this study recommends far greater prevalence of it as a management technique, (albeit under careful scientific, advisory and welfare scrutiny). It is a tool that could work in many conservation settings, not least naturalistic grazing. Outside of the existence of permanent herds, like Knepp's, there would be scope for translocating discrete herds of pigs to various sites at various times, depending on the management aims (Conservation Pigs, n.d.). In winter, primary disturbance of woodland and grassland would be helpful; in summer, woodland undergrowth and heathland or grassland bracken removal would predominate (Randall, 2006). In autumn, pannage might return (Verderers, 2019), with a view to these being commercial herds providing wild forage meat. Most uses would require pulses of activity before too much damage is caused. Within the field of rewilding, stocking levels must be low enough to avoid large scale disturbance, or sites must be large enough to absorb it. Furthermore, the greatest benefits appear to result from greatly reducing grazing following pig disturbance, and this advice applies to Knepp Wildland. However, this is difficult to achieve under the auspices of rewilding in a size-limited system. Moreover, destocking herbivores like cattle, which would be the easiest solution, can destabilize the financial viability of such projects. The optimal percentage scale of pig disturbance in different habitats, and distance between disturbed areas needs evaluation, particularly from an invertebrate perspective, which likely require consideration in a manner similar to the sources and sinks of metapopulation theory. Medium herds could again financially benefit rewilders as pasture fed meat, but careful consideration of demographic removal must be applied to manage this R selection species. Conservation management dictates, whether large scale biodiversity benefits most from annual rooting or from less frequent disturbance, the ability to direct that effect is desirable. This would be resource, (but should be result), intensive. Contrastingly, rewilding ethos is to largely let the process regulate itself, which requires less management. However, how will the results compare? This juxtaposition will be an evolving debate, that can only be resolved by observing both approaches replicated at scale. In our increasingly anthropogenic landscape, it is likely that a compromise will be required.

This research has various limitations, requires further validation and generates manifold new inquiries. This study's findings are at odds with some of the literature, but that literature is often in forest systems, or with few statistical replicates and written from the standpoint of pigs as pests. Boar are the fastest reproducing ungulate, and generally increasing in both native and non-native ranges, yet detailed, long-term, replicated research on their benefits and impacts is still decidedly lacking (Massei and Genov, 2004) , and that needs to change. Future replication would benefit from a comparable control for both invertebrate surveys. Equally, standardization of vegetation with invertebrate surveys (both sample quantity and sample area/randomness) should be addressed. Additionally, replication through the invertebrate season (April to October) would be useful to reduce bias from insect emergence and from migrant strategists. Incorporation of bioindication tools, like Pantheon classification (Webb *et al.*, 2017), would add an appropriate method of intersite and interstudy comparison.

The role of FI is open to discussion. On the one hand it provides a quick, volunteer-friendly determination of habitat usefulness for invertebrates. However, it is more suited to inform sweep net than ground surveying techniques, it is presently only helpful in grassland, it is probably overly simplistic for this level of enquiry and hence highly subjective, as demonstrated by FI not being able to differentiate between the different grazing regimes in LU and CW.

Repeating this study on a bi or tri annual basis (at least initially) would improve understanding of the successional interplay on invertebrate diversity, and replicating it in different rootled and grazed fields to re enforce the results, and to further understand the interplay of different grazing levels is paramount. Then to study pig rootling in this manner: a) in different habitats e.g. woodland, wetland; b) on different undisturbed successional stages and c) with different management follow-up e.g repeat rootling, grazing, resting and combinations, would be extremely compelling and informatory for this and other sites.

Furthermore, this is just one herbivore of five at Knepp. To further understanding of their various roles in invertebrate biodiversity, if any, study of their grazing and disturbance regimes in a similar manner to this project, would be greatly beneficial and would inform the overall relationship between naturalistic grazing and invertebrates. On a wider scale, other herbivores are used in rewilded systems, (e.g. bison, elk, beaver, geese and rabbits), and their future role, and management would profit from similar knowledge of their direct and indirect relationships with invertebrates.

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7 | SUPPORTING INFORMATION

7.1 | ADDITIONAL SUPPORTING INFORMATION

Additional supporting information, including the master data is available on request from the author.

Various resources, including monitoring and surveying studies are freely available to view from the Knepp Wildland website. Further data *may* be available upon request to interested parties from the Knepp Estate Office.

7.2 | REFERENCE IMAGES OF SITES AND TECHNIQUES

FIGURE S1 | Sites and surveys at Knepp, spring/summer 2019. Clockwise from top right: Charlwoods (CW); Charlwoods Barn (CB); pitfall trap with lid; exclosure with pitfall; Lucas (LU) showing winter 2018/19 pig rootling; sweep net in Trollards Barn (TB). Image credits: Richard Godbehere 2019