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Hedgerow rejuvenation management affects invertebrate communities through changes to habitat structure

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Abstract

Hedgerows are an important semi-natural habitat for invertebrates and other wildlife within agricultural landscapes. Hedgerow quality can be greatly affected either by over- or under-management. Neglect of hedgerows is an increasingly important issue as traditional management techniques such as hedgelaying become economically unviable. In the UK, funding for hedge management is available under agri-environment schemes but relatively little is known about how this impacts on wider biodiversity. We used a randomised block experiment to investigate how habitat structural change, arising from a range of techniques to rejuvenate hedgerows (including more economic/mechanised alternatives to traditional hedgelaying), affected invertebrate abundance and diversity. We combined digital image analysis with estimates of foliage biomass and quality to show which aspects of hedge structure were most affected by the rejuvenation treatments. All investigated aspects of habitat structure varied considerably with management type, though the abundance of herbivores and predators was affected primarily by foliage density. Detritivore abundance was most strongly correlated with variation in hedge gap size. The results suggest that habitat structure is an important organising force in invertebrate community interactions and that management technique may affect trophic groups differently. Specifically we find that alternative methods of hedgerow rejuvenation could support abundances of invertebrates comparable or even higher than traditional hedgelaying, with positive implications for the restoration of a larger area of hedgerow habitat on a limited budget.

Zusammenfassung

Hecken sind ein wichtiger halbnatürlicher Lebensraum für Wirbellose und andere Wildtiere in der Agrarlandschaft. Ihre Eignung als Habitat kann sowohl durch zu intensives Management als auch durch Vernachlässigung beeinträchtigt werden. Vernachlässigung von Hecken wird mehr und mehr zu einem Problem, da traditionelle Pflegemaßnahmen wie z.B. das „Knicken" wirtschaftlich nicht mehr tragbar sind. Im Vereinigten Königreich stellen Programme zur Förderung umweltgerechter Landwirtschaft Fördermittel für Hecken-Pflegemaßnahmen zur Verfügung, aber wenig ist darüber bekannt, wie solche Maßnahmen sich auf die Biodiversität von Hecken-Lebensräumen auswirken. Ein Block-randomisiertes Experiment diente uns dazu, zu erforschen, wie strukturelle Änderungen durch eine Reihe von Methoden der Hecken-Verjüngung die Häufigkeit und Diversität von Wirbellosen beeinflussen. Zu diesem Zweck kombinierten wir Methoden der digitalen Bildanalyse mit Schätzmethoden zur Bestimmung der Biomasse und Qualität des Blattwerkes, um zu bestimmen, welche Heckenstruktur-Aspekte am meisten von der Wahl der Verjüngungsmethode beeinflusst wurden. Alle untersuchten Aspekte der Habitatstruktur wurden durch die Art der Pflege deutlich beeinflusst. Hingegen wurden die Abundanzen von herbivoren und prädatorischen Wirbellosen primär durch die Dichte des Blattwerkes beeinflusst. Die Detritivoren-Häufigkeit korrelierte am stärksten mit der Variabilität der Lückengrößen der Hecken. Unsere Ergebnisse sind Beleg dafür, dass strukturelle Aspekte deutlichen Einfluss auf die Interaktionen innerhalb der Invertebraten-Zönose ausüben und dass Hecken-Pflegemaßnahmen verschiedene trophische Gruppen in unterschiedlicher Weise beeinflussen. Hierbei können alternative Methoden der Heckenverjüngung vergleichbare oder sogar höhere Abundanzen von Wirbellosen zur Folge haben als das traditionelle „Knicken" von

Hecken. Dies wiederum hat bedeutende Konsequenzen für die großflächige Renaturierung von Hecken-Lebensräumen bei begrenzten finanziellen Mitteln.

Keywords: Conservation hedging; functional groups; hedge-laying; higher level stewardship; wildlife hedging;

Introduction

Habitat structure, defined as the composition and arrangement of objects in space (McCoy & Bell, 1991), is widely known to affect interactions within invertebrate communities (Langellotto & Denno, 2004). However, the direction and magnitude of these effects are dependent on the system in question, and the way in which structure is quantified. A meta-analysis of 67 manipulative studies found that enhancement of habitat structure resulted in a significant increase in predator and parasitoid abundance (Langellotto & Denno, 2004), concluding that increases in predators did not follow prey abundance but rather occurred through increased efficiency of prey capture. Predators may also be impaired by increased complexity of habitat structure, for example through reduced foraging efficiency (Legrand & Barbosa, 2003), or a higher number of refuges for prey (Sanders et al., 2008).

At the within-habitat scale, structure may affect invertebrate interactions by altering the availability of resources for herbivores (Denno et al., 2002; Sanders et al., 2008), the ease with which predators are able to capture their prey (Schmidt & Rypstra, 2010), or the degree of interference among predators (Janssen et al., 2007). Alterations to habitat structure may concurrently alter resource quality. For example, the proliferation of young leaves resulting from mechanical disturbance have a decreased ratio of total carbon (C) to nitrogen (N; Havill & Raffa, 2000; Mediene et al., 2002), which can have effects on herbivores that cascade to other trophic levels (Chen et al., 2010).

Hedgerows are a man-made linear habitat covering over 450,000 km in England alone

(Norton et al., 2012), supporting a wide range of plants (Critchley et al., 2013), birds, mammals (Barr et al., 2005), and over 1500 species of invertebrate (UK Steering Group, 1995). Traditional management by hedgelaying, whereby some stems are removed and those remaining are partially cut near the base and laid along the line of the hedge, has given way to intensive cutting by modern tractor and flail machinery or in some cases neglect. Resulting widespread changes in the structural quality of hedges (Croxton et al., 2004) include reductions in berry resources for wildlife (Staley et al., 2012) and 'gappy' hedges (Croxton & Sparks, 2002) or lines of trees (Croxton et al., 2004). A 6% decrease in the length of hedgerow between 1998 and 2007 was attributed largely to under-management, and in 2007 it was also estimated that only 48% of hedges were in 'good' structural condition (Norton et al., 2012). Valued as a priority habitat for conservation (JNCC & Defra, 2012), sensitive management of hedgerows, including rejuvenation, is promoted in the UK through agri-environment scheme funding (Natural England, 2013), making investigation into the potential of more economical methods pertinent.

Few formal comparisons have been made between the impacts of hedge rejuvenation management on invertebrates (Henry et al., 1994) though different methods lead to widely divergent habitat structures which are likely to impact differently on invertebrate community composition. In this study, we tested how invertebrate abundance and diversity in hedgerows was affected by changes in localised habitat structure (i.e. woody biomass distribution) and habitat quality (nutritional value of foliage for herbivores) using a multi-site manipulative field experiment at which hedgerow rejuvenation treatments were applied. We also measured foliage biomass, recognising that this represents both a structural and resource component of the system. We focussed on differences between trophic groups, hypothesising that increasing the spatial variation of (within-habitat) hedgerow structure would increase predator abundance but that herbivores would be more affected by the nutritional quality of food resources. Secondly, we hypothesised that hedges rejuvenated with more economical methods, used in place of traditional hedgelaying, will support a similar abundance and trophic diversity of invertebrates as those rejuvenated with traditional hedgelaying.

Materials and methods

Experimental design

A randomised block experiment was established at four lowland arable sites in East and Southeast England; Newbottle Estate (NE; Buckinghamshire), Utcoate Grange (UG; Bedfordshire), Monks Wood (MW; Cambridgeshire) and Wimpole Hall (WH; Cambridgeshire). At each site, four rejuvenation techniques and an unmanaged control (Table 1) were randomly allocated and applied in October 2010 to 15 m contiguous sections (plots) of uniform hedgerows that had received little management for some years. Treatments were replicated two or three times at each site, depending on the length of hedgerow available, giving 10 experimental blocks in total (each treatment replicated once per block). All experimental plots within one block were on the same hedge, and orientation varied between the hedges in the experiment. Hedges were typical for lowland England being largely dominated by hawthorn (*Crataegus monogyna*), with some blackthorn (*Prunus spinosa*) and field maple (*Acer campestre*;

French & Cummins 2001).

Invertebrate sampling

Invertebrates were sampled from each plot on three occasions during 2011 (May, July & September). At 3 m, 6 m & 9 m along the plot a 2 m length of guttering was inserted through the hedge (approximately 50 cm above ground level). The canopy was beaten five times with a stick 1 m above each guttering length. Falling invertebrates were swept from the guttering into a labelled plastic bag with a soft paintbrush and refrigerated (Maudsley et al. 2002). Transferred to 70% Industrial Methylated Spirits, samples were later sorted to order or in some cases family (i.e. Coleoptera) and assigned to a trophic group where possible (predators, herbivores and detritivores; supplementary material Table A1). For each group, the Shannon diversity index (H') of taxa was calculated as $H^{'} = -\sum p_i \ln(p_i)$. where i = order and p = proportion of invertebrates in that order.

Habitat structure and foliage quality: destructive sampling

Destructive leaf samples were collected in July 2011 from four three-dimensional (8000 cm^3) quadrats per plot, at 70 cm height; two positioned at the outer edge of the hedge and two half way into the centre, to encompass variation in foliage density. Leaves were dried at 80 °C for 48 hours and biomass determined. Within these quadrats the length (cm) and width (<0.5 cm, 0.5-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm) of each twig was measured, from which woody volume (v) was estimated using the equation $v = \sum_{i=1}^{6} (\pi {a_i}^2) b_i$, where a is the median width and b is the total length of the twig recorded for each class *i*.

In spring 2011, hedge height and width (at 1 m height) was measured with a pole to the nearest 10 cm at five positions for each plot, and mean height and width calculated per plot. Leaves from six *C. monogyna* branch tips collected at random alongside each invertebrate sample were freeze-dried (Heto PowerDry PL3000) and finely ground. Total carbon (C) and nitrogen (N) content was determined by gas chromatography (Matejovic, 1995) in a Costech Elemental Combustion System CHNS-O (MI, Italy).

Habitat structure: digital image analyses

Digital photographs were taken of plots in January 2011, with leaves absent, holding a white sheet behind the hedge to illuminate gaps. Images were converted to a standard resolution (0.25 cm/pixel) and a standardised area of interest was used for analysis (30-90 cm above hedge base; compatible with invertebrate sampling region). Pixels were assigned to binary values denoting either hedge or gap, using a signature file created iteratively from the image(s) in a batch supervised classification with ERDAS IMAGINE 9.3 software (Fig. 1; Intergraph, 2013). For each gap the coordinates of the centre point and area (cm^2) were extracted using ENVI 5.1 software, from which the number of gaps and coefficient of variation (CV) of gap area was then calculated. The ratio of woody hedge:gap was also calculated as the proportion of total pixels of each value.

Data analyses

The invertebrate abundance data were multiplied by the height of each hedge plot, as the beating method used sampled a constant height of the hedge above the guttering collection tray (1 m). This scaled invertebrate abundance to the dimensions of each experimental plot. Linear models were used to test relationships between rejuvenation treatment and habitat structure (coefficient of variation in gap area, number of gaps /m^2, lateral branch volume, hedge:gap ratio, foliage biomass) and the quality of herbivore resources (C:N ratio of foliage). This analysis was repeated for invertebrate data scaled by hedge height. Site and block were initially included as factors in linear models. Block did not contribute to the explanatory power of the models, and so was removed from final analyses.

The effects of rejuvenation treatment and habitat variables on abundance and diversity of invertebrates in different trophic levels were tested. Spearman's rank correlation was calculated and a cut-off coefficient value of 0.5 used to identify excessively collinear explanatory variables (Zuur et al., 2009), resulting in hedge:gap ratio being excluded from the analysis. Linear models containing these variables, and site, were constructed for each of nine responses relating to invertebrate community composition (abundance and diversity, and ratios between each trophic group), and simplified using backwards selection. Where a significant effect of rejuvenation treatment was shown *post hoc* Tukey tests were used to determine which treatment levels differed. As habitat variables were collinear with treatment, separate models containing only treatment and site were used to assess management effect. The fits of the two models were compared using Corrected Akaike's Information Criteria for small sample sizes (AICc) to assess the relative importance of treatment versus the continuous measures of hedge structure that may represent mechanistic drivers behind the impacts of management on invertebrate responses.

Data were transformed (natural log, square root, arcsin or squared) to meet assumptions of normality where necessary and untransformed means (± standard error) reported in results. All analyses were carried out in R version 3.0.1 (R Core Team, 2013), with packages glmulti (Calcagno & Mazancourt, 2010) and multcomp (Hothorn et al., 2008).

Results

In total 10,769 invertebrates were collected from beating the hedge canopy in 2011; no interactions were found between treatment and month so data were summed across months for further analysis. The most abundant taxa in decreasing order were Collembola (n = 4554), Acari (n = 1322), Coleoptera (n = 1197), Araneae (n = 811), Psocoptera (n = 597), Heteroptera (n = 570), Diptera (n = 447) and Psylloidea (n = 400). For all other taxa <250 individuals were sampled. Of the predators the most abundant taxa were Araneae (60%), parasitic Hymenoptera (17%) and Dermaptera (11%). Herbivores were more diverse, but dominated by Psyllidae (31%), Curculionidae (17%) and Aphididae (11%), and the most abundant detritivore taxa were Collembola (79%), Psocoptera (10%) and Lathridiidae (10%).

Relationships between rejuvenation treatment and invertebrate community composition

Rejuvenation method affected the number of invertebrates in each trophic group (Fig. 2 and Table 2). In the three laid treatments detritivores were on average 2.1 and 1.5 times more abundant than the control or circular saw treatments respectively (Tukey's HSD $P<0.01$), and herbivores were on average 1.4 times more abundant than in the latter (Tukey's HSD $P< 0.05$). The abundance of predators was 1.9 times greater in the Midland-style hedgelaying and wildlife hedging than either the control or the circular saw treatments (Tukey's HSD $P< 0.01$) .

When data were scaled to account for hedge height, the effect of rejuvenation treatment remained significant for predators ($F_{(4,42)} = 8.21$, $P = <0.001$) and herbivores ($F_{(4,42)} = 9.23$, $P <0.001$) similarly. The control treatment supported 2.2 times more herbivores and 1.9 times more predators than the average of all other treatments except the wildlife hedging. The Midland and wildlife hedging treatments also had 1.6 times more herbivores (Fig. 2A) and 1.7 times more predators (Fig. 2B) than the circular saw treatment (Tukey's HSD $P < 0.05$). Detritivore abundance scaled by hedge height was 1.3 times greater in the Midland and wildlife hedging than the circular saw treatment (all Tukey's HSD $P < 0.05$; overall treatment effect $F_{(4,42)} = 3.91$, $P <0.001$; Fig. 2C).

Relationships between rejuvenation treatment and habitat factors

Treatment affected all habitat variables tested (Table 3). The C:N ratio of foliage was lowest in the circular saw and highest in the control. The midland-style and conservation hedgelaying, and the wildlife hedging were intermediate. All three laying techniques increased foliage biomass (g/m^3), particularly the Midland-style, which was was over 2.5 times that of the control and 1.5 times that of the wildlife hedging (Table 3).

The control had a smaller volume of lateral branches per unit area than the conservation hedgelaying and wildlife hedging (Table 3). The coefficient of variation of gap area (CV), which indicates a more variable structure containing open areas (see Fig. 1), was largest in the control and circular saw treatments, and smallest in the wildlife hedging. The total proportion of hedge:gap was collinear with lateral branch volume and CV (Spearman rank correlation: $r_s = 0.56$ and $r_s = 0.67$ respectively, $P < 0.001$), but in contrast differed between wildife hedging and other laid treatments. The lowest proportion of hedge:gap was found in the circular saw treatment and the highest in the wildlife hedging.

Although some treatments showed concomitant increases in foliage biomass and decreases in CV, the Midland-style hedgelaying treatment had a significantly higher foliage biomass than the wildlife hedging, but no difference in CV. A very weak correlation (Spearman rank correlation: $r_s = -0.24$, $P = 0.09$) between width and foliage biomass x CV, suggests there were no confounding effects of increased width (i.e. of wildlife hedging).

Habitat factors affecting invertebrate community composition

Foliage biomass had a positive effect on herbivore and predator abundance, with a 500 g/m^2 increase equating to an average increase of five and 15 individuals respectively (Table 2; Fig. 3A and 3B), although there was no effect on the ratio of predators to herbivores. Detritivore abundance was related most strongly (negatively) to CV (Fig. 3c), decreasing from approximately 200 to just a few individuals over the measured range. The ratio of detritivores to predators was also negatively correlated with CV (Table 2; Fig. 3d), and to herbivores slightly less so (Table 2). The quality of resources for herbivores (C:N ratio of foliage), was not a significant factor for any invertebrate community response variable tested, despite differing between treatments. Treatment did not affect the Shannon diversity index for any trophic group. The diversity of herbivores was negatively correlated with CV, with a slightly positive relationship to number of gaps /m^2 (Table 2); across the range of CV there was an average loss of three herbivore taxa ($F_{(1,45)} = -2.52$, $P < 0.05$).

Variation in most invertebrate community response variables was better explained by treatment than by the structural variables (Table 2). As the management treatments are the cause of structural changes, this is to be expected, but one exception was the detritivore to predator ratio, for which the variation in gap size had an effect independent of treatment.

Discussion

Hedgerow management affecting invertebrates

Hedge rejuvenation method resulted in considerable immediate differences in the structure and quality of hedgerow habitat which had knock-on effects on invertebrate communities. Techniques where the hedge was laid increased foliage biomass, though less so in the mechanical wildlife hedging. A positive relationship between foliage biomass and invertebrate abundance corroborates previous findings, particularly for spiders (Gunnarsson, 1990), and herbivores (Whitfeld et al., 2012). Greater net positive effects of foliage biomass on predator abundance compared to herbivores were found, which could potentially reflect increased availability of refugia from intra-guild predation for predators (Gunnarsson, 1990), or increased prey availability enhancing population growth (Denno et al., 2002). However, the ratio of these two trophic groups did not relate significantly to either treatment or habitat structure parameters, so the data does not strongly support the hypothesis that within-habitat spatial variation in structure differentially affects herbivores and predators. An increase in the foliage quality for herbivores (C:N ratio; Mattson, 1980), was found in treatments where considerable cutting had occurred (circular saw, Midland-style and conservation hedgelaying; Mediene et al., 2002), but the hypothesis that herbivore abundance would be more affected by the nutritional quality of foliage than by habitat structure, was not supported. It is possible that fecundity increased (Awmack & Leather, 2002) whilst other factors such as interactions with predators and parasitoids reduced abundance (Havill & Raffa, 2000). Further research employing smaller-scale mesocosm experiments (e.g. Langellotto & Denno, 2004; Woodcock & Heard, 2011) could be used to elucidate these mechanisms.

Detritivore abundance has previously been shown to correlate with branch biomass (Halaj et al., 2000). However, we found heterogeneity (CV) of gaps to be more relevant with lower CVs (less variation) related to higher abundances. Psocoptera and Lathridiidae are specifically associated with bark (New, 1970; Lawrence & Newton, 1980), while Collembola benefit from the retention of dead foliage within the canopy habitat, both of which a more closed and clumped distribution of branches (lower gap area CV) is likely to provide. Why less variation in gap size related to increased diversity of herbivorous taxa is less clear. One line of enquiry that could be explored in future studies is whether there is any relationship to the provision of nectar and pollen resources important to herbivores (Wäckers et al., 2007).

Implications for rejuvenation management practice

Our study is unique in its use of a multi-site, replicated manipulative field experiment to compare the relative effects of different hedgerow rejuvenation techniques. Few previous studies addressing habitat structural effects on invertebrate abundance have also quantified resource quality for primary consumers within an arboreal context (but see Facey et al., 2014). We found that when the overall size of hedge was taken into consideration, the unmanaged hedge supported the highest abundances of predatory and herbivorous invertebrates. However, rejuvenation treatments are designed to prevent hedgerows from developing into a line of trees and in this context management impacts are important to consider if farmer goals (e.g. management efficiency and effectiveness) are to be better aligned with optimising the value of hedge habitats for wildlife. Farmer goals are rarely about optimising invertebrate abundance, but rather the maintenance of a reasonably compact hedge habitat. Moreover, we assessed the response of invertebrate community over the spring – autumn following winter hedgerow rejuvenation. Over the longer term the effects of rejuvenation may reduce as the hedgerow plants grow and structural differences diminish, especially between the three laid rejuvenation methods.

In contrast to Henry et al. (1994), where number of insect orders increased with hedgelaying (though their comparison was only against pollarding), treatments had no effect on invertebrate diversity at the level of order/family. While reshaping a hedgerow with a circular saw reduced the adundance of invertebrates in the first year after management, other techniques performed similarly to the traditional Midland-style laying. This supports our hypothesis that the wider use of these more economical methods is unlikely to have detrimental effect on the abundance of invertebrates. Consideration of ease of future management is required for some techniques e.g.Wildlife hedging, but this should be offset with their potential benefits e.g. supporting more invertebrates than other techniques. Overall the techniques we tested reduced the cost of traditional hedgelaying from half to less than a quarter. As such they represent a more efficient and cost effective way of rejuvenating a greater number of hedgerows (e.g. under AES) without compromising a key element of the biodiversity they foster.

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Appendix A. Supplementary data

Allocation of invertebrate taxa sampled to trophic level, assigned according to Cooter & Barclay, 2006 & Barnard, 2011 can be found, in the online version, at XXXXX.

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Table 1: Description of experimental hedge management treatments.

Management	**Description**
Midland-style hedgelaying (MH)	Traditional style designed for heavy stock-proofing; some branches are removed, the rest laid to one side of the hedge with frequent stakes and top binders to secure. Results in all foliage being pushed to one side of the hedge, with the other side remaining relatively devoid of foliage during the following year
Conservation hedgelaying (CH)	Reduced labour method of hedgelaying; similar to the Midland-style but with stems laid along the line of the hedge rather than to one side, stakes used extremely sparingly, and binders omitted
Wildlife hedging (mechanical laying; WH)	Novel method where the hedge is layed using heavy machinery; a chainsaw is used to make basal cuts, and a tractor with telescopic handler pushes the hedge over along its length. No brash is removed, and some stems may be severed
Circular saw re-shaping (CS)	A tractor with circular saw attachment is used to re-shape the hedge. This gives a much cleaner cut than the flail attachment used for regular management, and enables larger volumes of brash to be cut and easily removed from the hedge
Control (C)	The hedge remains unmanaged

Table 2: Relative effects of treatment and habitat variables on invertebrate community composition. Results of separate models containing explanatory variables of treatment (M 1) or habitat variables (M 2) on those measures of invertebrate community composition for which significant effects were found.

Response[1]	Model	Parameter	Estimate (±SE)	$F_{(d.f)}$	P	Adj. R^2	AICc
P abundance	M1	Foliage biomass	0.03 (0.009)	$11.14_{(1,45)}$	<0.01	0.43	408.27
	M2	**Treatment**		**$6.29_{(4,42)}$**	**<0.001**	**0.58**	**65.47**
H abundance	M1	Foliage biomass	0.001 (0.038)	$7.50_{(1,45)}$	<0.05	0.37	69.42
	M2	**Treatment**		**$5.20_{(4,42)}$**	**<0.001**	**0.47**	**65.56**
D abundance	M1	CV for gap area	-0.33 (0.06)	$26.13_{(1,45)}$	<0.001		
	M1	**Number of gaps**	0.001 (0.0004)	**$5.54_{(1,45)}$**	**<0.05**	**0.71**	**119.62**
	M2	Treatment		$7.71_{(4,42)}$	<0.001	0.72	122.44
H:D ratio	M1	CV for gap area	0.028 (0.01)	$12.10_{(1,45)}$	<0.001	0.61	-71.49
	M2	**Treatment**		**$2.87_{(4,42)}$**	**<0.05**	**0.59**	**-63.13**
D:P ratio	M1	CV for gap area	-0.037 (0.012)	$7.38_{(1,45)}$	<0.01	0.62	n/a
H diversity	M1	CV for gap area	-0.057 (0.02)	$7.90_{(1,42)}$	<0.01		
	M1	Number of gaps	0.00037(0.00013)	$7.90_{(1,42)}$	<0.01	0.47	n/a

[1] Trophic groups are summarised as P (predators), H (herbivores) and D (detritivores). Response data were transformed prior to analysis to meet assumptions of normality with log (all abundance variables) square root (H:D ratio) or squared (D:P ratio) transformations. Only significant results are reported. [2] Foliage biomass is measured in g/m^3

Table 3: Relative effects of treatment on habitat variables and mean (±SE) per treatment. Treatments are control (C), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH), and effect is significant at $P<0.05$ where direction is specified, according to *post hoc* Tukey's HSD test.

Response	**C**	**CS**	**CH**	**MH**	**WH**	**$F_{4,42}$**	**P**
Mean C:N ratio of foliage	0.36 (0.02) a	0.27 (0.01) c	0.32 (0.01) ab	0.31 (0.02) bc	0.33 (0.01) ab	8.91	<0.001
Foliage biomass (g/m^3)	247 (39) b	225 (26) b	581 (53) a	637 (72) a	432 (72) a	20.11	<0.001
CV for gap area (cm^2)	4.90 (0.62) a	4.25 (0.35) a	2.62 (0.33) b	2.31 (0.29) b	1.68 (0.33) c	13.45	<0.001
Lateral branches (% vol.)	0.32 (0.11) b	0.30 (0.11) b	0.88 (0.28) a	0.77 (0.18) a	0.55 (0.11) a	4.4	<0.01
Ratio of hedge:gap	0.66 (0.06) c	0.63 (0.05) c	0.80 (0.03) b	0.88 (0.02) b	0.95 (0.02) a	21.62	<0.001

Figure captions

Fig.1. Classified images. Example binary images of treatments (average height m ± SE) (A) circular saw (1.85 m ± 0.11), (B) wildlife hedging (2.00 m ± 0.12), (C) Midland-style hedgelaying (1.45 m ± 0.03), (D) control (4.17 m ± 0.10) and (E) conservation hedgelaying (1.40 m ± 0.04) treatments.

Fig. 2. Mean abundance (± SE) of (A) herbivores, (B) predators and (C) detritivores, against rejuvenation treatment. Bars are white for sample abundances, and grey for abundances scaled by the mean hedge height (m). Treatments are control (C), circular saw (CS), conservation hedgelaying (CH), Midland-style hedgelaying (MH) and wildlife hedging (WH).

Fig. 3. Relationships between (A) foliage biomass and predator abundance (B) CV gap area and herbivore abundance (C) CV gap area and detritivore abundance, and (D) CV gap area and detritivore:predator ratio. Regression lines (solid) and 95% confidence intervals (dashed) are univariate relationships only, included to provide a visual reference.

Fig. 1

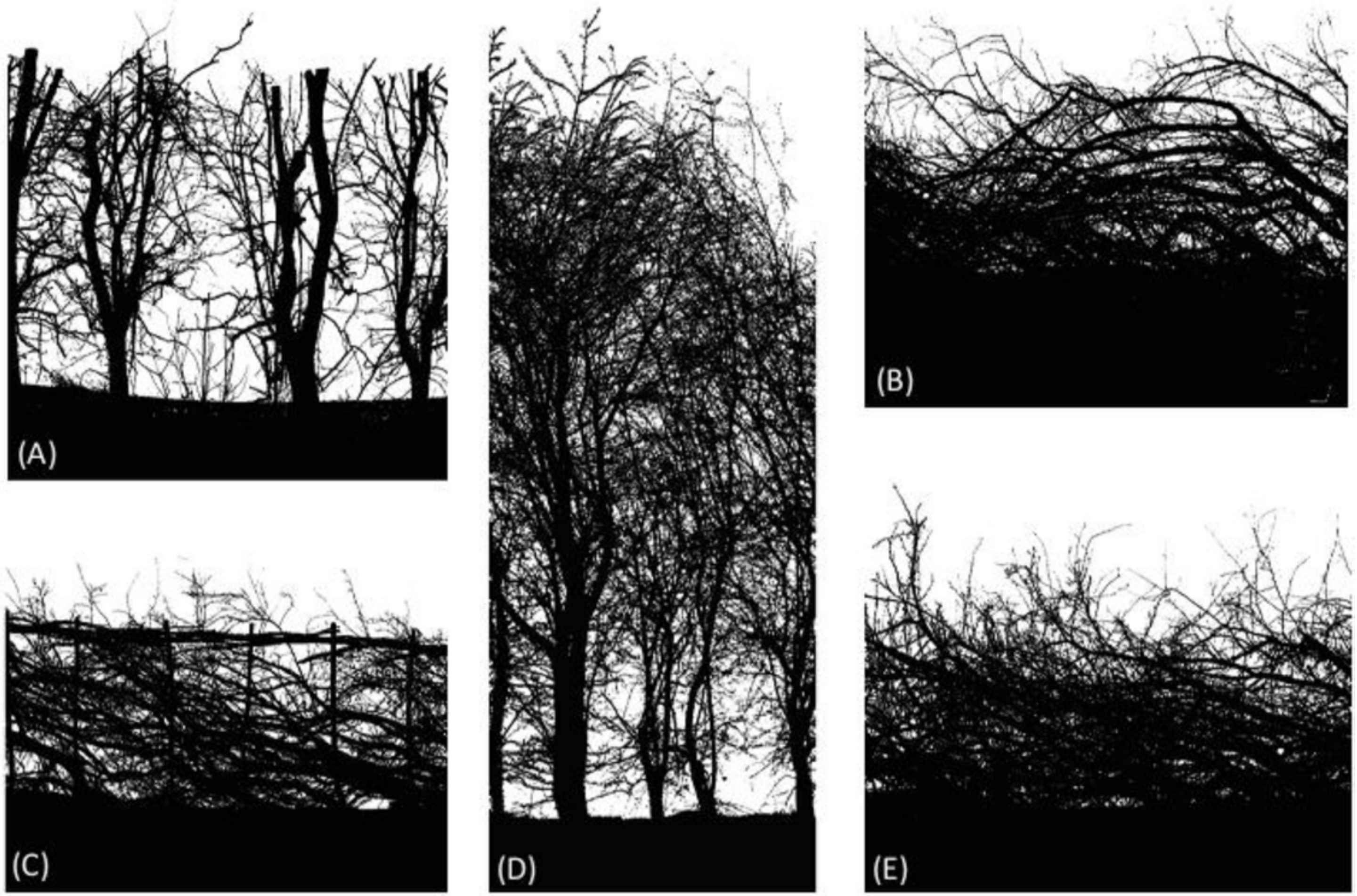
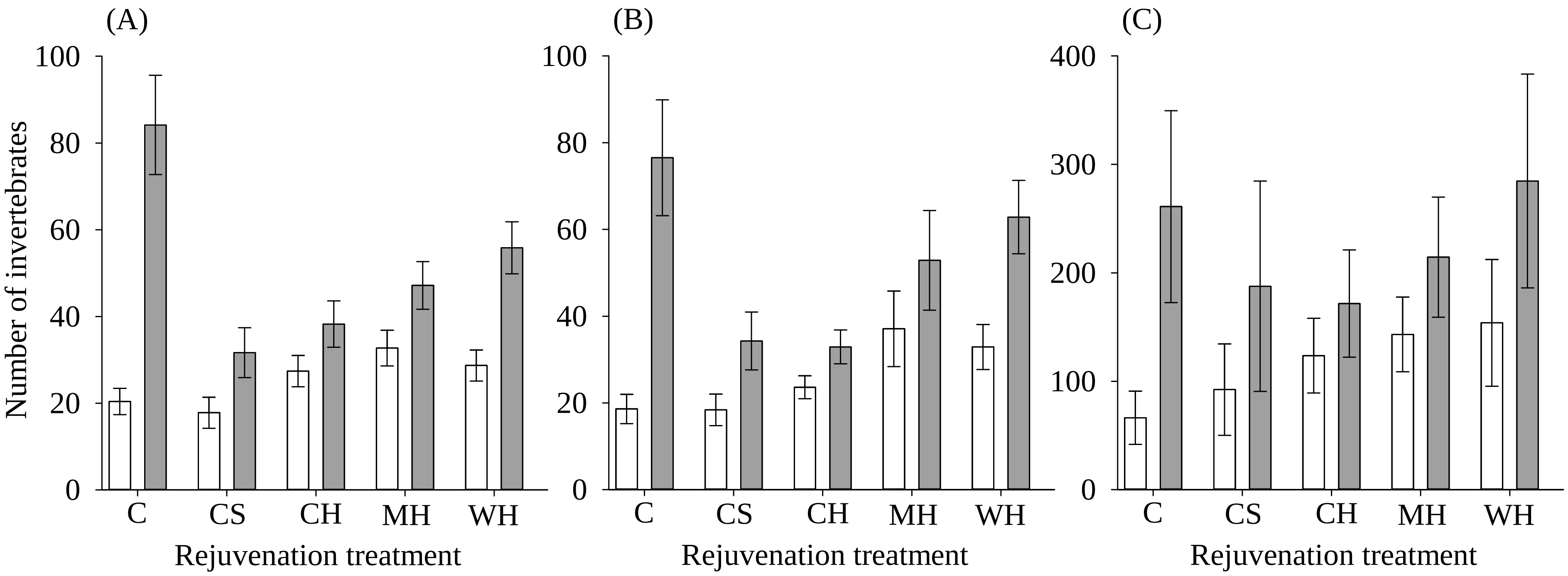
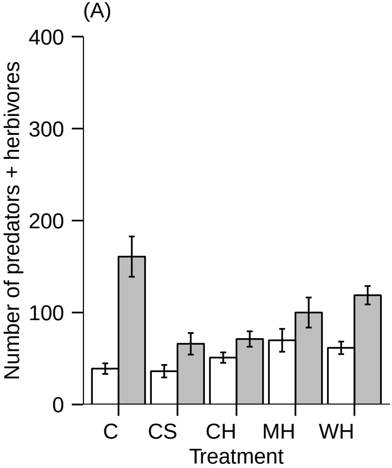
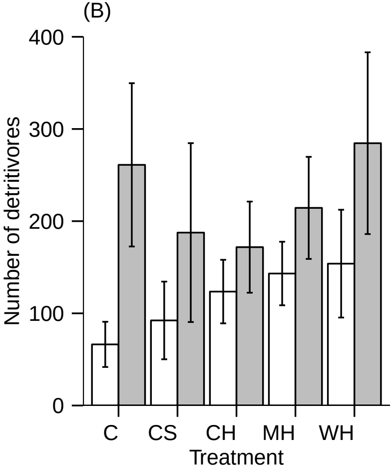
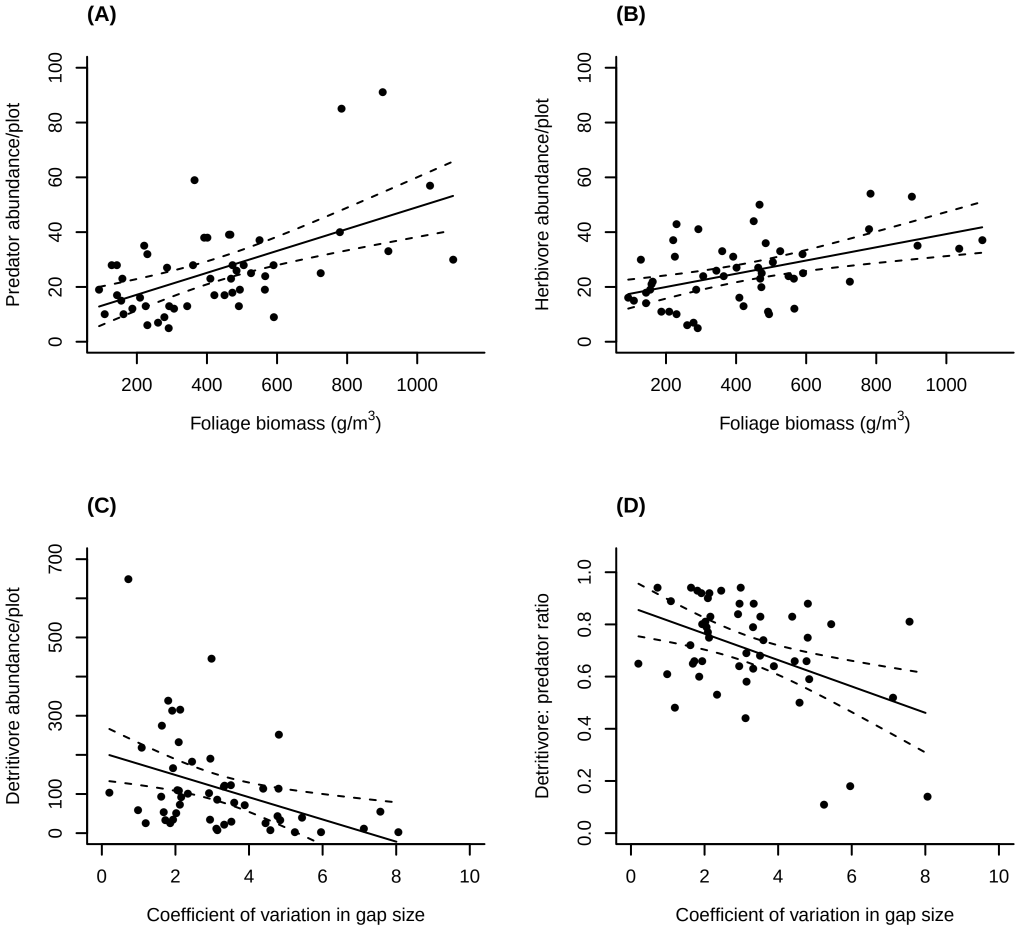


Fig. 2


(A)
(B)
(C)
Number of invertebrates
0
20
40
60
80
100
0
20
40
60
80
100
0
100
200
300
400
C
CS
CH
MH
WH
C
CS
CH
MH
WH
C
CS
CH
MH
WH
Rejuvenation treatment
Rejuvenation treatment
Rejuvenation treatment


(A)
Number of predators + herbivores
400
300
200
100
0
C
CS
CH
MH
WH
Treatment


(B)
Number of detritivores
400
300
200
100
0
C
CS
CH
MH
WH
Treatment


(A)
Predator abundance/plot
0
20
40
60
80
100
200
400
600
800
1000
Foliage biomass (g/m^3)
(B)
Herbivore abundance/plot
0
20
40
60
80
100
200
400
600
800
1000
Foliage biomass (g/m^3)
(C)
Detritivore abundance/plot
0
100
300
500
700
0
2
4
6
8
10
Coefficient of variation in gap size
(D)
Detritivore: predator ratio
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
Coefficient of variation in gap size