

Environment and Rural Affairs Monitoring & Modelling Programme (ERAMMP)

ERAMMP Report-43: Analysis of National Monitoring Data to Inform Future Land Management Schemes in Wales

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Abbreviations Used in this Report

AES	Agri-environment scheme
AIC	Akaike's Information Criterion
AWI	Annual Population Survey
BAP	Biodiversity Action Plan
BTO	British Trust for Ornithology
CLMS	Copernicus Land Monitoring Service
DAFOR	Dominant, Abundant, Frequent, Occasional, Rare
ERAMMP	Environment and Rural Affairs Monitoring & Modelling Programme
GAM	Generalised Additive Model
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
GMEP	Glastir Monitoring and Evaluation Programme
HNV	High Nature Value (farmland)
LMS	Land management scheme
UKCEH	UK Centre for Ecology & Hydrology
WLF	Woody Linear Feature

Contents

1	Policy Summary	2
2	Executive Summary	5
3	Background & Headline Findings	6
	3.1 Benefits of Woody Linear Features creation depend on landscape context.....	6
	3.2 Flower-poor fields have potential for wild pollinators	8
	3.3 Semi-natural surroundings buffer effects of fertility on plant species richness	9
	3.4 Ideal management depends on the taxon of interest	10
4	Case Study 1: Flowers and Woody Linear Features for Pollinator Abundance	13
	4.1 Background.....	13
	4.2 Approach.....	14
	4.3 Results	16
	4.4 Discussion	19
5	Case Study 2: Woody Linear Features for Bird Species Abundance	21
	5.1 Background.....	21
	5.2 Approach.....	22
	5.3 Results	25
	5.4 Discussion	31
6	Case Study 3a: Landscape Heterogeneity for Plant Biodiversity.....	33
	6.1 Summary.....	33
	6.2 Background.....	33
	6.3 Approach.....	36
	6.4 Results	37
	6.5 Discussion	40
7	Case study 3b: Hedgerows for Plant Biodiversity	42
	7.1 Summary.....	42
	7.2 Background.....	42
	7.3 Approach.....	43
	7.4 Results	44
	7.5 Discussion	47
8	Case Study 3c: Grassland Extensification for Plant Biodiversity	49
	8.1 Summary.....	49
	8.2 Background.....	49
	8.3 Approach.....	50
	8.4 Results	51
	8.5 Discussion	55
9	Annex A: Further Details on Case Study 2	57
	9.1 Detailed model results	57
	9.2 Species-level results.....	59
10	References	74

1 POLICY SUMMARY

The purpose of this work was to provide more in-depth analysis of the field survey data collected under the GMEP project between 2013 – 2016 to inform both future analysis of Glastir outcomes and the design of the Sustainable Farm Scheme in Wales.

Key policy relevant outcomes include:

1. Hedge creation funded by Glastir payments happens most frequently where there is already moderate to high density of hedges (> 50m/ha). Hedge creation benefits most birds until 120m/ha. Above this threshold, birds associated with more open field and boundary environment decline (e.g. Skylark and Lapwing).

Intervention: Hedge creation

Outcome: Birds

Spatial context: Existing hedge cover

Policy message: Focus payments for hedge creation to support birds in lower density areas (< 120m/ha) but take care to minimise potential risk to open habitat bird species. Exception only if scrub and woodland bird species are the known target species for that location (e.g. Yellowhammer and Song Thrush).

2. Hedge cover is always linked to a net benefit for pollinator abundance and diversity however this is species and context dependent.

Intervention: Hedge creation

Outcome: Pollinators

Spatial context: Existing hedge cover

Policy message: Hedge creation creates a net increase in pollinator abundance and diversity. Note that not all species benefit equally and other actions in grassland and arable systems will have more benefit for some species and perhaps more benefit overall.

3. Benefits of hedges for honey bees is only observed where cover of broadleaved woodland cover is low (< 25%) where an increase in honeybee abundance approximately doubling for every additional 100m/ha of hedges. Above there is no increase.

Intervention: Hedge creation

Outcome: Honey Bees

Spatial context: Existing hedge cover

Policy message: If woodland cover is < 25%, hedge creation will double honey bees for every 100m/ha created. But hedge creation will not benefit honey bees if woodland cover is > 25%. Focus hedge creation where woodland cover is low if honey bees are the target.

4. Higher flower cover in farmland increases insects and pollinators up to 60% flower cover in farmland. This rate of increase was greatest where flower cover was low (< 5%).

Intervention: Flower cover in farmland

Outcome: Insects and pollinators

Spatial context: Existing flower cover

Policy message: Consider providing more payments to increase flower cover in farmland as benefits for insects and pollinators are observed from 0 - 60% existing flower cover (and there is an increase in plant diversity too). Consider targeting payments for introducing flower cover into flower poor farmland to derive most benefit.

5. Honey bees are not a reliable proxy of other pollinator and insect groups as they display different habitat use behaviours.

Intervention: Habitat creation

Outcome: Honey bees

Spatial context: N/A

Policy message: Data about the use and value of different habitats by honey bees should not be used as a proxy for all pollinator and insect groups.

6. High cover of woodland and hedges is linked to high plant species richness of hedges.

Intervention: Hedge creation

Outcome: Plant species richness

Spatial context: Existing hedge and woodland cover

Policy message: Prioritise payments for new hedges near to existing woodland and hedges if hedge ground flora plant diversity is the outcome required. But note whilst plant species may benefit, some pollinators and birds may benefit more where new hedges are in locations where woodland and hedges cover is low. There is a trade-off.

7. Grassland fertility is linearly related to a decline in plant species richness except where surrounding habitat diversity is high.

Intervention: Grassland extensification

Outcome: Plant species richness

Spatial context: Landscape Heterogeneity / Semi-natural land

Policy messages: Payments to maintain areas of high habitat diversity around fertile grassland will help maintain a higher level of in-field plant diversity.

Grassland extensification payments could be focussed on areas where this buffering effect is not present.

It should be noted however that payments for more active interventions will be needed to improve diversity in a field already depleted to introduce species back into the pool.

8. Landscape heterogeneity / Habitat diversity is linked to increased species richness of plant species up to a maximum of 1.5 habitats / 1 km square but only for generalist species. Specialist species decline.

Intervention: Habitat diversity

Outcome: *Plant species richness*

Spatial context: *Landscape Heterogeneity / Semi-natural land*

Policy messages: *Payments to create more landscape heterogeneity where current habitat diversity is < 1.5 habitats/ 1km square will benefit generalist plant species but may act against specialist species.*

Payments to support areas suitable for specialist species need to be created as well as support of payments to create more landscape heterogeneity.

In summary, outcomes of interventions are observed to be highly variable depending on the taxa and clear thresholds have been demonstrate to help guide spatial targeting of payments e.g.

Hedge creation (often linked to connectivity and resilience)

- New hedge creation where current cover is low (< 100h/ha) will result in more increases for insects; more bird abundance; but lower plant species richness in hedge ground flora.
- Hedge creation where cover is high (> 100m/ha) will result in less net increase for insects; declines for some bird species; but higher plant species richness in hedge ground flora.

Flower cover

- Any increase in flower cover in farmland creates a net benefit for insect abundance. Most benefit is seen where current cover is currently (< 5%) although increases are seen up to 60% cover.

Grassland extensification

- Extensification payments will have most benefit for plant species richness where surrounding habitat diversity is low.
- Habitat diversity payments will help to sustain ongoing high plant diversity levels where habitat diversity is high.

Landscape heterogeneity, diversity and extensification (often linked to resilience)

- Habitat diversity up to 1.5 habitats in 1 km squares will benefit plant species richness but benefits are for generalist species with declines of plant specialists.

Ultimately there are often winners and losers when land management is changed. Therefore, spatial targeting to support specific taxa and ecosystem outcomes is essential if unintended consequences are to be avoided. Payments to create a mix of landscape types has most benefits for a mix of taxa including those required by specialist taxa.

The occurrence of ecological and spatial contextual thresholds have been identified for Wales from this analysis of GMEP national field survey data which can help to guide spatial targeting to maximise benefits derived from: hedge creation; increased flower cover; grassland extensification; and habitat diversity creation for plants, insects and pollinators and birds.

2 EXECUTIVE SUMMARY

This report develops Wales' evidence base, to inform targeting of Land Management Schemes (LMSs) that will replace Glastir. We present analyses of data from the Glastir Monitoring and Evaluation Programme (GMEP), 2013-2016. We focus on plant, bird and pollinator biodiversity, but use methods that could be applied to a wide range of other environmental outcomes. We produce advice to optimise management interventions, using patterns and relationships among environmental variables in Wales. Most importantly, we show how co-located environmental observations from a structured national field survey can be deployed to address a variety of applied policy questions. Our key findings are as follows:

Birds

The first Wales-specific assessment of bird responses to Woody Linear Features (WLFs) & landscape context

Benefits of hedgerow creation for field and boundary specialists, from Blackbirds to Yellowhammers (Fig. 2.1.)

Particularly where existing WLF density is low

Need to consider effects of interventions on all taxa, regardless of whether they are direct targets

Some negative effects of WLFs for open field birds

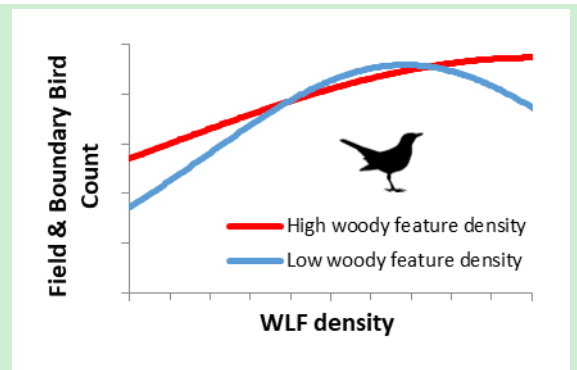


Figure 2.1. Non-linear effects of WLFs on abundance of field & boundary birds

Pollinators

Further investigation into the drivers of pollinator abundance in Wales, where broadleaf woodland is key

Clear benefits of WLFs for overall pollinator abundance, particularly for hoverflies & honeybees (Fig. 2.2.)

For honeybees, if broadleaf cover nearby is low

Flower cover is critical, but low on improved grassland
Interventions need to increase flower cover, with steeply positive effects in flower-poor areas

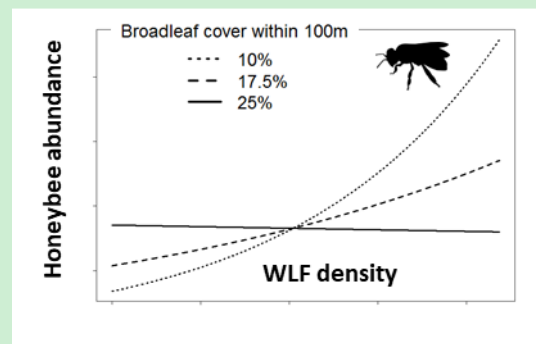


Figure 2.2. Context-dependent effects of WLFs on honeybee abundance

Plants

Several in-depth studies, including further insight into indicators of High Nature Value (HNV) farmland in Wales

Land use intensity decreases species richness of hedge ground flora and farmed grassland swards
But high habitat diversity may buffer declines

Wider landscape context affects local plant diversity, especially surrounding woody cover and habitat diversity
But habitat diversity mainly benefits generalists

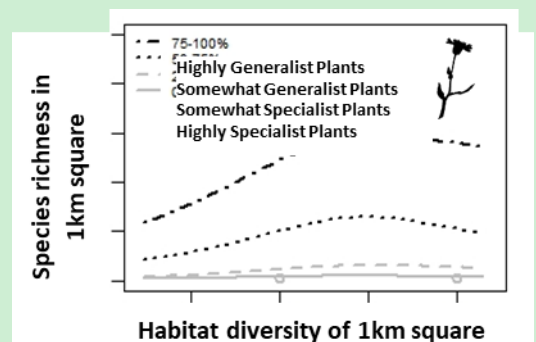


Figure 2.3. Positive effects of habitat diversity mainly apply to generalist plant species

3 BACKGROUND & HEADLINE FINDINGS

Land management schemes (LMSs), including agri-environment schemes (AESs), are a major policy tool to improve environmental outcomes on farmland, and farmland covers ~90% of land in Wales (Armstrong et al. 2016). LMSs also represent a significant public expenditure. As of 2012, £89 million a year was made available for the Glastir Land Management Scheme in Wales (Davies, 2012). Around the same time, £400 million a year was invested in AESs in England (Natural England, 2009). Clearly LMSs need to fund the right interventions - in the right locations - to maximise their environmental benefits. When restoring biodiversity and other environmental outcomes on farmland, landscape context is particularly important. For example, LMS interventions in isolated landscapes might not be colonised by species. On the other hand, there may be redundancy to LMS interventions in landscapes which are already diverse and semi-natural (Tschardt et al. 2005). Management context is another important consideration. For example, residual fertility can impede grassland restoration on improved land (Critchley et al. 2003).

Aiming to inform LMS targeting in Wales, this report presents in depth analyses of relationships between biodiversity and agricultural management parameters (e.g. woody linear features, flower cover, habitat diversity). Many of the presented relationships are likely to have direct, causal, underlying mechanisms. For example, woody linear features (WLFs) may increase bird, plant and pollinator biodiversity by providing nesting habitats, refugia and floral resources. A similar approach could be taken for a wider set of environmental outcomes in future work – for example with respect to freshwater quality.

Here we summarise the policy implications of our results, reinforcing them based on new analysis of data from the Glastir Monitoring and Evaluation Programme (GMEP) national field survey – in the context of wider literature. In particular, we identified several biodiversity responses which are non-linear or context-dependent, with implications for LMS management and targeting. We also present data on the uptake of relevant Glastir interventions across key landscape gradients. For example, we present uptake of hedgerow creation options across gradients of existing WLF density. These data provide an informative backdrop against which to devise future LMS targeting strategies.

In this report, we attempt to understand causal relationships based on patterns within, and correlations between, environmental variables. As stated above, the relationships presented are probably underpinned by causal mechanisms. However, in analysing environmental observations recorded within a narrow time window (2013-2016), we can at best only approximate causality. Causality is best understood through experimental manipulation. While experimental manipulation is nearly impossible at the spatial and temporal scales considered here, we advise careful consideration of causality during application of the findings. Furthermore, future surveys are scheduled within GMEP squares – for example under the ERAMMP 2021 field survey. As such, future advice to inform LMS targeting strategies could draw on temporal trends, alongside spatial patterns, in the data.

3.1 Benefits of Woody Linear Features creation depend on landscape context

We found non-linear and/or context-dependent relationships between density of WLFs on Welsh farmland and the abundance of birds and pollinators. We also found impacts of the

surrounding landscape on hedgerow ground flora. These results have implications for the targeting of LMS interventions.

3.1.1 Birds

We investigated how the non-linear relationships between the abundance of three ecological groups of bird species and WLFs were affected by background landscape context: other woody habitat within the surveyed area and in the surrounding landscape, and the areas of arable farmland and all improved land in the surveyed area. There were significant effects for all groups, most notably showing that increasing hedgerow density would have more effect on bird species that require both field and boundary habitats - particularly in areas with lower levels of existing woody habitat cover. Species that use the habitat mosaic in farmland benefit from the heterogeneity that WLFs introduce into farmed land, but less so at higher WLF densities, where only scrub and woodland species benefit.

Once again, the results provide direct, quantitative evidence to inform targeting of future management. While previous studies have demonstrated the qualitative benefits of interventions such as hedgerow creation, this is the first to present quantitative data for Wales and information on trade-offs across species of interest.

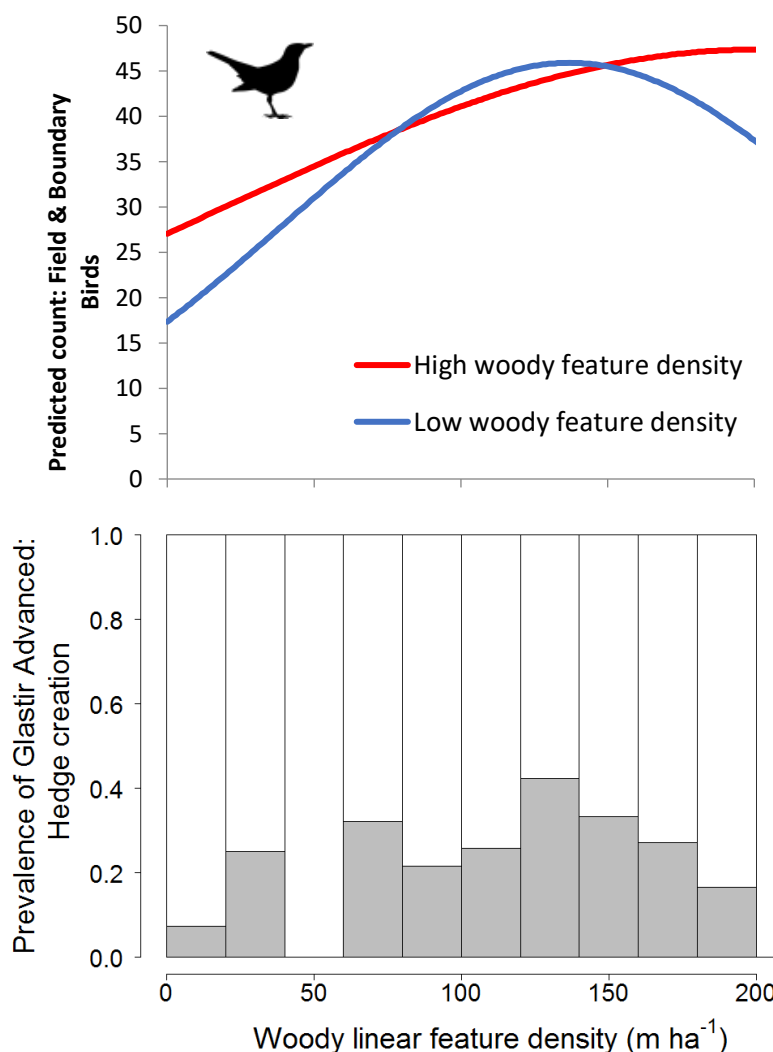


Figure 3.1. Top: Woody linear features (WLFs) benefit field & boundary specialist birds (total count of individuals) on lowland farmland in Wales - especially where there is low density of other small woody features (blue line). There is evidence of diminishing returns for birds as WLF density increases (i.e. the curves are saturating). Creation of WLFs might thus make the biggest difference on farms with low existing WLF density.

Bottom: Proportion of squares containing Glastir hedge creation, across a gradient of WLF density. Hedgerow creation under Glastir happens frequently on farms where WLF density is already high. This might not maximise benefits for populations of relevant bird species.

3.1.2 Pollinators

We found that the effect of WLFs on honeybee abundance at the farm-scale was dependent on low broadleaved cover in the surrounding landscape. This highlights the spatial complexity of pollinator responses to introduced floral resources; individuals may exploit certain floral resources in place of others. This is probably particularly true of honeybees, which frequently collect pollen from trees (Jones et al. 2021) and can communicate within the colony to focus foraging toward productive areas (Balbuena, Molinas, & Farina, 2012). We found that honeybees did not show the same saturating response to flower cover as the wild pollinator groups, suggesting a tendency to concentrate in the most flower-rich areas. Honeybee abundance is not a reliable proxy for the abundance of other pollinator groups.

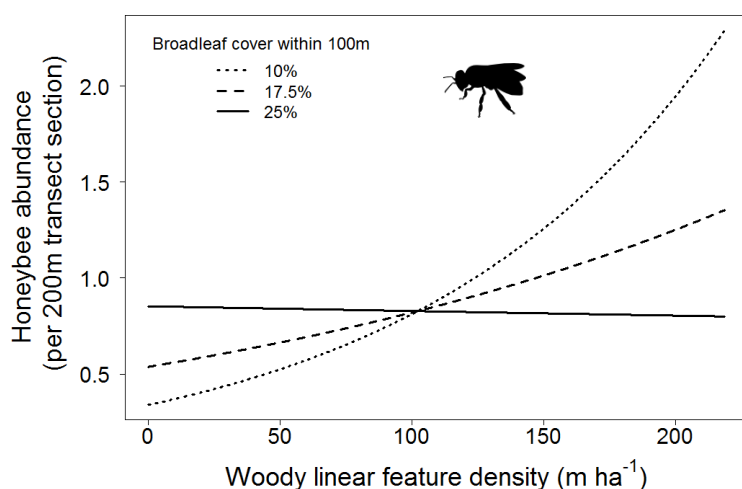


Figure 3.2. Positive effects of WLFs on honeybee abundance were conditional on low surrounding broadleaf cover.

This result complements many other studies, especially based in England, which find that benefits of agri-environmental interventions depend on the landscape context. For example, specialist moth responses to created grass margins depend on nearby semi-natural habitat (Alison et al., 2016). On the other hand, bumblebee responses to sown forage patches are actually greater in arable-dominated areas (Heard et al., 2007).

3.1.3 Plants

Landscape context affects local plant diversity. In particular, we find that high density of woody features or woodland in the surrounding landscape is associated with high species richness of hedge ground flora. This is scale dependent; at the local scale small woody features are significant, while at larger scales small woody features and also larger areas of woodland are significant. As covered in section 3.4, the relationships differ between richness of general ground flora and ancient woodland indicators. The intensity of adjacent land showed a strong negative relationship with species richness, including richness of ancient woodland indicators.

3.2 Flower-poor fields have potential for wild pollinators

Flower cover was universally important for abundance of eight insect pollinator groups. Furthermore, for wild pollinators, flower cover had the steepest positive effect on abundance at the flower-poor end of the spectrum. Clearly wild pollinators are able to exploit scattered, small patches of flowers in otherwise bare fields. Furthermore, the effect

of a given increase in flower cover on local pollinator abundance may be greatest in such flower-poor fields. This saturating effect of flower cover on abundance applies in absolute terms.

While floral resources are critical for pollinators across habitat and ecosystem types, we identified that few interventions under Glastir were targeted towards introducing flowers or increasing flower cover on farmland. Future land management or agri-environment schemes in Wales might include measures to introduce more flowering plant species to farmland, especially grassland swards. However, appropriate timing and intensity of cutting or grazing would also be necessary to ensure increases in flower cover and floral resource provision.

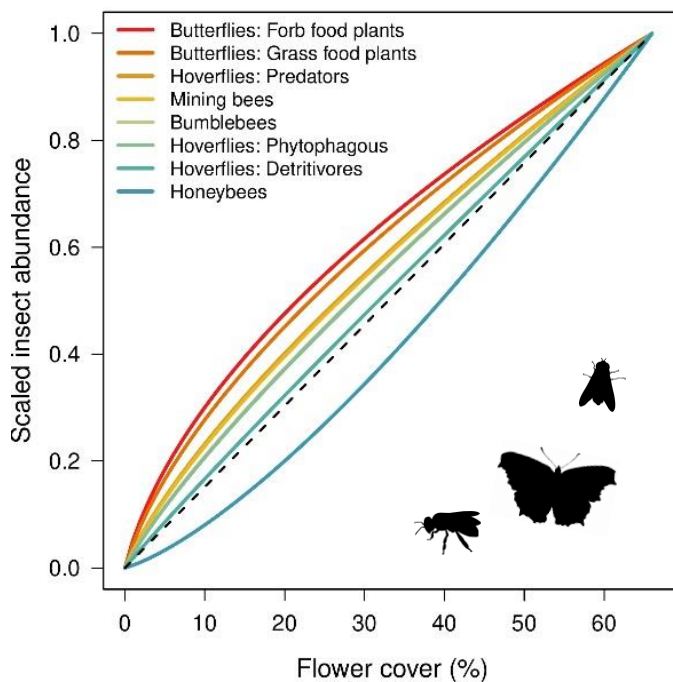


Figure 3.3. Flower cover increases the abundance of eight pollinator groups. For wild pollinators, there are diminishing returns; we expect roughly twice the increase in abundance with an increase in flower cover from 0-5%, as compared with 10-15% (wild pollinators are above the dashed 1:1 line; honeybees are below it).

3.3 Semi-natural surroundings buffer effects of fertility on plant species richness

We explored whether landscape context can interact with fertility to enhance in-field species richness. We found that there is a steep decline in species richness at higher fertility in improved and neutral grasslands. Species richness is highest in the plots with the highest habitat diversity and total species richness in the square in both improved and neutral habitats. Despite the decline in species richness with fertility, there may be buffering from landscape context. In improved grasslands higher habitat diversity or the abundance of semi-natural land appears to be interacting with fertility to maintain species richness. In neutral grasslands, this seemed to be the case for the amount of semi-natural land.

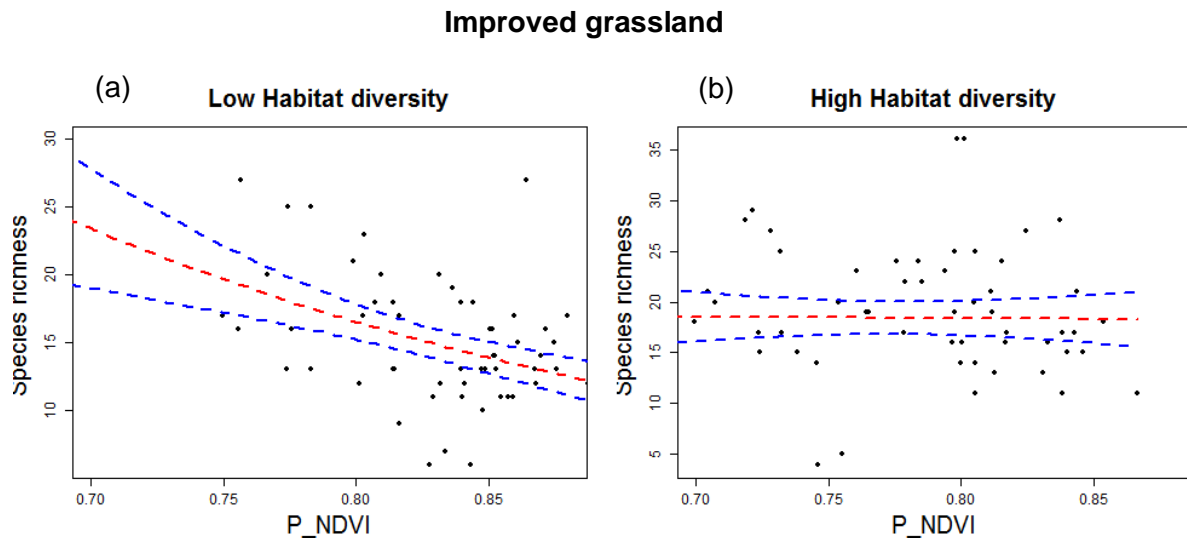


Figure 3.4: Relationship between fertility (plot scale NDVI) and species richness in plots grouped by quantiles of habitat diversity a) Low, b) High, in Improved grassland.

These results suggest that in diverse landscapes, high species richness can be sustained despite high fertility. This means there may be an advantage in targeting interventions to areas that are not buffered by landscape diversity. However, if the species pool has been depleted by raised fertility and simplification then reducing fertility in a simple landscape may not elicit a response (e.g. Marrs et al. 1996), particularly for specialists associated with semi-natural habitats and lower fertility (Kleijn et al. 2011). In more intensively managed landscapes, more active interventions may be required such as addition of grass, forb and legume species by reseedling, oversowing, or slot seeding. More advanced interventions could include introduction of plug plants or feeding animals with high quality hay containing seeds (from nearby sites). This would increase costs, however (Keenleyside et al. 2020, Torok et al. 2018).

This work also demonstrates that it is advantageous to consider implementing packages of several different interventions that increase the amount of semi-natural land and colonisation sources at the farm or landscape level as these can be helpful in sustaining diversity even where fertility is high.

3.4 Ideal management depends on the taxon of interest

We find that responses to management vary between taxa, with some common themes.

3.4.1 Birds

Many farmland bird species have declined and are hence conservation priorities due to agricultural intensification, but this general pattern summarises across a range of specific relationships with environmental change. This includes effects of fertiliser use, re-seeding of grassland, hedgerow loss and simplification of arable cropping patterns. Management to reverse declines must therefore consider the critical factors for individual target species, or ecological groups. For example, hedgerows are expected to benefit many species, such as Yellowhammer or Song Thrush, but could negatively affect open field species,

such as Skylark and Lapwing. It is appropriate to consider the range of effects of an intervention on a diversity of taxa, regardless of whether those species are direct targets.

Here, we consider the responses of the abundance of three ecological groups of birds to the density of WLFs (e.g. hedgerows) in Welsh farmland. All groups showed non-linear responses, but responses differed between groups. Species that use woody habitats and species that use a combination of hedgerow and field centre habitats were most common between 0.05 and 0.13 km/ha of hedgerow, but decrease in abundance in farmland above that range (the maximum in the data was 0.23 km/ha). Conversely, open-field species were rather unaffected by hedgerows up to 0.10 km/ha, but were increasingly negatively affected above this point. This has clear implications for targeting hedgerow creation, and highlights trade-offs between management to benefit, say, Lapwing and Yellowhammer.

3.4.2 Pollinators

Previous work showed how pollinator abundance across habitats and ecosystems in Wales differed between pollinator groups (Alison et al. *in prep.*). Here we show that responses to WLFs, landscape context and flower cover also differ between groups. This implies divergent responses to management. For example, we found evidence to suggest that honeybees and hoverflies are more likely to benefit from hedge laying than mining bees. Similarly, grass-feeding butterflies are more likely to benefit from arable reversion to grassland than forb-feeding butterflies.

However, there are shared themes in expected responses to management across pollinator groups. For example, all pollinator groups showed a strong positive relationship with flower cover. Similarly, broadleaved woodland consistently supports relatively high abundance of all pollinator groups (Alison et al. *in prep.*). Finally, we didn't find any significant negative effects of WLFs on pollinator abundance – suggesting net gains to pollinator abundance and diversity following hedgerow creation.

3.4.3 Plants

LMSs often build heterogeneity on farmland, with possible benefits for plant biodiversity. However, we find that some aspects of plant biodiversity respond more positively than others. We looked at the relationship between landscape heterogeneity and plant species niche width, finding that it is the species with a broad niche width (i.e. generalists) that benefit most from increased heterogeneity. As heterogeneity increased, species with the narrowest niche width (i.e. specialists) actually tended to decline. Overall, increasing heterogeneity in simple landscapes is expected to benefit biodiversity. However, as heterogeneity increases further, we highlight that gains in generalist species could be offset by losses of specialists, or possibly species associated with more open conditions (Concepción et al. 2012, Maskell et al. 2019). This shows that targeting of LMSs will depend on the intervention type, and particularly whether it is applied to generalist or specialist species.

We also found different responses to landscape context between overall ground flora and Ancient Woodland Indicator (AWI) plant species. We analysed relationships between landscape context and hedgerow ground flora. For overall ground flora, there was a slight positive relationship between species richness and woody cover. However, AWIs were more responsive to landscape context; with positive/unimodal relationships between AWI richness and surrounding woodland cover. This implies a greater role for hedgerows as refugia for AWIs where there is woodland nearby.

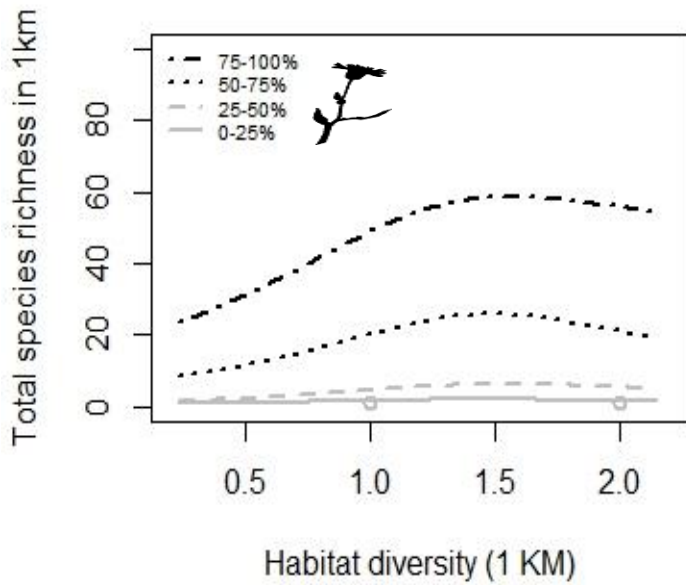


Figure 3.5. Generalist species, with broad niche-width (black lines), respond more positively to landscape-scale habitat diversity than specialist species, with narrow niche-width (grey lines). Generalist species thrive where there are small patches of a wide variety of habitats, such as on Type II high nature value farmland. The four lines represent four quarters of plant species after ranking them based on how generalist they are (75-100% = most generalist, 50-75% = upper middle, 25-50% = lower middle and 0-25% = least generalist).

4 CASE STUDY 1: FLOWERS AND WOODY LINEAR FEATURES FOR POLLINATOR ABUNDANCE

4.1 Background

'Pollinators' describes a wide variety of wild and managed animals, particularly insects, that enable pollination and fertilisation of flowers (Potts et al., 2016). Pollinators provide economic benefits by enhancing global food production (Gallai et al., 2009), 35% of which comes from animal-pollinated crops (Klein et al., 2007). However, they are also functionally critical to sustain populations of wild plant species (Biesmeijer et al., 2006), while some groups – especially bees – carry immense social and cultural value (Christmas et al., 2018). Non-crop-related benefits of pollinators may be especially important in Wales, a region dominated by improved grassland agriculture (Armstrong et al., 2018).

Trends of pollinator abundance in Wales are poorly understood. In Great Britain, volunteer-submitted records show that, since 1970, more moth, bee, hoverfly and butterfly species have declined than increased (Fox et al., 2014; Powney et al., 2019; Thomas et al., 2004). Similar declines are evidenced in wider Europe (Carvalho et al., 2013). In Wales, data for non-butterfly pollinator groups, e.g. bees and hoverflies, are particularly scarce. A Wales-level indicator of abundance of bees and hoverflies is still in development under the UK Pollinator Monitoring Scheme (PoMS). For butterflies, analysis during GMEP demonstrated that abundance of seven specialist species declined since 1970, while abundance of 19 wider countryside species was stable (Fig. 4.1., Smart et al., 2015).

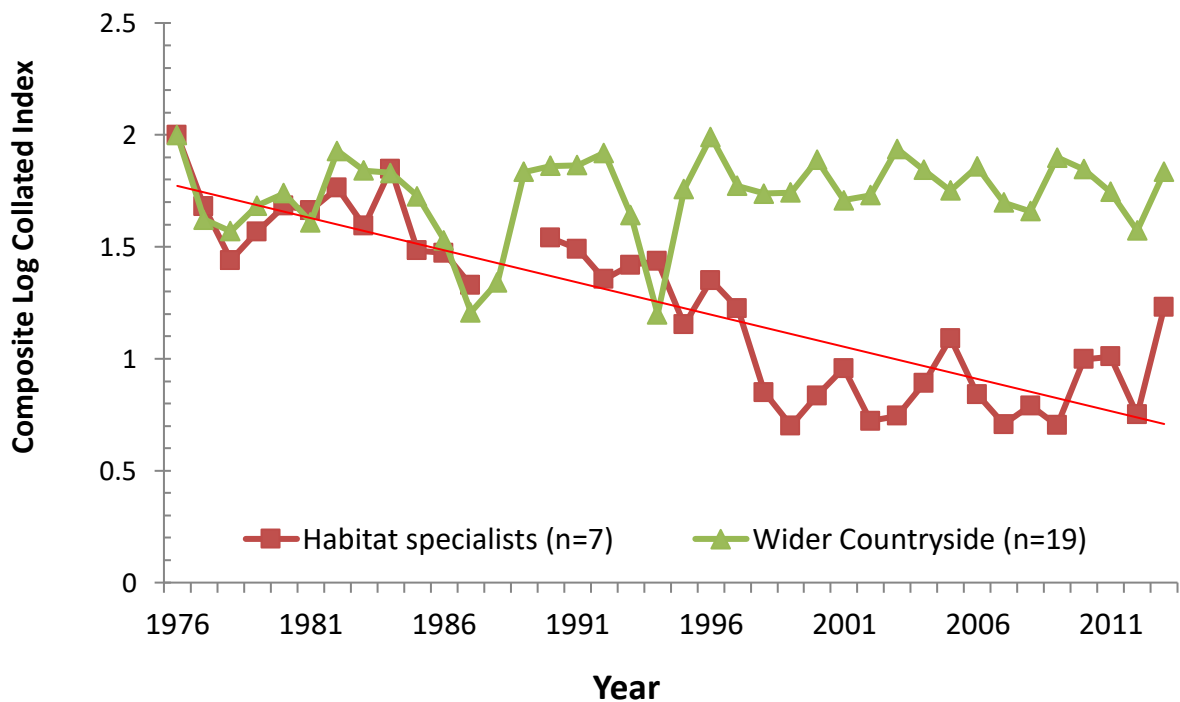


Figure 4.1. Composite abundance indices for 7 habitat specialist butterfly species (red squares) and 19 wider countryside species (green triangles). Adapted from Smart et al. (2015).

Until recently, the state of pollinators across Wales' varied habitats was poorly understood. The GMEP field survey included pollinator transects in 300 1km squares across Wales, where habitats and linear features were also mapped at high resolution. Analysis of pollinator transect data has shown positive effects of flower cover, woodland, woody linear features (WLFs) and even cropland for abundance of multiple pollinator groups (Alison et al., *in prep.*) with some corresponding benefits for pollinator diversity (Maskell et al., 2019). Interventions that create hedgerows or increase flower cover could therefore benefit pollinators in Wales, but questions remain about where such interventions might be most effective. Previous work in England has demonstrated how benefits of agri-environmental interventions can depend on suitable habitat in the surrounding landscape (Alison et al., 2016), but few such studies have been carried out in Wales.

We present detailed analysis of effects of flower cover and WLFs on the abundance of pollinator groups across three insect orders. First, we test for non-linear effects of flower cover at local-scales. Second, we test for non-linear and context-dependent effects of WLFs at the farm-scale. In Section 6, we discuss what these results mean for pollinator-friendly management in Wales – focussing on implications for agri-environmental targeting.

4.2 Approach

Data on pollinating insects, flower cover, habitats and woody linear features across Wales were collected through the Glastir Monitoring & Evaluation Programme from 2013-2016 (GMEP; Emmett & the GMEP team, 2017). For details of the field survey design, and selection of 300 GMEP squares, see Emmett & the GMEP team (2014, 2017).

4.2.1 Pollinator and flower surveys

Two visits - one in July and one in August - were made to each of 300 GMEP squares by trained insect and flower surveyors. Visits were made between 10am and 4pm on warm, dry, calm days following the UK Wider Countryside Butterfly Survey method (Brereton et al., 2011). During each visit two 1km transects, divided into sections of roughly 200m, were surveyed for adult butterflies (Lepidoptera: Rhopalocera), bees (Apoidea) and hoverflies (Syrphidae). Pollinator transects were walked at a steady, even pace. All identifiable insects observed within a 5m box around the observer were recorded. Butterflies were identified to species-level; bees were identified as honeybees, bumblebees, or one of two groups of solitary bee based on pollen collection strategy (pollen on legs: mostly mining bees, e.g. *Andrena*; pollen on abdomen: mostly leafcutter or mason bees, family Megachilidae); hoverflies were identified to one of three morphological groupings, which were broadly reflective of larval feeding strategies (predatory, detritivorous or phytophagous).

Percentage flower cover (*not* vegetative cover) within 5m of each transect section was recorded using a DAFOR scale (Dominant >30%≥ Abundant >10%≥ Frequent >5%≥ Occasional >1%≥ Rare >0%) for each of 10 plant groups (Apiaceae, Asteraceae (yellow), Asteraceae (purple), Dipsacaceae, Ericaceae, Fabaceae, Lamiaceae, Rosaceae, Scrophulariaceae or “other”). Flower cover was an absolute measure, not a relative measure (i.e. cover of different families were not expected to sum to 100).

4.2.2 Habitat and WLF mapping

Habitat and WLF surveys were carried out in all GMEP squares during the same year as pollinator and flower surveys. Following the methodology of the Countryside Survey of Great Britain (Wood et al., 2018), every permitted and accessible land parcel in the square was assigned a UK Biodiversity Action Plan (BAP) broad habitat type (Jackson, 2000). WLFs (hedgerows and lines of trees < 5m wide, minimum length 20m) were also mapped in and around those parcels.

4.2.3 Data analysis

Pollinator abundance, total flower cover, habitat type, WLF density and other contextual data were extracted from the GMEP database at two scales: (1) local-scale: defined as individual 200m transect sections and (2) farm-scale: defined as the arable, neutral grassland and improved grassland (hereafter “farmed”) areas of each GMEP square.

Farm-scale WLF density calculations were inclusive WLFs on boundaries between farmed and non-farmed habitats. Local-scale analyses were carried out for each of eight insect groups: (1) bumblebees, (2) honeybees, (3) mining bees, (4) butterflies with grass larval food-plants (hereafter “grass-feeding butterflies”); (5) butterflies with forb larval food-plants (“forb-feeding butterflies”), (6) hoverflies with larvae that are predatory (“predatory hoverflies”), (7) hoverflies with larvae that are detritivorous (“detritivorous hoverflies”) and (8) hoverflies with larvae that are herbivorous (“herbivorous hoverflies”). Farm-scale analyses were not possible for mining bees and herbivorous hoverflies because they were not sufficiently represented on farmland.

- (1) To investigate local-scale effects of flower cover**, we used flower cover to predict insect abundance along 200m transect sections. Flower cover was represented as the sum of the midpoints of DAFOR measurements (rounded up: 65%, 20%, 8%, 4% and 1% respectively) of all recorded plant families along a 200m transect section. We tested for non-linear effects of flower cover, and controlled for effects of many other variables including habitat type, temperature, sunshine, wind speed and WLF density within 10m of the transect section. We used generalised linear mixed effects models (GLMMs) with negative binomial error structures.
- (2) To investigate farm-scale effect of WLFs**, we used the density of WLFs to predict mean insect abundance across farmed 200m transect sections in a square (mean counts were rounded up to the nearest integer). We tested for non-linear or context-dependent effects of WLF density, as well as non-linear effects of contextual variables (e.g. broadleaved cover within 100m). A different contextual variable was selected for each insect group on the basis of previous analysis – specifically we represented habitat types previously associated with high numbers of each group (Table 4.1). We used generalized linear models (GLMs) with negative binomial error structures.

For both analyses, inference was made based on effects present in the best model. Which was taken to be the simplest model with $\Delta AICc < 2$ (see Alison et al., *in prep* for further methodological details and analysis).

4.3 Results

4.3.1 Local-scale effects of flower cover

Flower cover had non-linear effects on the abundance of all insect groups (Fig. 4.2.). Resulting relationships between abundance and percent flower cover were concave (i.e. saturating) for wild pollinators (bumblebees, mining bees, butterflies and hoverflies) and convex for honeybees. As such for wild pollinators, abundance gains per percent flower cover were greater if flower cover was <10%. For honeybees, however, abundance gains per percent flower cover were greater if flower cover was >10%. Habitat type, WLFs and weather also affected the eight insect groups to various extents (see Alison et al., *in prep* for expanded results).

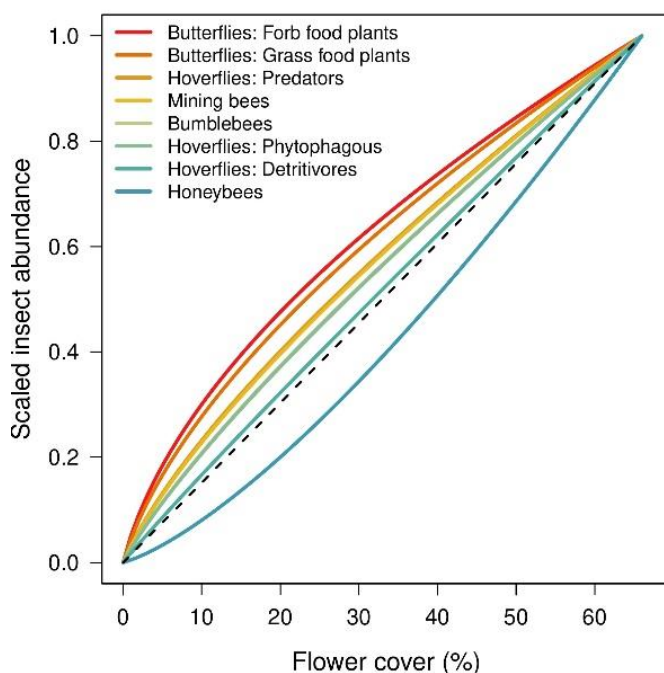
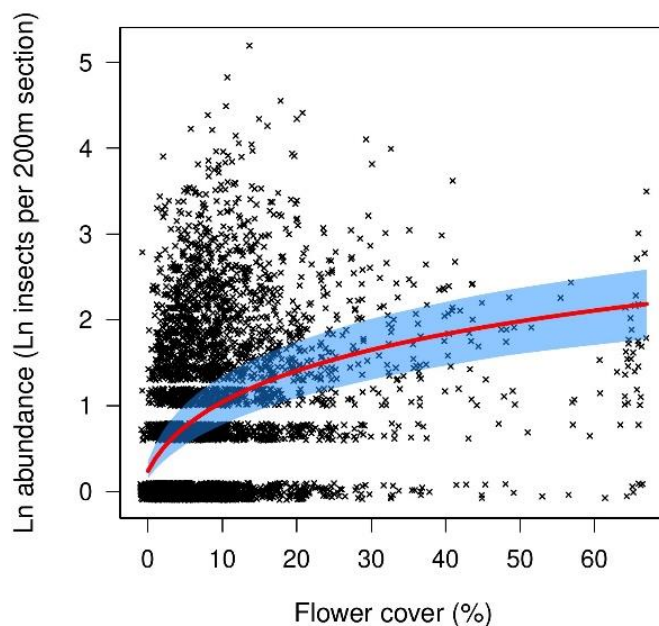


Figure 4.2. Top: Local-scale effects of flower cover on scaled abundance of eight pollinator groups. Relationships between abundance and percent flower cover were principally concave (i.e. saturating) for wild pollinator groups and convex for honeybees. Coloured solid lines represent scaled predictions from the best model for each pollinator group. The dashed black line represents linearity.



Bottom: The above relationship for bumblebees with counts displayed (black crosses). Counts have been log-transformed, and "jitter" (noise) has been added to points along both axes to visualise the scatter of the data. Both panels are reproduced from Alison et al., (*in prep.*).

4.3.2 Farm-scale effects of WLFs

WLFs had linear positive effects on abundance of honeybees, predatory hoverflies and detritivorous hoverflies in the farmed areas of GMEP squares (Table 4.1.; Fig. 4.3., top & bottom). Furthermore, positive effects of WLFs for honeybees on farmland were contingent on low (<20%) surrounding broadleaf cover (i.e. the proportional area within 100m which is either small woody features or broadleaved woodland; Fig. 4.3., top).

Increased arable proportion benefitted predatory hoverflies in a linear fashion, but showed a saturating relationship with abundance of forb-feeding butterflies (Table 4.1.; Fig. 4.3., middle). Increased proportions of neutral grassland benefitted grass-feeding butterflies, while increased surrounding broadleaf cover benefitted detritivorous hoverflies and honeybees.

Table 4.1. Farm-scale effects of landscape context (either proportion arable, proportion neutral grassland or broadleaf cover within 100m), density of WLFs and the interaction between the two variables. Greyed out cells represent that a variable was absent from the best model, '+' indicates a positive effect, 'r' represents a positive, saturating effect.

Group	Landscape context	WLF density (m ha ⁻¹)	WLF density × landscape context
Bumblebees	(broadleaf cover within 100m)		
Honeybees	+ (broadleaf cover within 100m)	+	WLF effect positive where broadleaf cover within 100m is low
Butterflies: Grass l.f.p.	+ (proportion neutral grassland)		
Butterflies: Forb l.f.p.	r (proportion arable)		
Hoverflies: Predators	+ (proportion arable)	+	
Hoverflies: Detritivores	+ (broadleaf cover within 100m)	+	

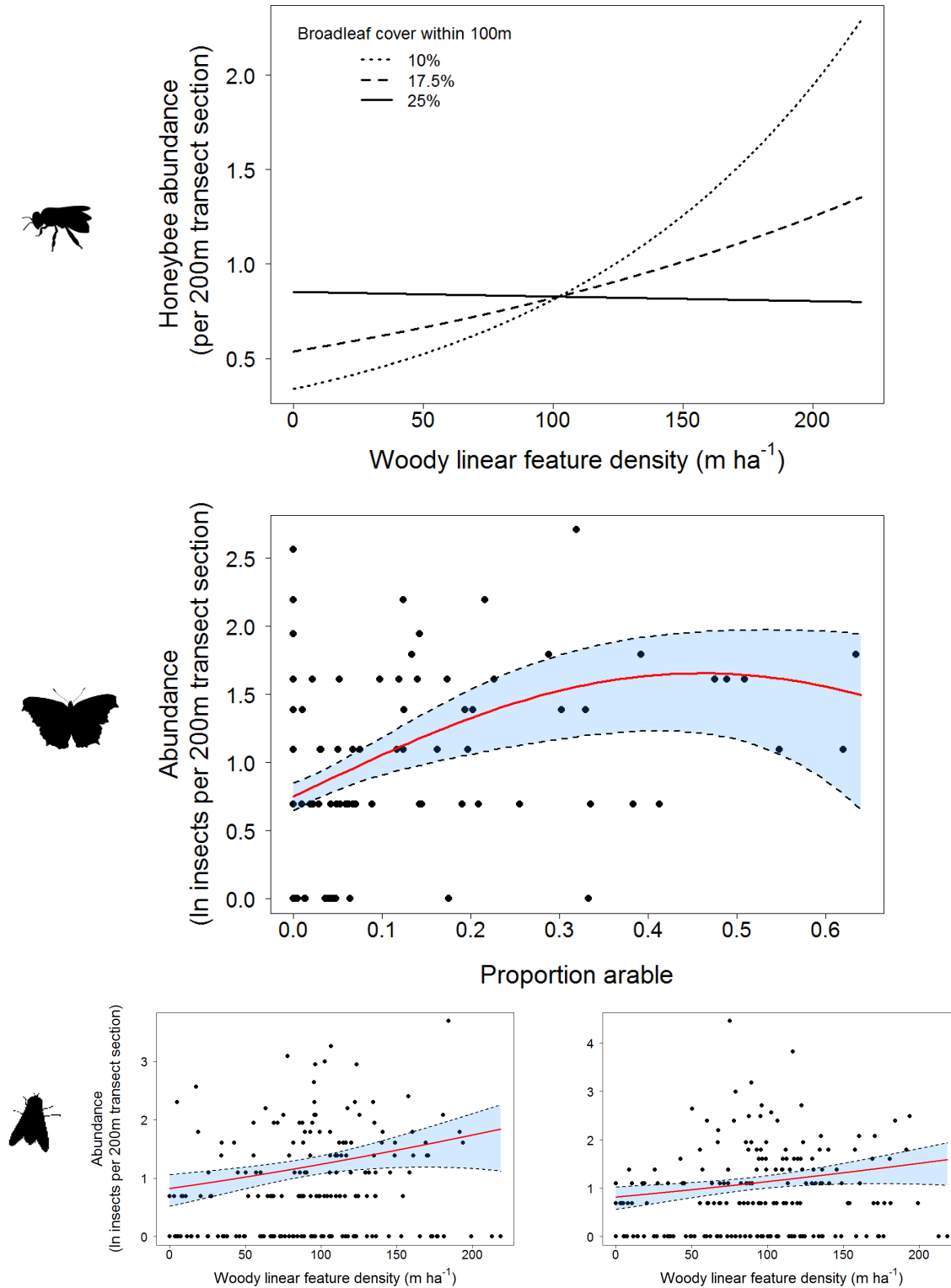


Figure 4.3. Farm-scale effects of context and WLFs on abundance of pollinator groups. **Top:** Positive effects of WLFs on honeybee abundance were conditional on low surrounding broadleaf cover. **Middle:** hump-backed relationship between the proportion of arable and abundance of forb-feeding butterflies. **Bottom:** Linear, positive relationships between WLF density and abundance of predatory (left) and detritivorous hoverflies (right).

4.4 Discussion

4.4.1 Local-scale effects of flower cover

We find strong effects of flower cover on the local abundance of all pollinator groups studied, showing how crucial pollen and nectar resources are for a variety of insect species. The universality of the effect of flower cover suggests that, above all, interventions to increase floral abundance are likely to benefit pollinators in Wales. Most interestingly, we show that there may be diminishing returns for pollinators as flower cover increases. For example: Compared with an increase from 20-30%, an increase in flower cover from 0-10% corresponds to almost twice the increase in abundance of grass- and forb-feeding butterflies (Fig. 4.2., top). A likely reason for this would be that as flower cover increases, populations of pollinating insect species become limited by non-floral resources. For example, solitary mining bees and common bumblebees such as *Bombus terrestris* may become limited by abundance of suitable ground-nesting sites (Gardner et al. 2020). Similarly, butterflies may become limited by the availability of larval food plants, while hoverflies may become limited by abundance of aphid prey, decaying plant material or dung.

The shape of the relationship between flower cover and local abundance is remarkably similar across wild pollinator groups. However, honeybee abundance did not show a saturating response to flower cover, which could relate to distinct foraging behaviour. For example, information exchange between honeybees, through “dance following” and mouth-to-mouth fluid exchange, could allow colonies to focus on the most flower-rich areas of a landscape (Balbuena, Molinas, & Farina, 2012). Population dynamics of honeybees are also very different to those of wild pollinators; honeybee nesting in Wales is limited by the quantity and quality of hives and beekeepers, and not natural or semi-natural habitats.

4.4.2 Farm-scale effects of WLFs and arable proportion

Farm-scale benefits of WLFs for honeybees and hoverflies probably relate partly to floral resources. For honeybees, Hawthorn (*Crataegus monogyna*) and Blackthorn (*Prunus spinosa*) in WLFs provide critical early-season pollen and nectar (Jones et al., 2021). In general, DNA meta-barcoding work led by the National Botanic Garden of Wales shows how plants typical of woodlands and hedgerows dominate honeybee forage in the early season (De Vere et al., 2017). For hoverflies, WLFs could also provide shelter and microclimatic buffering, allowing insects to regulate their temperature throughout the day. Furthermore, hedgerows probably provide resources for different groups of hoverflies in the form of aphid prey, food plants and leaf litter.

For both hoverflies and honeybees, we did not find evidence that effects of WLF density on abundance were non-linear. As such, we expect an increase from 0-50 m ha⁻¹ of hedgerows on a farm to lead to roughly the same increase in pollinator abundance as an increase from 100-150 m ha⁻¹. It seems that widespread pollinator species can benefit from isolated WLFs just as well as those on WLF-rich farms.

While we also found that WLFs increase honeybee abundance, we found that benefits were reduced where surrounding broadleaf cover was high (e.g. >20%; Figure 4.3., top). In Wales, broadleaved woodland is associated with very high local abundances of honeybees (Alison et al., 2021). As such, it is possible that honeybee foraging around WLFs is displaced to nearby broadleaved woodland where such habitat is available. This would make sense in light of (1) collective foraging behaviours of honeybees (Balbuena,

Molinas, & Farina, 2012) and (2) the fact that honeybee population size is limited by the number of hives in the surrounding landscape. Overall this finding highlights that when adding resources to a farm to benefit pollinators, these can interact in complex ways with existing resources in the surrounding landscape.

Finally, we show that increases in arable cover on a farm have positive, but highly saturating effects for forb-feeding butterflies. Abundance of forb-feeding butterflies only increases with arable proportion up to around 15% (Fig.4.3., middle). Previous work showed cropland to be associated with high forb-feeding butterfly abundance in Wales (Alison et al., 2021). Importantly, this result shows that cropland expansion would be unlikely to have positive outcomes for pollinators if it creates homogenous, arable-dominated landscapes.

5 CASE STUDY 2: WOODY LINEAR FEATURES FOR BIRD SPECIES ABUNDANCE

5.1 Background

Farmland birds have been the most conspicuous and widely publicised element of biodiversity in Europe, undergoing long-term declines and local extinctions (e.g. Krebs et al. 1999). Being conspicuous and appreciated by people, they have high cultural value and, hence, have been made principal targets of a range of conservation management measures, including many options in agri-environment schemes (AESs; see, e.g., Davey et al. 2010a, Baker et al. 2012, Dadam & Siriwardena 2019), including within Glastir in Wales (<https://gov.wales/glastir>).

Hedgerows are important habitat features for birds in farmed landscapes, principally providing nest sites (either in the hedge itself or adjacent semi-natural herbivorous vegetation), food resources and shelter (Davey et al. 2010b, Redhead et al. 2013, Siriwardena et al. 2012, Broughton et al. 2021). The latter two apply in winter as well as in the breeding season, but often for different species. Specifically, hedges may provide suitable habitat for species associated with scrub or woodland edge habitats in a landscape that would otherwise not support them, but also provide an important component of habitat for species that can exploit agricultural production habitats (i.e. open fields; e.g. Redhead et al. 2018). The latter typically use field boundary habitats for nesting or shelter, and in-field habitats for foraging. Therefore, it is to be expected that different species will respond differently to changes in the availability of woody linear habitats in the landscape, and that baseline landscape structure will affect the patterns significantly in many cases.

Hedgerow management is prominent within LMSs such as Glastir, including options supporting the creation of new hedgerows, the restoration of relict or degraded hedgerows and more biodiversity-friendly management of existing hedgerows (chiefly involving reduced cutting frequency to promote vegetation density and berry production; <https://gov.wales/glastir>). Creation and restoration measures require a long-term commitment, because new woody vegetation takes decades to mature to the point that a hedgerow provides the resources and ecological functions that will benefit birds in practice. Trial and error to find best management practice is, therefore, not practical and it would be beneficial to be able to predict the best locations, in terms of biodiversity benefit per unit investment, for such management *a priori*.

It would be predicted that species that depend entirely on woody features will be more abundant in landscapes with more woody cover, especially more hedgerows in farmland-dominated landscapes. However, the abundance of species that require a combination of field and boundary habitats is likely to respond non-linearly, or to depend on the landscape context (quantity of other woody cover). Species that avoid vertical structure and woody features will respond negatively to hedgerow cover, but potentially non-linearly, because positive responses to *length* of hedgerow are unlikely to be strictly reciprocal to those to *area* of in-field habitat. Community or assemblage metrics such as diversity, species richness or composite multi-species abundance indices will respond in complex and unpredictable ways, dependent upon the balance of the different species-specific responses that are found in the assemblage that is measured. Therefore, it will be most instructive to consider relationships with hedgerows in terms of individual species.

The Glastir Monitoring and Evaluation Programme (GMEP) included bespoke bird monitoring, tied in with the monitoring of other targets. Hence, all 300 1km survey squares in the survey were surveyed for birds (75 squares each year from 2013 to 2016), using a flexible transect approach in which all terrestrial habitat areas in each square for which access permissions had been secured were visited on three or four visits during the breeding season (April to mid-July). For details of the field survey design, and selection of 300 GMEP squares, see Emmett & the GMEP team (2014, 2017). Digital mapping of bird locations by field then allows all records in farmland to be considered with respect to the field boundary habitat types in the relevant fields. Together, the detailed bird data and their integration with habitat/vegetation survey data provide a unique resource for exploring relationships between birds and hedgerows.

Here, we present analyses of the responses of all relevant bird species, grouped into guilds with different expected dependences on hedgerows, to woody linear feature density, considering the evidence to support non-linear responses and their shapes, and the dependence of those relationships on the background habitat context.

5.2 Approach

5.2.1 Rationale

The analyses of bird and linear feature data aimed to do the following for birds with different predicted responses to the quantity of hedgerow in the landscape:

- (i) Describe the shape of the relationship (how bird abundance changes as the density of hedgerow in the landscape) – evaluated using flexible models that make no assumptions about what the relationship will be in advance.
- (ii) Show whether and how the relationships vary in different landscapes, i.e. where there are different amounts of arable land, intensive farmland, other woody features and woodland in the surrounding landscape – evaluated using simpler models that produce more easily interpreted test results.
- (iii) Infer the implications for birds of adding more linear features (hedgerows) to different types of landscape, and where there are different amounts of hedgerow present already.

5.2.2 General approach and principles

Maximum bird counts by species across all survey visits, selecting farmland land parcels from GMEP survey squares, were pooled with respect to a classification of habitat preferences (Table 5.1). These pooled total abundance variables with respect to habitat preference were used in statistical models, as described below. Analyses were also conducted for species-specific abundances and are reported in Annex A. To test the predictions we first tested whether there was evidence that relationships between abundance and length of woody linear feature per area of farmland surveyed were non-linear, using Generalised Additive Models (GAMs). This approach avoids specifying a shape for the relationship (it could take a linear form or any shape of smooth, non-linear variation), so does not constrain patterns to a form that is determined *a priori*. Comparing models in which smoothed functions of different levels of complexity described the relationship between bird abundance and density of woody linear features showed the extent of the non-linearity that was present, in the presence and absence of different landscape controls, without constraining the fits to a particular function form. The influences of controls and interactions with landscapes were then investigated further with

simpler models constraining relationships to be linear or quadratic (curvilinear, but with only a single turning point), as Generalised Linear Models (GLMs). This model structure allows interactions between woody linear feature length and other habitat variables to be considered in a way that is more tractable and interpretable than would be possible in the GAM framework, but at the cost that complex non-linear forms, if they occur, cannot be described.

Data on woody linear features within the surveyed farmed area, the areas of arable and of improved land in the farmed area, the proportion of the survey square covered by small woody features and the proportion of broadleaf woodland cover in the surrounding landscape were extracted from GMEP and Land Cover Map data, as described in Table 5.2.

Table 5.1. Species definitions that are predicted to determine responses to woody linear feature density. 'N' denotes sample sizes of 1km squares where counts were non-zero; the total sample size was 227.

Woody feature species			Field & boundary species			Open field species		
Name	BTO code	N	Name	BTO code	N	Name	BTO code	N
Blackcap	BC	138	Blackbird	B	210	Lapwing	L	15
Bullfinch	BF	80	Chaffinch	CH	208	Skylark	S	80
Blue Tit	BT	185	Goldfinch	GO	165			
Chiffchaff	CC	136	Greenfinch	GR	86			
Dunnock	D	188	Linnet	LI	130			
Great Tit	GT	170	Magpie	MG	153			
Garden Warbler	GW	53	Song Thrush	ST	142			
Long-tailed Tit	LT	63	Whitethroat	WH	111			
Lesser Whitethroat	LW	17	Woodpigeon	WP	180			
Robin	R	197	Yellowhammer	Y	19			
Reed Bunting	RB	36						
Wren	WR	211						
Willow Warbler	WW	150						

Table 5.2. Derivation of habitat variables used in the analyses. "Lowland farmed areas of 1km square" means all arable, improved grassland and neutral grassland in a square.

Habitat variable	Definition
ARABLE_AREA	Proportional area of parcels in lowland farmed areas of 1km square mapped as arable and horticulture broad habitat
INTENS_AREA	Proportional area of parcels in lowland farmed areas of 1km square mapped as improved grassland broad habitat + ARABLE_AREA
WLF_DENS_KM_HA	Length of woody linear features in (and bordering) lowland farmed parts of the square in km/ha
SWF_1KM_PROP	Proportional area of small woody features in the lowland farmed parts of the square – from Copernicus derived data (CLMS 2019), after selecting only small and linear elements from within 1km of lowland farmed parts of the square ("outside only" buffer).
BL_1KM_PROP	Proportional area within a 1km buffer of lowland farmed parts of the square ("outside only" buffer) which is either covered by small woody features (SWF_1KM_PROP) or covered by broadleaf woodland according to a combined layer of Land Cover Map 2015 and National Forest Inventory 2016.
FIELD_AREA_SUM	Total area of parcels (km ²) in lowland farmed areas of a square.

5.2.3 Analytical details and statistical models

The models considered counts per unit area, by modelling raw counts with an offset for area surveyed (FIELD_AREA_SUM, Table 5.2) because, although surveys were conducted in standard units of 1km squares, only the farmed components of squares were considered in these analyses. The predictor variables were all independent of area, in being feature densities or proportions. Squares with fewer than three farmland parcels or less than 10 ha of surveyed (farmland) area were omitted, because there will have been too few field boundaries present in the surveyed area to represent a landscape type clearly. Over dispersion was accounted for in GLMs using a correction to model fit based on Pearson's χ^2 value for the model (note that this option was not available in the software used to fit GAMs, but will affect only confidence intervals and significance tests, not modelled parameter estimates themselves). Models with different levels of smoothing or linear/quadratic functions to describe the variation in count with respect to woody linear feature density were compared using AIC values: for models fitted with the same algorithm (i.e. not GAMs versus GLMs; such comparisons would not be valid because different algorithms are used to estimate deviance), a lower AIC value would indicate stronger support for a model, with more deviance explained, but penalising the inclusion of more parameters. All models were fitted using SAS 9.4¹. The specific questions considered and models used are described in Table 5.3.

Table 5.3. Analytical questions posed and models fitted to bird count data to investigate relationships with the density of woody linear features.

Question	Model form (dependent variables are bird abundance)
Is there evidence for non-linear relationships with woody linear features for each species and group?	GAMs specifying different levels of smoothing (complexity) of the non-linear relationship with woody linear feature density GLMs specifying linear or quadratic effects for the relationship with woody linear feature density
Do the relationships with woody linear features vary with landscape context?	GLMs specifying linear or quadratic effects for the relationship with woody linear feature density and interactions with linear effects of the background variables, as detailed below:
The proportion of arable land cover in the survey area: do patterns vary with the type of farming?	Interaction with the area of arable farmland (ARABLE_AREA)
The proportion of arable + improved land cover in the survey area: do patterns vary with farming intensity?	Interaction with the area of more intensive farmland (arable and improved grass; INTENS_AREA)
The proportion of other woody cover within the survey area: do patterns vary with local woody context?	Interaction with the area of other woody features in the survey area (SWF_1KM_PROP)
The proportion of other woody cover in the surrounding landscape: do patterns vary with woody context in the surrounding 1km buffer?	Interaction with the area of woody cover in the surrounding area (BL_1KM_PROP)

¹ www.sas.com

The background predictor variables considered were essentially uncorrelated (Table 5.4). Woody linear feature density in the surveyed sample varied from zero to just over 200m per hectare, although data density was highest in the middle of this range and rather low towards the upper end (Figure 5.1). This will have led to relationships with the higher values of the predictor being more uncertain.

Table 5.4. Correlations between the chosen habitat/landscape variables (N=227 squares).

	INTENS_AREA	ARABLE_AREA	SWF_1KM_PROP	BL_1KM_PROP
INTENS_AREA	1	0.313	-0.003	-0.061
ARABLE_AREA	0.313	1	-0.092	-0.009
SWF_1KM_PROP	-0.060	-0.124	1	0.479
BL_1KM_PROP	-0.061	-0.009	0.401	1

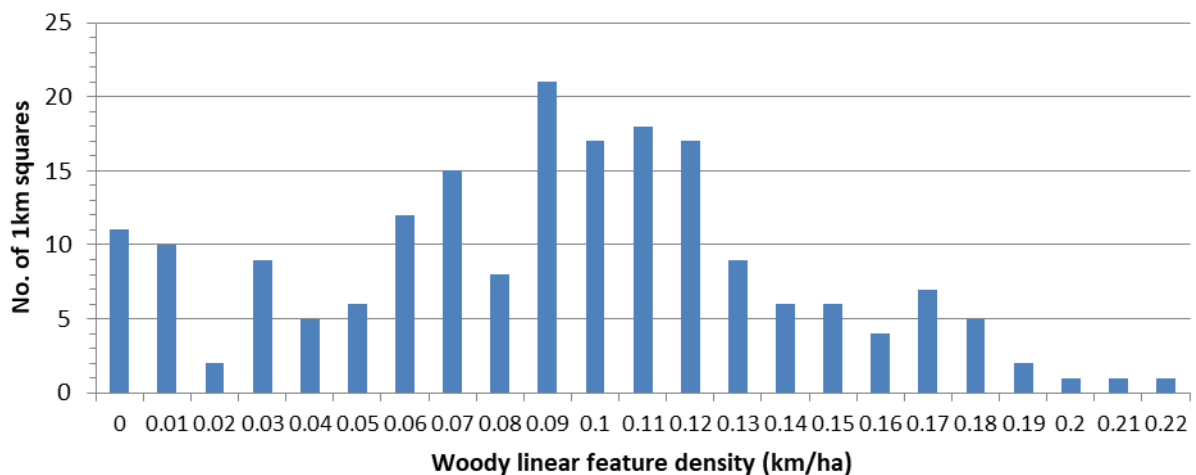


Figure 5.1. Frequency distribution of woody linear feature densities across 1km squares containing farmland habitat.

5.3 Results

5.3.1 Unconstrained relationships: GAM comparisons

Combining species into total abundances per guild or group (Table 5.1) revealed strong support for more complex smooth functions, with clearly decreasing AIC values with more degrees of freedom for the woody feature and field & boundary groups, and a clear rejection of the simplest smooth for the open field group (Annex A: Table 9.1). However, plots of the most complex function forms showed that the overall shapes were still quite simple, with the complexity being in small variations among the intermediate values of woody linear feature density (Figs 5.2 – 5.4).

Both species entirely dependent upon woody features and those that use them in combination with open fields showed overall increases in abundance up to a density of circa. 0.05km/ha of woody linear features and decreases in abundance as the density climbed above c. 0.13km/ha, but little effect over the intermediate range (Figs 5.2 and

5.4.). The open field species showed little effect below c. 0.1km/ha, but decreases above that point (Fig. 5.3).

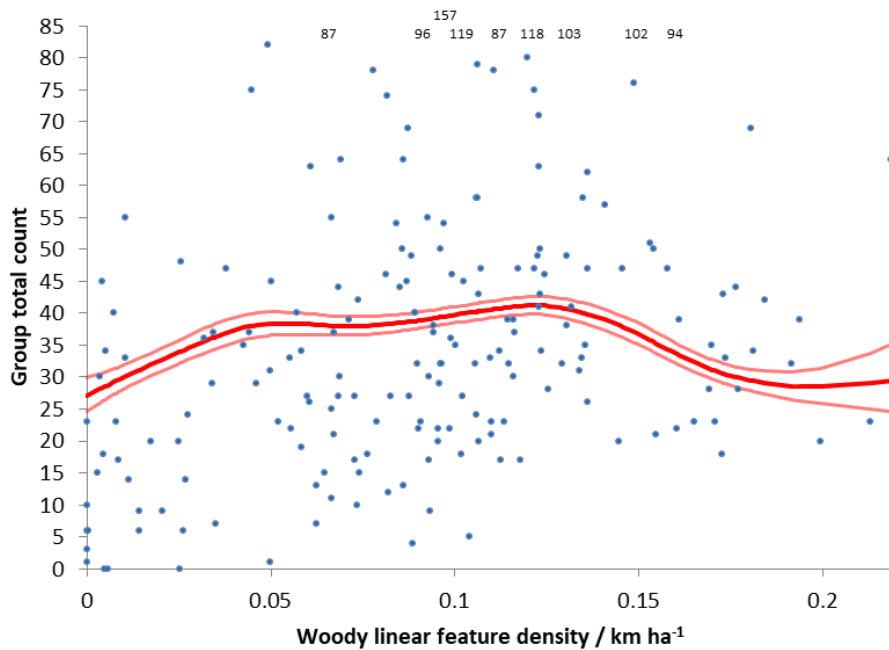


Figure 5.2. GAM smooth plots for the abundances of field & boundary species, with respect to woody linear feature density, using a smooth with 4df (the most complex one fitted). Dark red line shows smoothed fit and pale lines the fit's 95% confidence interval. Blue dots are raw data points; outlier abundance values are denoted by numbers at the appropriate point along the x-axis.

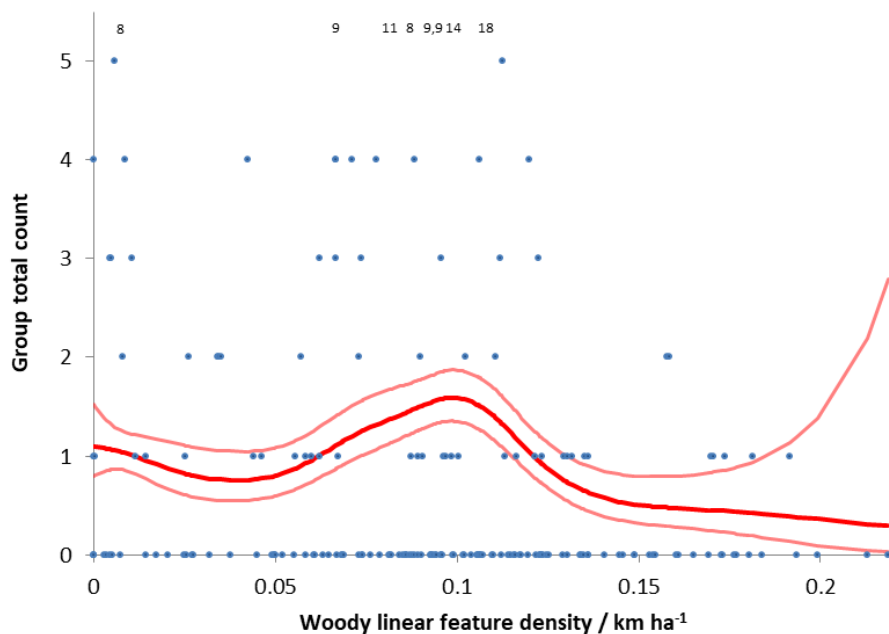


Figure 5.3. GAM smooth plots for the abundances of open field species, with respect to woody linear feature density, using a smooth with 4df (the most complex one fitted). Dark red line shows smoothed fit and pale lines the fit's 95% confidence interval. Blue dots are raw data points; outlier abundance values are denoted by numbers at the appropriate point along the x-axis.

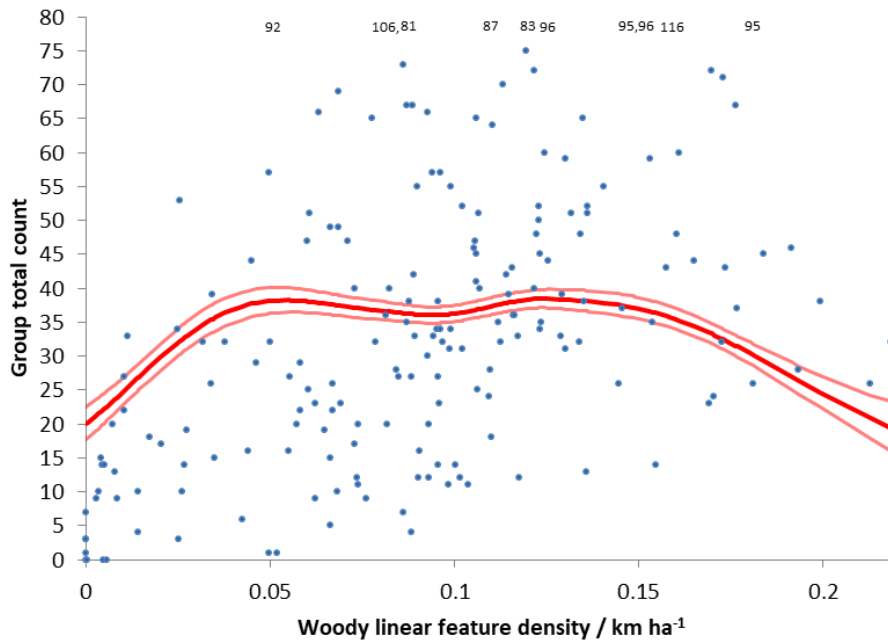


Figure 5.4. GAM smooth plots for the abundances of woody feature species, with respect to woody linear feature density, using a smooth with 4df (the most complex one fitted). Dark red line shows smoothed fit and pale lines the fit's 95% confidence interval. Blue dots are raw data points; outlier abundance values are denoted by numbers at the appropriate point along the x-axis.

5.3.2 Habitat effects on relationships: parametric functions in GLMs

Comparisons of models specifying constant (null), linear and quadratic (simple curvilinear) relationships between abundance and woody linear feature density supported the GAM results: quadratic models had the lowest AIC values, indicating the best fits, when all of the control variables were considered (Table 9.2). Again, there was strong evidence for non-linear relationships for all three groups of species.

There was evidence for a significant interaction between these non-linear patterns for all three species groups and at least one background habitat context variable, in that the relevant interaction model provided a better fit to the data than one with no interaction (Table 9.2). Once again, non-linear patterns were supported by the failure to select a linear interaction model in any comparison (Table 9.2). For field and boundary birds, quadratic interaction models were supported for local woody feature cover (small woody features, SWF_1KM_PROP) and broadleaf woodland cover in the landscape (BL_1KM_PROP). Inspection of the influences of the interaction effects on the shapes of the non-linear relationships indicates that the responses for both high and low small woody feature density were non-linear, with more birds found in areas with more woody field boundaries, but with the effect levelling off at higher levels of background small woody feature density (Fig. 5.5a). However, the effect was larger and the slope of the relationship steeper in landscapes with fewer small woody features, actually with evidence for a decline at the highest local woody feature densities. There was a similar general pattern in the interaction with the proportion of broadleaf woodland cover at the landscape scale, but with a more subtle effect (Fig. 5.5b).

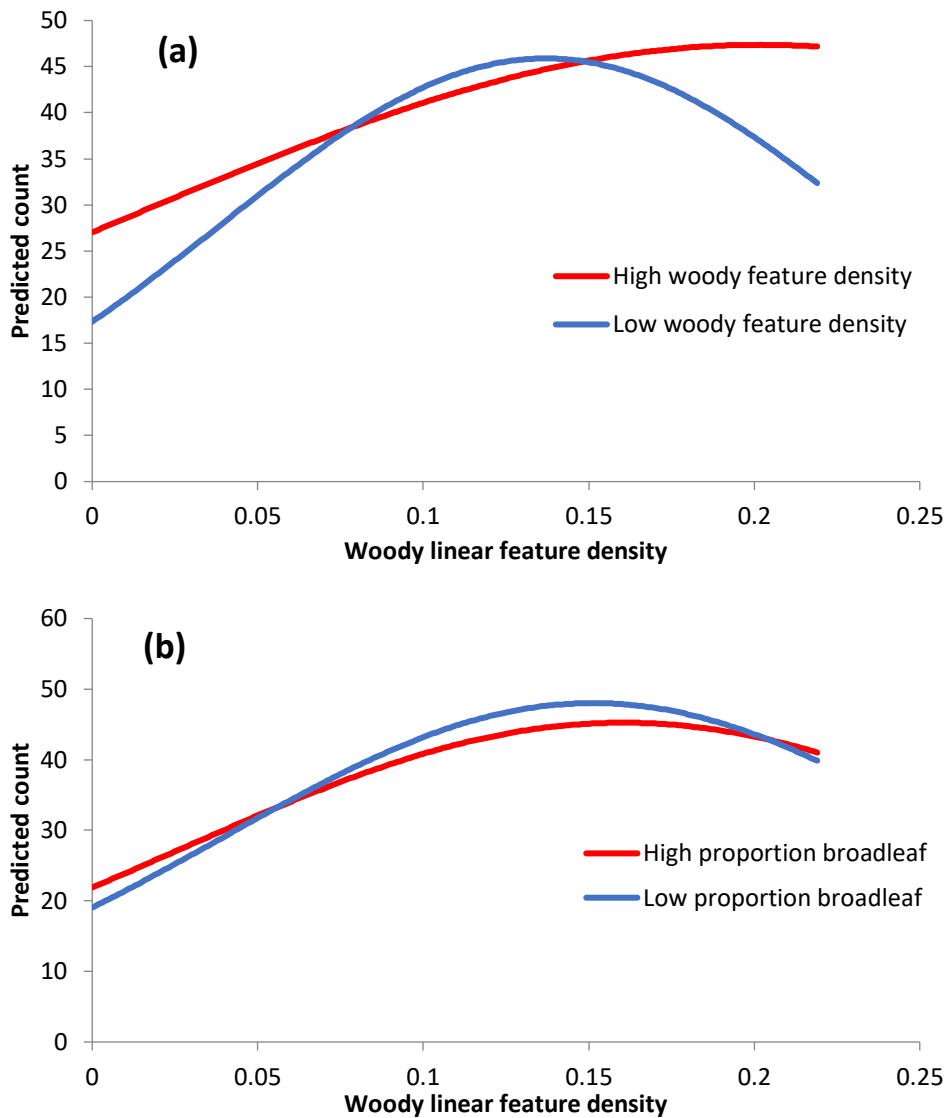


Figure 5.5. Predicted counts of birds that use field and boundary habitats with respect to the density of woody linear features, in survey areas with high (red) and low (blue) (a) local densities of other small woody features and (b) landscape levels of broadleaf woodland cover (see Table 5.2 for definitions; woody features are small areas of woody vegetation mapped separately from woody linear features). Plots show predicted values from GLMs including the relevant interaction terms, predicted for the first (low) and third (high) quartile values from the observed distributions of the habitat variable.

The same two habitat variables were important for woody habitat birds, as well as the area of arable land (ARABLE_AREA), although the latter effect was marginal ($\Delta AIC=2.8$, Table 9.2). There was a common pattern for predicted counts to rise smoothly with woody linear feature density, but mostly then to level off, or even to decline, at woody linear feature densities of greater than 0.15 km/ha (Fig. 5.6.). The interactions showed modifications of this pattern; counts were higher with high woody feature density in the surrounding area (Fig. 5.6a) and high broadleaf woodland land cover nearby (Fig. 5.6b), with less evidence of a decline at high woody linear feature density. Results were similar where arable cover was low (Fig. 5.6c).

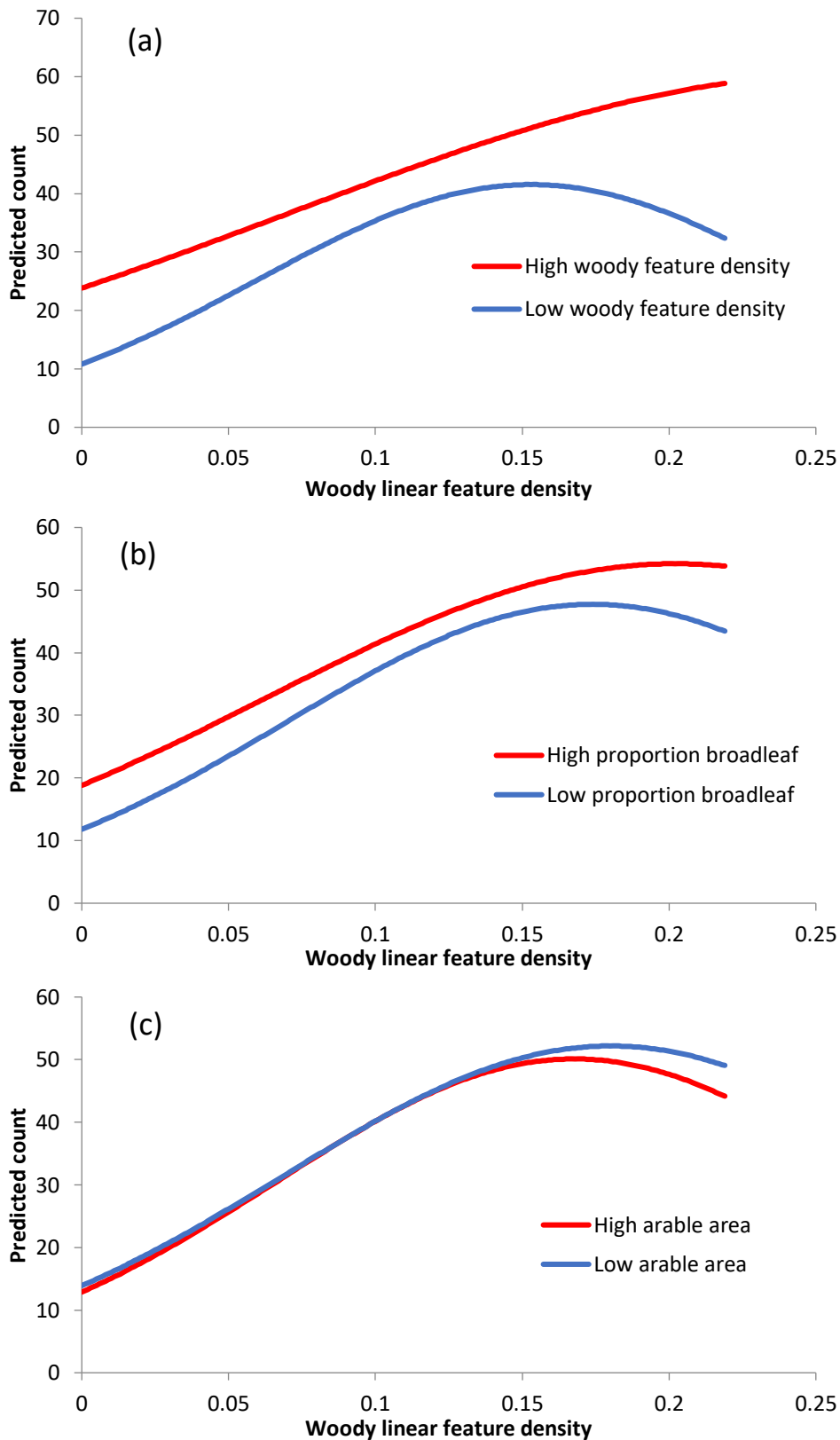
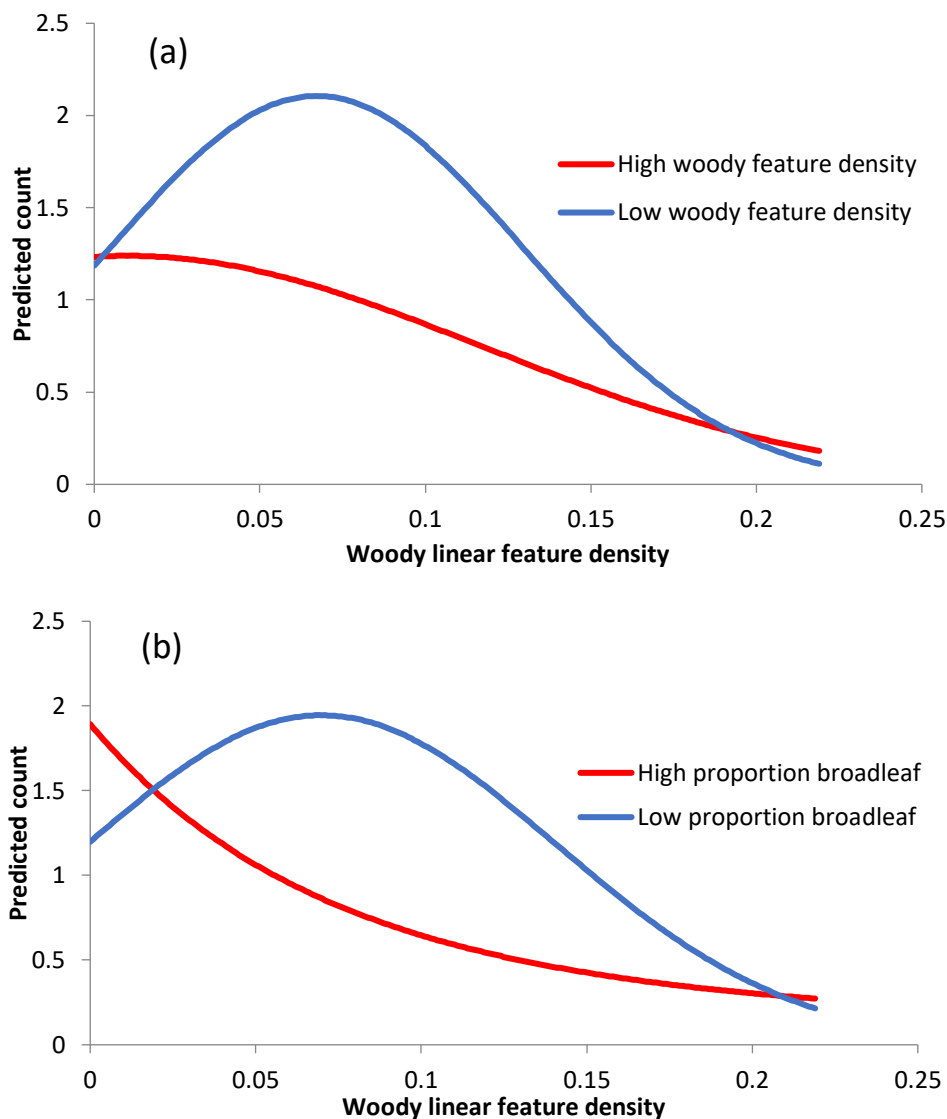


Figure 5.6. Predicted counts of birds that use woody habitats only with respect to the density of woody linear features, in survey areas with high (red) and low (blue) (a) local densities of other small woody features, (b) landscape levels of broadleaf woodland cover and (c) areas of arable cover. Plots show predicted values from GLMs including the relevant interaction terms, predicted for the first (low) and third (high) quartile values from the observed distributions of the habitat variable.

All four variables were important influences on the relationship for open field birds and the patterns predicted were more variable than for the other groups (Fig. 5.7.). In surveyed areas and landscapes with low woody cover, predicted counts peaked at around 0.075 km/ha of woody linear features, but with high local woody feature density, the relationship was largely flattened (Fig. 5.7a) and with high landscape broadleaf cover, it became a rapid decline (Fig. 5.7b). The pattern of rapid decline was also evident with low arable and high intensive farming cover, especially above 0.05 km/ha of woody linear features, but, at high levels of both arable and intensive farming, counts again peaked with high cover of the background variables (Fig. 5.7c,d).



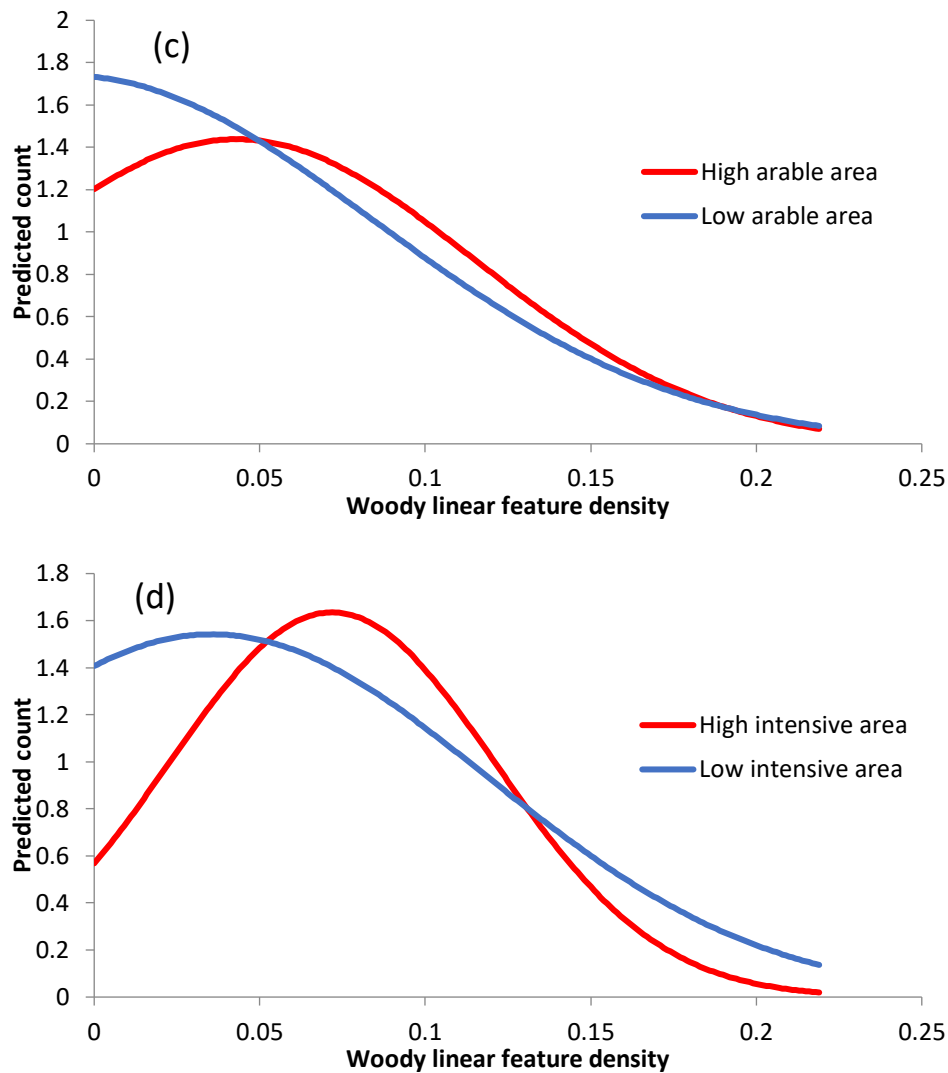


Figure 5.7. Predicted counts of birds that use open fields only with respect to the density of woody linear features, in survey areas with high (red) and low (blue) (a) local densities of small woody features, (b) landscape levels of broadleaf woodland cover, (c) areas of arable cover and (d) areas of intensive farming. Plots show predicted values from GLMs including the relevant interaction terms, predicted for the first (low) and third (high) quartile values from the observed distributions of the habitat variable.

5.4 Discussion

Non-linear responses of bird communities to the density of woody linear features have clear implications for the targeting of agri-environment management in the form of the creation or restoration of hedgerows. These implications are discussed in Section 6, in the context of the current distribution of relevant Glastir interventions. Here, we have found strong evidence for non-linear responses of all groups of farmland birds, as well as most individual species (Annex A). Moreover, although these relationships are at most only weakly affected by background habitats as simple, additive controls, they are frequently subject to strong interaction effects, changing form with landscape context.

Birds were divided into groups with different expected responses to woody linear feature density, based on their ecologies. The predicted responses of these groups were supported partially, but not entirely. Open field species indeed tended to be less common where there were more woody linear features, albeit with little effect across the low end of

the range of the variable (Fig. 5.3.), but increasing woody features from a very low base appeared actually to be a positive influence in areas with low local and landscape woody cover, or higher areas of arable or intensive farming (Fig. 5.7.). This pattern is counter-intuitive and may reflect subtle confounding factors, by which farmland suitability (e.g. grazing intensity) is somehow associated with variables such as woodland cover. This group variable may be particularly susceptible to such factors as it comprised only two species, one of which (Lapwing) is uncommon in Wales. Nevertheless, it is clear from the relationships in all contexts that the increasing hedgerow density above around 0.75 km/ha would be detrimental to open field species.

Birds that depend on woody habitats will only be found in woody linear features or other patchy woody habitats in most farmland areas. However, perhaps surprisingly, they did not simply increase in abundance with increasing woody linear feature density. Counts did increase up to 0.05 km/ha of woody linear features, but were then stable until actually falling at the upper end of the variable's range, above 0.15 km/ha (Fig. 5.6.). This may relate to the types of linear feature that are present in high density landscapes: perhaps they tend to feature less dense, wide or tall vegetation than otherwise similar boundaries where they are less common. This might be expected given that larger boundary vegetation will have proportionally more impact on the productive area in fields where fields are smaller and the density of boundaries is higher. It may also reflect the types of landscape in which more boundary habitats are found, with them being used more because populations spill out from core, higher quality (from the perspective of woodland birds) habitats. This is supported by the interaction test results: predicted counts were higher and declined less at high woody linear feature densities with high local and landscape densities of woody habitats (Fig. 5.7a,b). The latter decline was also marginally more pronounced in areas with higher arable cover (Fig. 5.7c), which may again reflect boundary habitat quality and more active management of hedgerows in such landscapes because of effects on accessibility of land to farm machinery. However, differences at the upper end of the woody linear feature gradient should be interpreted with caution because sample sizes were smaller (Fig. 5.2).

Like woody habitat species, those that prefer open fields and hedgerows in combination showed a peak in predicted abundance between 0.05 and 0.13 km/ha of woody linear features, but then a decline (Fig. 5.2). As with woody feature-dependent species, this could indicate an effect of lower habitat quality at the high end of the range, but it may also reflect optimal combinations of boundary habitats (for nesting and shelter) and open fields (for feeding) for the species concerned. The less sensitive non-linear functions fitted to test for interaction effects showed the increase in abundance with woody linear feature density was steeper in areas with lower levels of woody cover, especially locally but also at the landscape scale, and that the pattern of increase up to intermediate woody linear feature levels was a stronger pattern than the decline at higher woody linear feature levels (Fig. 5.5). The latter probably reflects the lower sampling density at that end of the gradient (Fig. 5.2), while the interaction effect suggests that the benefit of additional hedgerows would be greater in landscapes with lower initial covers of woody features in general and of woody linear features, specifically.

Overall, the patterns for groups and for individual species (Section 10 - Annex A) suggest that the patterns of response to woody linear features are non-linear for most species, and for combined abundances, but are not hugely complex patterns, or at least the patterns can be described acceptably by simple function shapes. Further, additional analyses incorporating smooth spline, instead of linear, functions for the background habitat controls produced near-identical results to those presented here. This supports the use of simple functions in parametric analyses.

6 CASE STUDY 3A: LANDSCAPE HETEROGENEITY FOR PLANT BIODIVERSITY

6.1 Summary

- In this section we explore the relationship between habitat heterogeneity and plant species richness using GMEP data. We aim to understand how and where land management scheme (LMS) interventions might successfully increase plant biodiversity.
- We found positive relationships between species richness and heterogeneity, particularly at local scales.
- However, we found that habitat diversity may have diminishing returns when it comes to regional plant species richness (Fig. 3.4).
- The species that benefit most from increased heterogeneity are those with a wider niche, i.e. generalists. Species with a narrow niche, i.e. specialists, actually decline with increased heterogeneity.
- Targeting for LMSs should consider the landscape context, particularly heterogeneity. However, components of heterogeneity, e.g. boundary features and habitat diversity, may differentially affect plant species. As such the package of measures being applied to a farm/landscape is also critical.
- Targeting will also depend on intervention type, and whether it is applied to generalist or specialist species.

6.2 Background

The analyses presented here aim to determine whether there is a positive linear relationship or non-linear relationship between habitat heterogeneity and plant species richness. This is important for understanding how the location of agri-environment interventions interacts with landscape context. For instance, if high heterogeneity promotes high species richness then interventions in heterogeneous landscapes might be more successful.

Previous work used GMEP data and remotely sensed data to estimate heterogeneity representative of high nature value (HNV) type 2 farmland in every 1km square in Wales. The map in figure 6.1 was created from the heterogeneity axis identified in that work (Maskell et al. 2019). With an understanding of how different levels of heterogeneity might influence outcomes, such a map could be used to target action both in implementing individual options and the package of options agreed within an area.

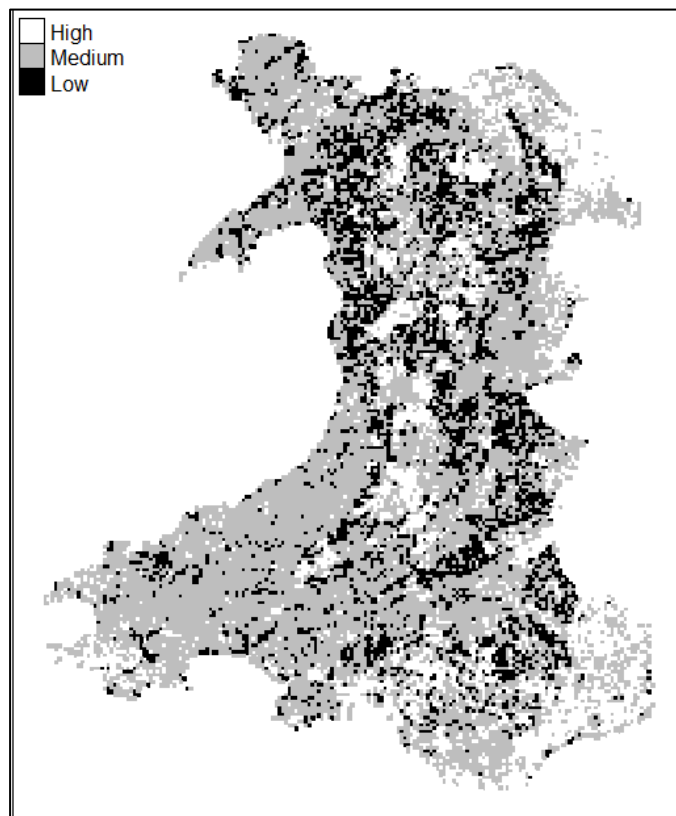


Figure 6.1: Map of High Nature Value farmland Type 2 Heterogeneity in Wales. This map was created from an ordination of GMEP field survey data (response variables; different types of biodiversity, explanatory variables; % semi-natural land, structural variables such as hedgerows and woodland connectivity). To extrapolate across Wales, remotely sensed data for explanatory variables was added to the ordination. Scores along the axes land-use intensity and habitat heterogeneity have been extracted and categorised (based on the 20th percentile) into 'High' (top 20 percentile), 'medium' (middle 60 percentile) and 'low' (lowest 20 percentile).

This section builds upon the previous work to explore further; (1) the concept of heterogeneity, including some additional metrics, (2) relationships between species richness and different metrics of heterogeneity at different scales and (3) which types of species might benefit/be adversely affected by heterogeneity, i.e. generalist or specialist species.

There are two common assumptions that have been the basis for theories of species diversity distribution in ecology, evolution and island biogeography for many years (Rosenzweig 1995, MacArthur 1965). These are: (1) as the area of a habitat increases, it's capacity to support more species also increases (Allouche et al. 2013), and (2) as environmental heterogeneity increases, there is a wider niche space to meet species' ecological requirements of species, thus species-richness increases (Heidrich 2020). Heterogeneity is the spatial variation in abiotic and biotic factors that influence habitat and landscape structure. For plants, this may mean heterogeneity in soils, nutrient availability, pH, soil compaction, water content, micro-topography, or microclimate.

However, there may be a trade-off between area and heterogeneity (Allouche et al. 2012, Heidrich et al. 2020, Ben-Hur & Kadmon 2020). As environmental heterogeneity increases, the available space for individual species decreases, leading to reductions in population size and ultimately stochastic extinctions. Figure 6.2 demonstrates the potential relationships.

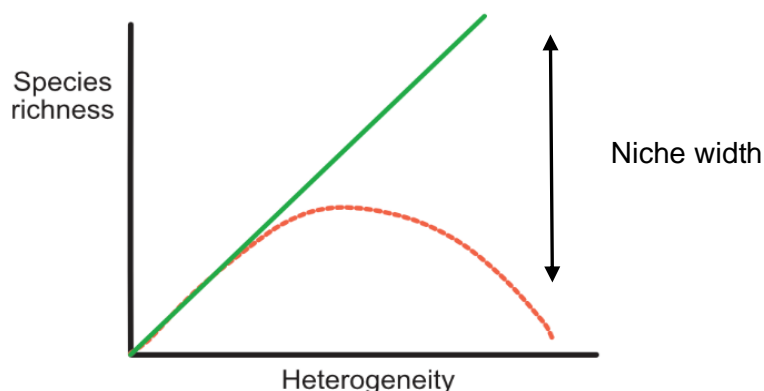


Figure 6.2. Conceptual diagram of relationships between heterogeneity and species richness

Habitat fragmentation may increase with increasing heterogeneity, causing species loss. When a threshold, or inflection point, is reached between species gains from heterogeneity and losses due to reductions in available area, species richness declines. This results in a non-linear unimodal relationship between heterogeneity and richness (Allouche et al. 2012, Heidrich 2020). The trade-off is expected to be more noticeable in species with a narrow niche width (Allouche et al. 2012), and might also depend on dispersal ability.

There is conflicting evidence about the relationship between area and heterogeneity, and whether a trade-off exists. Some authors have suggested that the relationships between area and heterogeneity are not necessarily easily and constantly predictable, and may vary by context (Heidrich et al. 2020, Batary et al. 2011). For example, the scale of the study, the habitat or ecosystem, selected taxa, trophic level and functional groups, the definition and measurement of heterogeneity, and the length of the gradient of chosen variables (short heterogeneity gradients may under-represent trade-offs). Results are also complicated by the many different definitions of heterogeneity; there is a great deal of ambiguity in concepts and terminology, and many different metrics have been used to represent heterogeneity (Stein and Kreft, 2016).

In previous work with GMEP data (Maskell et al. 2019) we analysed potential explanatory variables and created an ordination space where HNV type 1 land was represented by a land use intensity gradient and HNV type 2 by a heterogeneity gradient. Such landscape perspectives are important for targeting of LMSs and AESs, because some studies suggest that AES interventions have greater impact on species richness and abundance in simple, and not complex, landscapes (e.g. Tschardtke 2005, Scheper et al. 2013). However, such results are taxon and habitat specific (Batary et al. 2011). To increase the diversity and abundance of specialist species associated with semi-natural habitats, it may instead be best to target interventions toward complex landscapes where source populations exist (Keenleyside et al. 2020, Kleijn et al. 2011, Alison et al. 2016).

In this work, we build on the work of Maskell et al. (2019) looking at a wider set of landscape variables, including some new remotely sensed data. We explore relationships between plant species richness and multiple heterogeneity metrics at multiple spatial scales. We aim to improve understanding of how and where LMS interventions might be most beneficial for plant biodiversity.

6.3 Approach

Data were collated from the GMEP field survey, from remotely sensed data and from other third party sources (e.g. elevation data from NextMap DTM). Data were extracted at different spatial scales by buffering around the vegetation plot (Fig. 6.3).

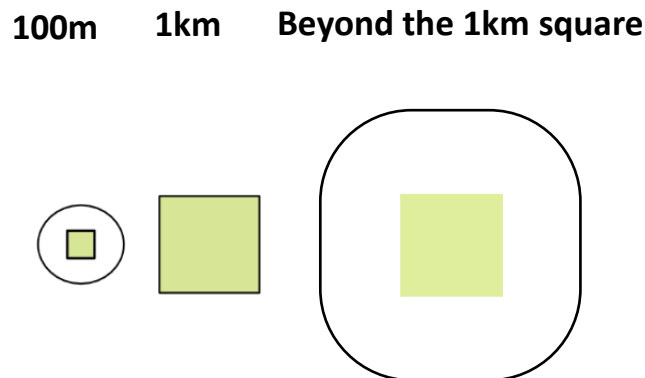


Figure 6.3 scaling used for data extraction

We carried out much initial data exploration to check for correlations between variables to ensure robust statistical analysis and inference (Section 10 - Annex A). For instance, we correlated variables from field survey with remotely sensed data. Where relationships were strong and significant we proceeded with remotely sensed alternatives which were available both inside and outside the square. There were very strong relationships between the small woody features data (Copernicus data; CLMS 2019) and the density of woody linear features from field survey ($r^2=0.69$). There were strong relationships between land cover of improved and semi-natural habitats from land cover map 2015 (LCM) and GMEP ($r^2=0.7$). Habitat diversity between GMEP data and LCM was slightly less well correlated but still $r^2=0.44$ at 1km scale.

In order to produce a composite heterogeneity metric, we carried out an ordination. Variables included in the ordination were Habitat diversity, NDVI (Normalised Differential Vegetation Index; extracted from 30m resolution composite, cloud-free Landsat-8 satellite imagery from 2013-2016) mean and standard deviation (STD represents variation in vegetation greenness), the % of semi-natural and improved land, woody cover, and different types of woody feature (from LCM and GMEP). At the 1km square scale this included the number of trees, length of woody linear features and elevation. An ordination (redundancy analysis; RDA) of explanatory variables was carried out at all 3 scales. As with previous, similar analyses (Maskell et al. 2019), Axis 2 of the ordination represented a composite heterogeneity metric. This meant that scores for Axis 2 could be used to represent compositional heterogeneity (Perovic et al. 2018), along with some individual variables such as habitat diversity.

Species richness data were taken from vegetation plots in the GMEP field survey (X, Y and U plots, see Wood et al. 2017 for details about vegetation survey methodology). Data from small 2m x 2m plots and large 200m² plots were used in analyses, but only the large plots are presented here. We calculated the number of species in each plot, as well as the total species richness across each 1km square.

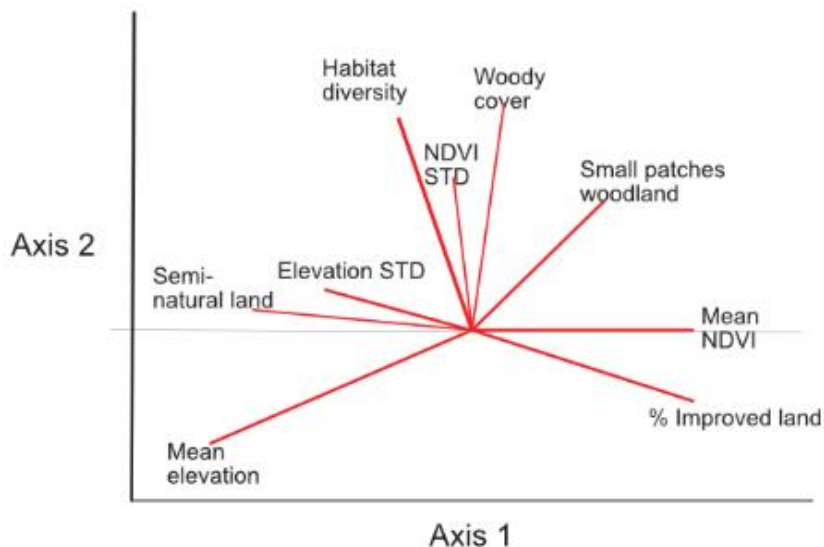


Figure 6.4 results from ordination of potential explanatory variables from field and remotely sensed data.

Generalised Additive Mixed Models (GAMMs, Poisson error structures) in R were used to analyse the effects of heterogeneity metrics on (1) plot-level and (2) square-level species richness. The 1 km square was incorporated as a random intercept in plot-level analyses. The number of plots per square was included as a predictor in the square-level analysis.

Niche hypervolumes can be used to characterise a species' ability to tolerate a wide variety of environmental conditions in an n -dimensional space. We calculated niche hypervolume for 375 plant species from the GMEP database in R (SVM method; Blonder et al. 2018). Species were classified by niche hypervolume into four groups (by quantiles) and species richness was calculated for each group.

GAMMs were used as above to explore relationships between heterogeneity and species-richness of different niche groups, and models also accounted for productivity (% of improved land in square).

6.4 Results

There were positive relationships between species richness and the heterogeneity axis at two different scales (within a plot and within a square, Fig. 6.5).

To look at whether these relationships vary by habitat type/ecosystem, we have plotted the same relationship for the plots in each individual habitat (Fig. 6.6). The relationships vary by habitat/ecosystem, with positive relationships in semi-natural grasslands, mountain, moor & heath, fen, marsh & swamp but no relationship in broadleaved woodland.

If habitat diversity is used instead of the heterogeneity metric the relationship is still positive between plots but at the 1km square scale the relationship is unimodal (Fig. 6.7).

Results from analyses of different variables at different scales can be seen in table 6.1. There were positive relationships between heterogeneity and species richness at the local and 1km scales. However, at 1km scales, relationships with habitat diversity became unimodal. Woody cover tended to have a positive effect on species richness at all scales.

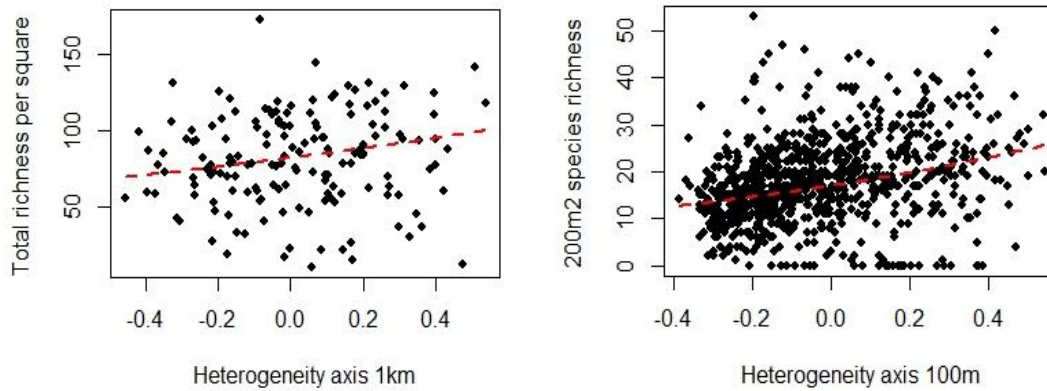


Figure 6.5. Effects of the composite heterogeneity axis (scores from the ordination) on species richness in 200m2 plots (left) 1km squares (right).

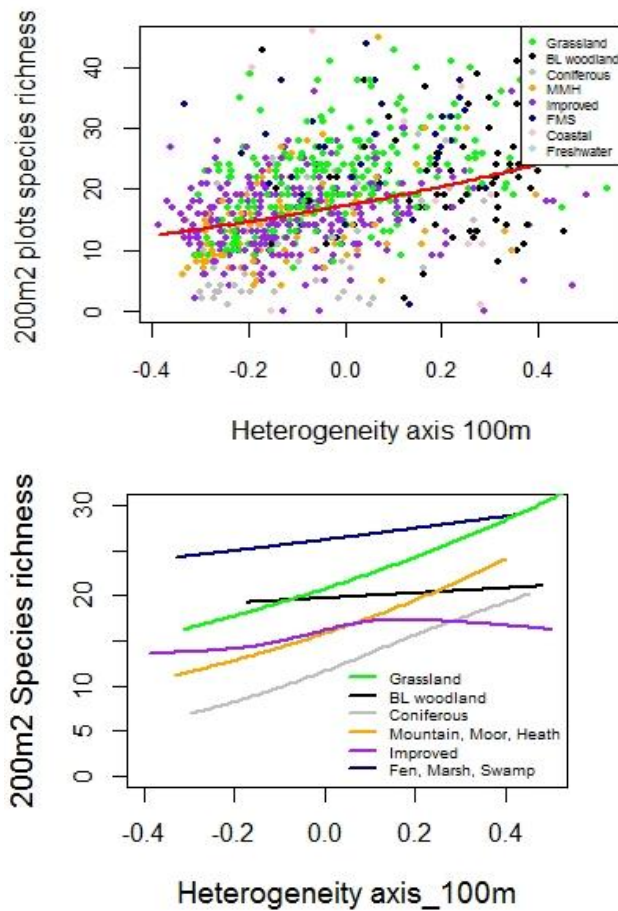


Figure 6.6 As for figure 6.5 above this is the relationship between heterogeneity axis and species richness in 200m2 plots a.) points are coloured by habitat type b.) fits from the GAMM model are shown for each habitat type.

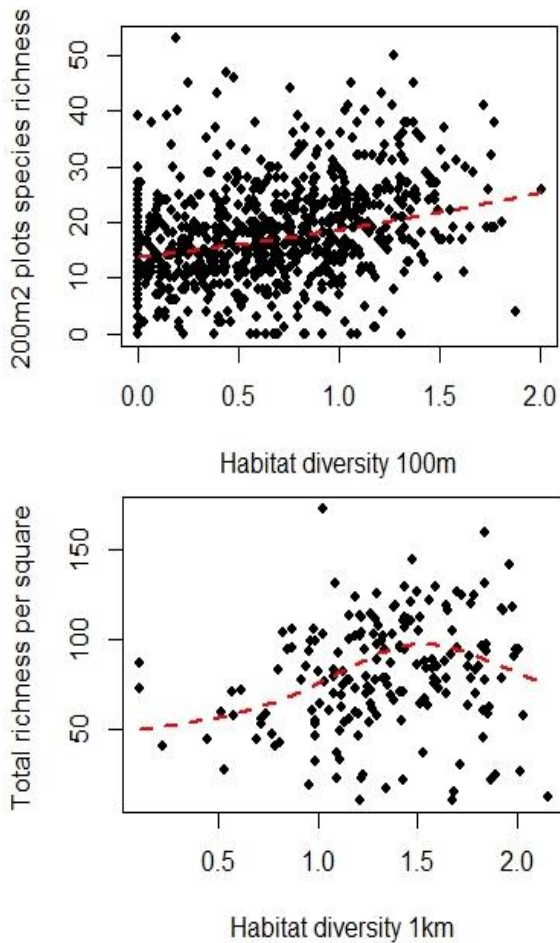


Figure 6.7. Relationships between Habitat diversity and species richness in a.) 200m2 plots and b.) 1km squares.

As predicted, species with the greatest niche width (i.e. highly generalist species) were positively related and species with the smallest niche width were negatively related to heterogeneity (Fig. 6.8.).

When habitat diversity was used as an explanatory variable there was a positive relationship between species with the greatest niche width and habitat diversity at the plot scale, however, there was a unimodal relationship between species with the greatest niche width and habitat diversity at 1km scale.

Table 6.1 Results from analyses of different metrics at different scales. ns= not significant, '+' indicates a positive effect, '∩' represents a hump-backed effect 'NA' means Not applicable, in this case that there is no data at this scale.

Scale of response variable	Heterogeneity axis (Scale of predictor)			Habitat diversity			Woody cover		
	Local	1km	Beyond 1 km	Local	1km	Beyond 1 km	Local	1km	Beyond 1 km
200m ²	+	ns	ns	+	∩	ns	+	+	+
1km	NA	+		NA	∩	ns	NA	+	+

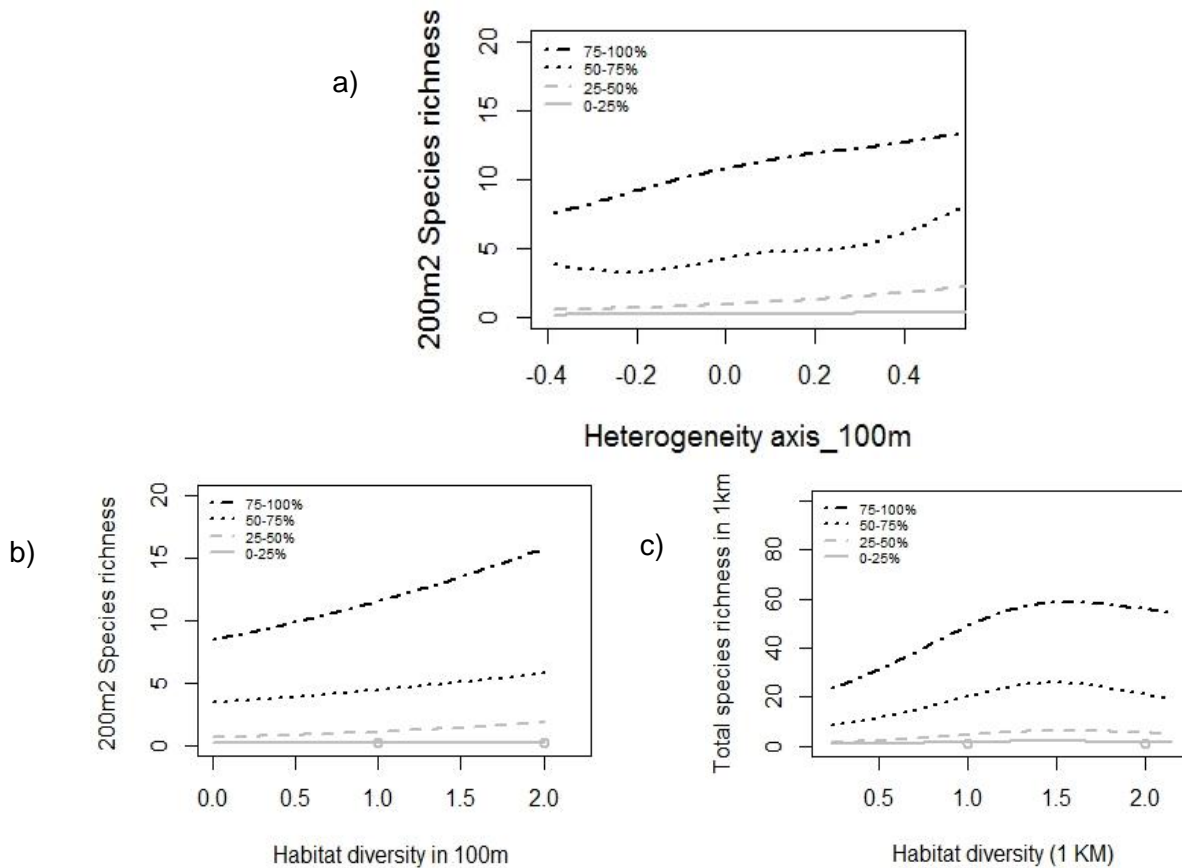


Figure 6.8: Relationships between species richness within four groups with different niche width, the species with the broadest niche are those at the top of the legend (75-100%) (a) heterogeneity, (b) habitat diversity and richness in 200m2 plots and (c) heterogeneity and richness in 1km squares.

6.5 Discussion

Understanding the relationship between heterogeneity, area and species richness is important for restoring and reconnecting habitats and their biodiversity, particularly in highly modified landscapes. Although we expected that heterogeneity might have stronger effects on plant species at local scales, we found significant relationships at all scales.

The composite heterogeneity metric is useful to summarise many aspects of the landscape, because the ordination axes were very strong. However, a composite metric makes it difficult to tease out which elements of landscape heterogeneity are most important – the metric included woody cover, WLF’s, the number of trees, variation in NDVI and elevation. The results using composite heterogeneity suggested that species richness was maintained at high heterogeneity, implying that negative effects from reducing the area of habitats were less substantial. It is also possible that when working with a composite heterogeneity metric, a strong positive effect of woody cover masks a unimodal effect of habitat diversity. Perhaps woody features provide additional niche space that exceeds any corresponding effect of habitat fragmentation.

We found generally positive relationships between species richness and heterogeneity, particularly at local scales. However, we also highlight a trade-off between an increase in the number of habitats (habitat diversity) and species richness at slightly larger scales. In other words, increased habitat diversity corresponds to increased local richness, but with diminishing returns for regional richness (Fig. 6.8). Theory suggests that this might result

from increased habitat fragmentation which can be associated with increased habitat heterogeneity. Some authors have predicted and found that the effects of agri-environment options on species richness will be maximal in landscapes of intermediate complexity (Tscharntke et al. 2005), decreasing to zero in the simplest and the most complex landscapes (Concepcion et al. 2008, Concepcion et al. 2012). This is based on the assumption that relationships between landscape complexity and field scale species richness are non-linear and that these interact with local management effects (Concepcion et al. 2008, Concepcion et al. 2012).

The results from the classification of species by niche width show that it is the species with a broad niche width, the generalists, that benefit most from increased heterogeneity. Smart et al. (2006) found that as alpha-diversity (local diversity within small vegetation plots) declined, plant communities became functionally more similar, while species-compositional similarity declined. Different communities converged on a narrower range of winning generalist trait syndromes, but species identities diverged as different species came to dominate more species-poor patches of different habitat types within each 1 km square. The reverse trends in beta-diversity (1km square species richness) occurred where alpha-diversity increased.

Relationships with productivity and species richness could follow similar patterns, We did try to account for the effect of productivity, firstly in the heterogeneity axis score (because axis 1 was a productivity gradient) and secondly as an additional variable in analysis.

Increased heterogeneity will generally be beneficial but there may be a point where habitat diversity is high, available niche space is filled, and increases in species richness are offset by species losses. The species declining are likely to be more specialised species with narrower niches; possibly those species associated with more open conditions e.g. Farmland birds (Concepción et al. 2012, Maskell et al. 2019). Targeting for LMSs will thus depend on intervention type and whether it is applied to generalist or specialist species. Consideration must also be given to the package of measures applied, and which aspect of heterogeneity it is expected to enhance.

7 CASE STUDY 3B: HEDGEROWS FOR PLANT BIODIVERSITY

7.1 Summary

- We explore whether landscape context influences the ground flora richness of hedgerows. We look at relationships between landscape metrics and species richness (overall and ancient woodland indicators; AWIs) at multiple spatial scales. We also analyse the influence of different hedgerow management parameters.
- Species richness of hedge ground flora was lower when adjacent to improved land.
- Heterogeneity at larger scales (beyond 1km) positively affected species richness of hedge ground flora. However, individually, habitat diversity and proportion of semi-natural habitat were not significantly related to overall species richness or AWIs.
- At local scales, species richness responded most clearly to elevation, improved land and small woody features within a 100m radius. Beyond 1km, cover of large woodlands also affected species richness. However, at the 1km scale effects of woodland and small woody features were weak.
- Relationships between species richness of AWIs and cover of woodland were unimodal. Significant relationships were found between AWIs, small woody features and large woodlands at the 1km scale and beyond the 1km square.
- In terms of management, vertical gaps in hedgerows were unimodally related to species richness. The management of neighbouring and surrounding land was apparently more important than hedgerow structure in determining ground flora.

7.2 Background

As discussed in Section 6, relationships between landscape complexity and species richness could be positive or non-linear, and are likely to interact with local management effects (Concepción et al. 2008, Concepción et al. 2012). It has been recommended that targeting of interventions should include assessment of landscape-scale dispersal sources, e.g. the density of linear features (Török et al. 2018).

Landscape context is important as a source of species for colonisation after the implementation of an intervention. Hedgerows may operate as refugia for species lost from a wider modified matrix. However, they also benefit from the 'refugia' effect of semi-natural (particularly woody) habitats to increase species pools and provide sources for colonisation.

We explore whether landscape context influences the ground flora richness of hedgerows. We do so firstly in a general sense, analysing relationships between different landscape context metrics and species richness (total and Ancient Woodland Indicator species; AWIs) to test the hypothesis that the ground flora of hedgerows is richer where there are larger species pools i.e. more semi-natural and particularly woody cover at local, 1km or landscape (1km+) scales. We also explore how hedgerow management relates to species

richness and how it might be influenced by landscape context. Hedgerow management options could include (1) “gapping up” (planting regionally relevant new hedgerow plants in gaps at an appropriate spacing and density - this could be a response to loss of trees through tree disease); (2) rejuvenation through hedge laying or coppicing and other locally relevant (traditional) management practices that would influence the height and width of the hedgerow, (3) fencing on both sides to restrict livestock access during establishment and regeneration, and (4) improvement of ground flora by limiting stock access, stopping application of fertilizer (Maskell et al. 2020). Here we have used some management metrics from “D plots”, which record the proportion of vertical gaps, hedgerow height, width, base height, the distance to managed adjacent land and the width of perennial vegetation (i.e. margin width).

7.3 Approach

7.3.1 Modelling species richness

In these analyses we fitted generalized additive mixed models (GAMMs, poisson error structures) to predict plant species richness (overall richness and AWI richness). Using mixed models enabled us to add a random variable to account for spatial autocorrelation of plots being nested within squares. Furthermore, GAMMs allow for unconstrained and smooth non-linear relationships. Models were fitted using the R package *gamm4*, and comparisons between models were made using AIC (second-order Akaike’s information criterion). AIC was extracted from the “mer” object of the fitted model. Following Burnham and Anderson (2002), we ranked them by their values of AIC, with the best fitting model having the lowest AIC. We look at effects of small woody features, hedgerows, lines of trees and number of trees, Habitat diversity, the % of semi-natural land, elevation (from NextMap DTM) and mean and STD of NDVI (Normalised Differential Vegetation Index; extracted from 30m resolution composite, cloud-free Landsat-8 satellite imagery from 2013-2016) as context. Management effects included the height, width of the hedgerow, percentage of vertical gaps, the base height (height from ground to canopy) and the distance of adjacent managed or ploughed land from midline of the Hedgerow.

7.3.2 Data

Vegetation plots were used to record the plant species composition of vegetation associated with hedge bottoms (1m x 10m, “B plots” and “H plots”, Wood et al. 2017). For a selection of the H plots, there is an adjacent hedge diversity Plot – the “D plot”. The hedge diversity plots span the width of the woody linear feature and are 30m long. In addition to species information, other data on the dimensions and condition of the feature were collected, as was information on the presence and width of adjacent buffer strips.

Data has been analysed separately for all B & H plots (N=244) and for those H plots associated with a D plot (smaller dataset, N=173).

The ground flora species richness of hedge and boundary plots has been calculated as in data analysis for SoNaRR reporting (Alison et al. 2020), in which the following negative indicators were excluded from species richness (species indicative of eutrophication and disturbance): *Urtica dioica*, *Rumex sp.*, *Galium aparine*, *Poa annua*, *Cirsium arvense*, *Cirsium vulgare*, *Bromus hordeaceus*, *Seneco vulgaris* and *Stellaria media*.

7.4 Results

7.4.1 All hedge plots – Effects of landscape context

The species richness of the ground flora was lower where the land adjacent to a hedge was improved (Figure 7.1). When improved/not improved status was included in models it consistently reduced AIC and improved model fit.

Table 7.1: Effects of landscape context (either habitat diversity, % semi-natural land, small woody features (taken from Copernicus data set; CLMS 2019), Large woodlands (NFI and LCM), density of WLFs and the heterogeneity axis calculated in Section 4. Analyses take place at different spatial scales, 100m around the plot, 1km and 1km around the square (i.e. 9km). ns= not significant, '+' indicates a positive effect, '∩' represents a hump-backed effect. NA= not tested.

Response variable	Scale	Landscape context						
		Habitat diversity	% semi natural land	elevation	Small woody features	WLF density	Large woodlands + small woody features	Heterogeneity axis
Total species richness of hedge ground flora	100m around the plot	ns	ns	∩	+	NA	ns	ns
	1 km square	ns	ns	∩	ns	ns	+	ns
	Beyond 1km (1km+)	ns	ns	∩	ns	NA	+	+
Ancient woodland indicator species richness of hedge ground flora	100m around the plot	ns	ns	∩	ns	NA	ns	ns
	1 km square	ns	ns	∩	ns	ns	+/∩	ns
	Beyond 1km (1km+)	ns	ns	ns	ns	NA	∩	ns

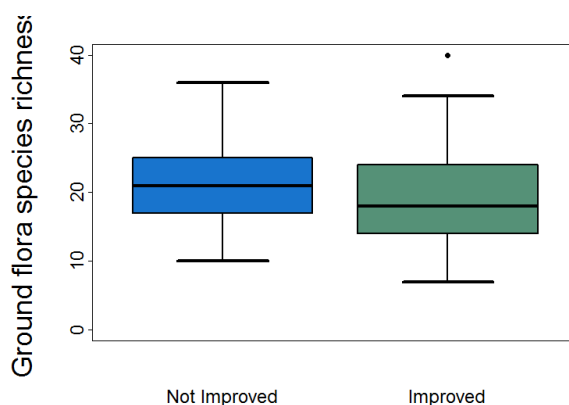


Figure 7.1: graph showing ground flora species richness where the adjacent land is improved vs. unimproved

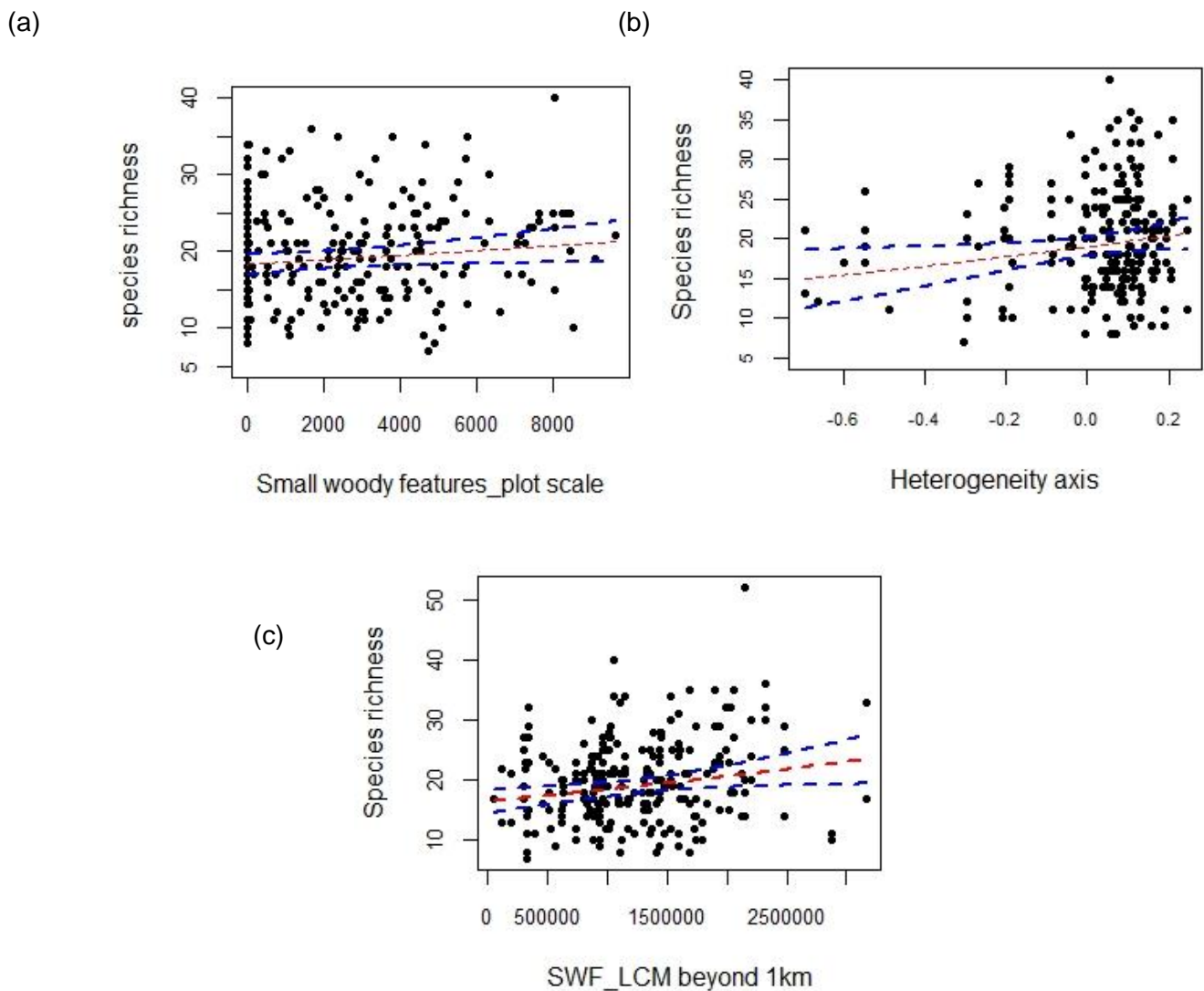


Figure 7.2. Relationships between species richness and a.) heterogeneity axis calculated in section 3. b) small woody features at 100m around the plot and c) large woodlands (LCM) and small woody features (SWF) in the 9km surrounding the 1km square. Elevation and improved land were included in b and c.

At 100m scale the best fit model for species richness includes elevation, improved land and small woody features.

At 1km square scale when elevation is added to the model for species richness, woodland is no longer significant, elevation and improved land only is the best fit model.

Beyond the 1km square scale the best fit model for species richness includes elevation, improved land, large woodlands and small woody features. There was also a significantly positive relationship with the heterogeneity axis at this scale.

The best fit model for woody indicators for square scale and beyond 1km is with improved land and large and small woodlands combined.

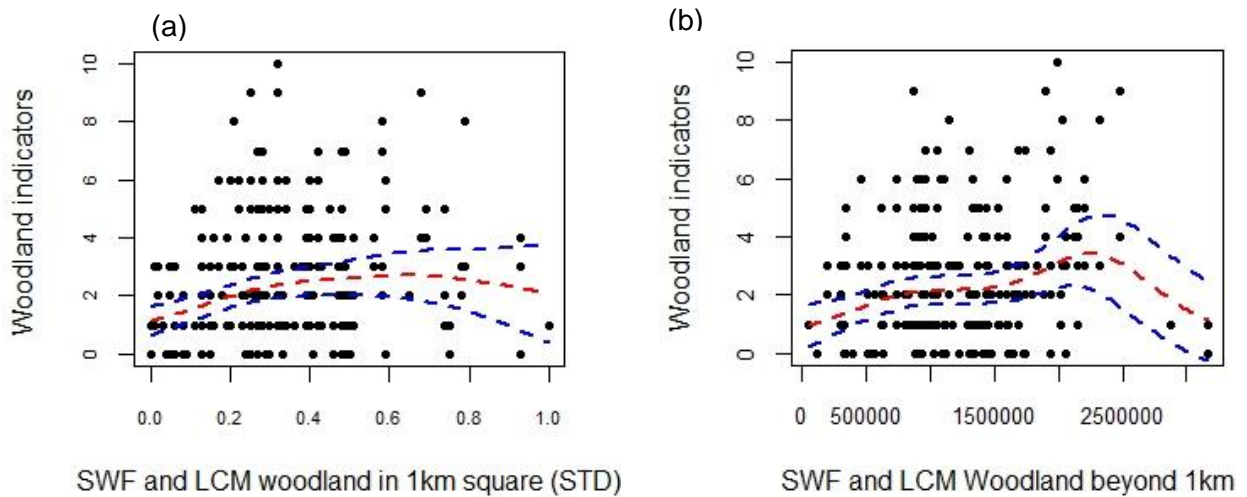


Figure 7.3 Significant relationships for the best fit models between woodland indicators and a) large woodlands (LCM) and small woody features (SWF) in 1km square scale for woodland has been standardised b) large woodlands (LCM) and small woody features (SWF) in the 9km surrounding the 1km square. Both models include whether or not improved land is adjacent.

To summarise the results from above with respect to species richness, woodland indicators and landscape context.

- Best fit models always include whether adjacent land is improved or unimproved.
- There were positive effects of the composite heterogeneity metric beyond the 1km.
- There was a positive relationship between species richness and small woody features within a 100m radius of the plot. At 1km and beyond 1km, small woody features and larger woodlands combined were positively related to species richness.
- Habitat diversity and the proportion of semi-natural habitat were not significantly related to species richness or woodland indicators in hedge ground flora. Relationships between species richness of woodland indicators and woodland were positive/non-linear. Significant relationships were between woodland indicators and combined cover of small woody features and large woodlands, at 1km square and beyond 1km square.

7.4.2 Subset of hedge plots – Effects of management parameters

The only significant relationship was a unimodal relationship between vertical gaps and species richness (Figure 7.4). The model fit was improved by adding small woody features and elevation. Habitat diversity and the proportion of semi-natural land did not improve the fit. There were no significant relationships between management and woodland indicators.

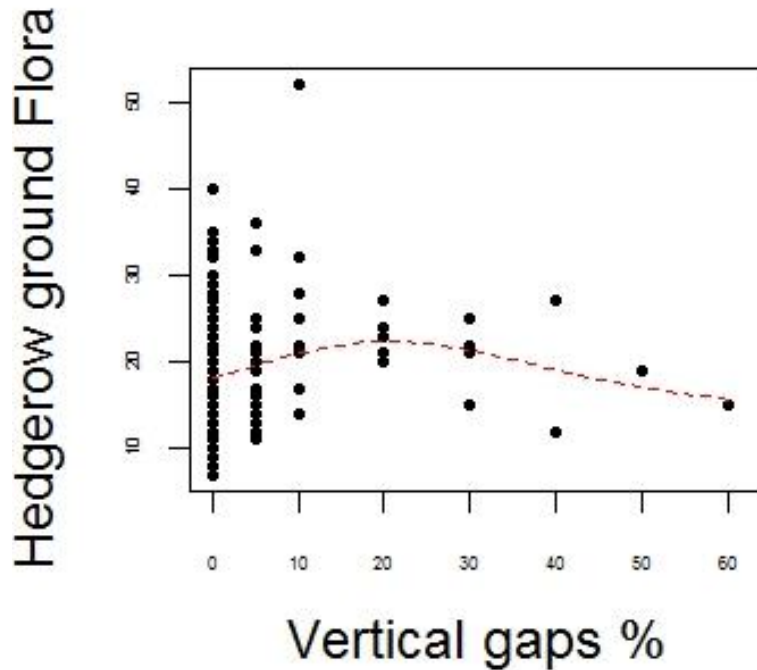


Figure 7.4: the relationship between vertical gaps (% of hedgerow) and species richness.

Table 7.2 Effects of habitat management on total species richness and woody indicators of ground flora. ns = not significant, '+' indicates a positive effect, '∩' represents a hump-backed effect.

Response variable	Vertical gaps	Width	Height	Base height	Distance from adjacent managed or ploughed land
Total species richness of hedgerow ground flora	∩	ns	ns	ns	ns
Woodland indicator species richness of hedgerow ground flora	ns	ns	ns	ns	ns

7.5 Discussion

In Wales, hedgerow ground flora has a relatively high species richness. In Countryside Survey (CS) 2007, mean species richness was 14 for the UK and 13.4 for England (this also included some of the negative indicators removed in this analysis) whereas in GMEP analysis shows that in Wales the mean species richness is ~20 (Alison et al. 2020). Here we show that hedge ground flora richness is generally high across different landscape contexts. Hedgerows can act as refugia, enabling species to be retained that would otherwise be lost from modified agricultural landscapes. Furthermore, there is potential for them to act as wildlife corridors allowing plant species to disperse between areas of semi-natural habitat (Hilty et al. 2006). However, the evidence for this is mixed and species specific, hedgerows may show extinction debts (time-delayed loss of species) and Litza

and Diekmann (2020) found that historical distance to forest was an important factor influencing ancient woodland indicator species richness.

Species richness increased along a composite heterogeneity axis (Fig. 7.2a). However, there are still many plots that have low species richness despite high heterogeneity, suggesting other influences that have not been captured in the analysis.

There is some evidence that landscape context, particularly the density of woody features around the hedgerow, does increase the species richness of the ground flora. However, this is scale dependent; at the local scale, cover of small woody features was significant while at larger scales, combined cover of woodland and small woody features was significant. The effect is weak for general ground flora richness, but there were relationships between woody indicator species and surrounding woodland features at larger scales.

It was surprising that there were so few significant relationships between species richness and management of hedgerows. Previous research suggests that management and the resulting structural attribute variability have a greater influence on biodiversity than hedgerow habitat spatial configuration and landscape context (Graham et al. 2018, Litza and Diekmann 2020, Deckers et al. 2004). Staley et al. (2013) found a trend towards taxonomic homogenisation of hedgerow ground flora driven by a decline in traditional hedgerow management techniques applied by hand, and increased eutrophication over time (from excess soil enrichment). Dense hedgerows may also limit drift of agro-chemicals into hedgerow basal flora (Tsiourus and Marshall 1998).

However, we did find that the intensity of land next to the hedgerow is very influential on species richness and woody indicators of hedgerow ground flora. Species richness was consistently higher where adjacent land is not improved, indicating the importance of management of adjacent land. Overall, it is apparent that management of neighbouring and surrounding land may be more important than hedgerow structure in determining hedgerow ground flora in Wales.

Generalist herbaceous species benefit from management practices that open up the canopy such as coppicing. Here, we found that species richness increased with gaps, up to a point at which it declined again. However, this may be at the expense of shade loving plant species including ancient woodland indicators (Staley et al. 2013).

8 CASE STUDY 3C: GRASSLAND EXTENSIFICATION FOR PLANT BIODIVERSITY

8.1 Summary

- We explored whether landscape context can interact with fertility to enhance in-field species richness.
- We used remotely sensed data (NDVI-Normalised Differential Vegetation Indices) as an explanatory variable for fertility. This is justified based on significant correlation between NDVI and Ellenberg fertility (a fertility indicator derived from plant community data).
- There is a steep decline in species richness at higher fertility in improved and neutral grasslands.
- While grassland richness trades off heavily with fertility, there may be buffering from landscape context. In improved grasslands, higher habitat diversity or cover of semi-natural land maintains higher species richness even where fertility is high. In neutral grasslands, this seemed to be the case for the amount of semi-natural land.
- Including square-level species richness, as a measure of the landscape species pool, improved model fit.
- These results suggest that in diverse landscapes, high species richness can be sustained despite high fertility. There may perhaps be an advantage in targeting interventions to areas that are not buffered by landscape diversity. However, if the species pool has been depleted by raised fertility and simplification, then reducing fertility in a simple landscape may not elicit a response e.g Marris et al. (1996), particularly for specialised species associated with semi-natural habitats and lower fertility (Kleijn et al. 2011).

8.2 Background

As discussed in the previous section, landscape context is important as a source of species for colonisation after the implementation of an intervention. If agricultural landscapes are a mosaic of well-connected early and late successional habitats, that support a high biodiversity (Concepción et al. 2012, Benton et al. 2003), there is more capacity for increases in the biodiversity of habitats after intervention. In simple landscapes there are few available species to colonise newly created habitat (Keenleyside et al. 2020).

There is good evidence that the performance of agri-environment scheme measures on farmland does vary with the habitat type, taxa considered and landscape context. Batary et al. (2011) conducted a meta-analysis of studies of both species richness and abundance across multiple taxonomic groups. AEM in grasslands was equally effective in complex and simple landscapes, with positive effects on plants and birds, independent of landscape complexity. However, other studies have not found this to be the case (e.g. Critchley 2003) where a lack of vegetation response to restoration management in UK Environmentally Sensitive Areas, highlighted the importance of residual fertility and lack of propagule sources particularly on improved land. It has been recommended that targeting

of interventions should include assessment of landscape-scale dispersal sources, e.g. proportion of semi-natural habitats (Török et al. 2018) as well as consideration of increasing small-scale heterogeneity alongside implementation of other measures.

This section relates to interventions on grasslands to reduce fertiliser, pesticide or herbicide use; and the use of organic rather than mineral fertilisers. High applications of fertiliser, particularly inorganic nitrogen, are used to encourage dense, fast-growing perennial grasses at the expense of other, less competitive grasses and flowering plants (Keenleyside et al. 2020, Cleland & Harpole 2010). The result is a reduction in species richness. Grassland systems in Wales are less intensively managed than in many other regions, but there is still potential to improve biodiversity by reducing inputs in some contexts. Evidence from the ESA schemes (Keenleyside et al. 2020, Critchley et al 2003) suggested that restoration to lower fertility and reduced abundance of plant species favoured by high nutrient loads was possible but dependent upon starting point. Semi-improved hay meadows showed good responses, semi-improved grasslands showed mixed responses and improved grassland starting points were much less responsive to restoration treatments (Keenleyside et al. 2020).

In this work we look at whether fertility interacts with the landscape context, or the regional species pool, to determine species richness of improved and neutral grasslands. The aim is to understand where interventions to reduce inputs may be most effective in Wales.

8.3 Approach

8.3.1 Modelling species richness

In these analyses we fitted generalized additive mixed models (GAMMs, poisson error structures) to predict plant species richness. Using mixed models enabled us to add a random variable to account for spatial autocorrelation of plots being nested within squares. Furthermore, GAMMs allow for unconstrained and smooth non-linear relationships. Models were fitted using the R package *gamm4*, and comparisons between models were made using AIC (second-order Akaike's information criterion). AIC was extracted from the "mer" object of the fitted model. Following Burnham and Anderson (2002), we ranked them by their values of AIC, with the best fitting model having the lowest AIC.

8.3.2 Grassland fertility and landscape context

We selected large randomly located "X plots" (200m², Wood et al. 2017) from neutral and improved grassland and calculated the total species richness for the plot. We then analysed relationships between species richness and fertility, accounting for landscape context, testing whether landscape context mediated the fertility-richness relationship. To represent fertility we explored relationships between different variables. There was a highly significant positive relationship between remotely sensed Normalised Differential Vegetation Index (NDVI; extracted from 30m resolution composite, cloud-free Landsat-8 satellite imagery from 2013-2016) and Ellenberg fertility at the plot scale (Fig. 8.1). We proceeded to use NDVI, as it could allow these relationships to be applied outside of vegetation plots in future.

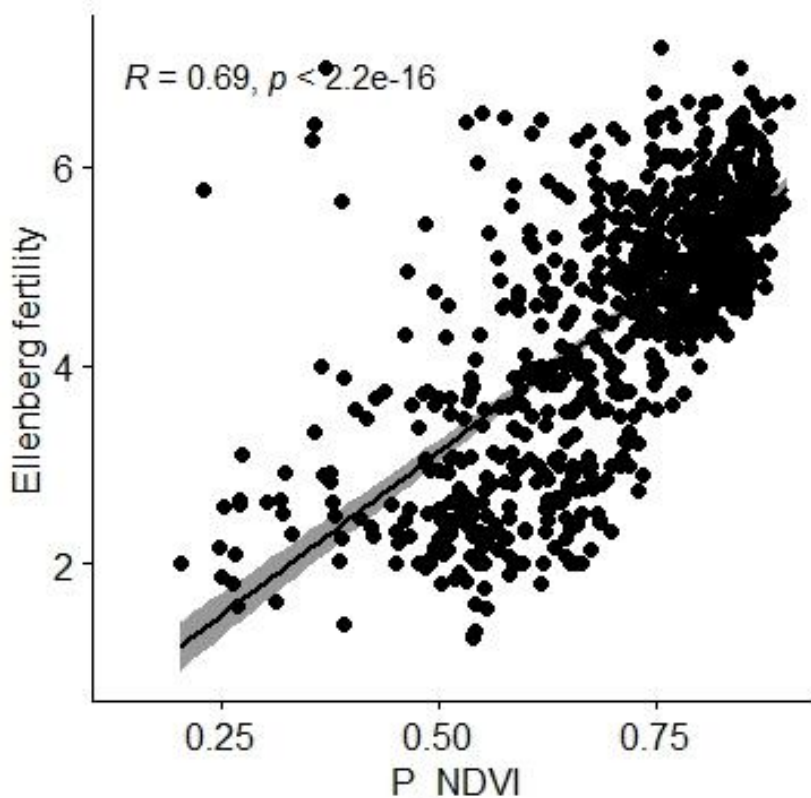


Figure 8.1: Relationship between Normalised Differential vegetation index (NDVI) and Ellenberg fertility score within a plot ($r^2=0.69$)

We also tested some other explanatory variables that could be used to explain nutrient status instead of NDVI. Effects of sward height, cattle, sheep and any stock were all tested, and only sheep were significantly related to species richness in improved grassland.

Explanatory variables were taken from the 100m surrounding the plot, the field scale and the square scale. So, for instance if NDVI values come from the 100m buffer around the plot then variables for habitat diversity, semi-natural land and elevation (from NextMap DTM) are also from the same scale. For the field scale NDVI, additional explanatory variables were used for the square and beyond the square (1km+). Explanatory variables include habitat diversity, the % of semi-natural land, species richness for a 1km square and elevation. Species richness for the square has been calculated by summing species richness from all plots and dividing by the number of plots. We also tested the interaction between landscape context and fertility.

8.4 Results

8.4.1 Fertility in improved and neutral grassland

Species richness is higher in neutral than improved grassland (Fig. 8.2). We analysed relationships between species richness, fertility and landscape context in improved and neutral grassland separately.

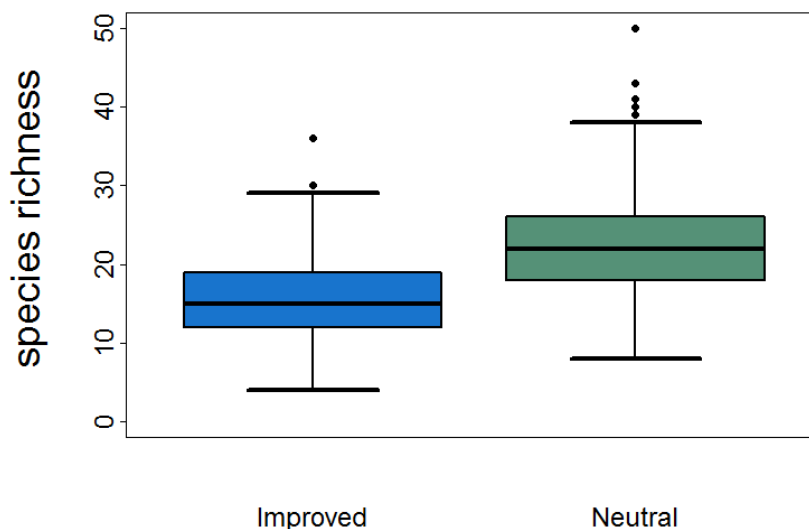


Figure 8.2. Total species richness in 200m² plots in Improved and Neutral grassland.

There was a steep decline in species richness at higher fertility in both habitats (Fig. 8.3). There is a hint of a unimodal relationship between fertility and species richness in improved grassland, whilst in neutral grassland the relationship is negative. Habitat diversity, species richness of the square and elevation also affected species richness (Table 8.1).

Table 8.1: Effects of fertility (NDVI) within 100m of a plot, or within the same field as a plot, on total species richness of ground flora and woody indicators. ns= not significant, '+' indicates a positive effect, '∩' represents a unimodal effect.

	Fertility NDVI 100m	Other variables in best model (100m)	Fertility NDVI Field	Other variables in best model (Field-scale)
Improved grassland	∩/-	Habitat diversity, square species richness and elevation	∩/-	Habitat diversity, square species richness and elevation
Neutral grassland	-	Habitat diversity, square species richness and elevation	-	Square species richness and elevation

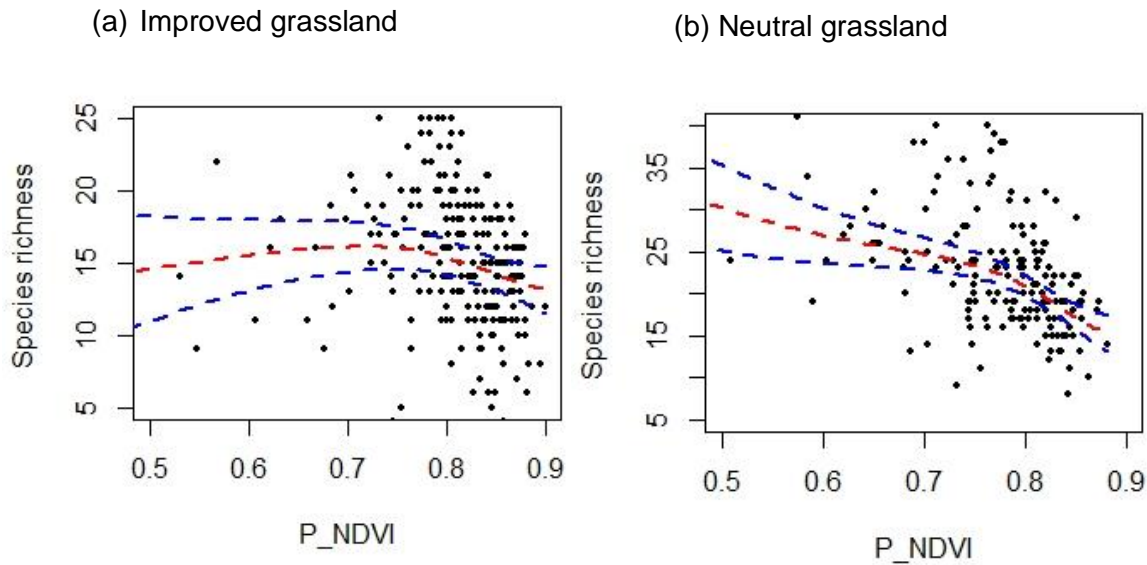


Figure 8.3: Relationship between fertility (plot scale NDVI) and species richness using the best fit model for (a) Improved grassland, (b) Neutral grassland

To see if the effect of fertility on species richness was stronger in certain landscape contexts, we tested for interactions between landscape context and fertility. We found that the effect of fertility depended on habitat diversity in improved grasslands, and depended on semi-natural land nearby on both improved and neutral grassland. To visualise the relationship between fertility and species richness in different landscape contexts, we repeated the analysis after classifying each plot into 4 groups (using quantiles) with low-to high habitat diversity and square species richness. The results for this analysis can be seen in Tables 8.2 and 8.3 and Figure 8.4.

In both improved and neutral grasslands, plot-level species richness is highest in plots with high habitat diversity and square species richness. On improved grassland, we observed no decline in species richness with fertility where habitat diversity was medium high or high (upper two quartiles, Fig. 8.4). However, where there was low habitat diversity, species-richness did decrease with fertility.

We found a similar effect of the amount of semi-natural land nearby for both improved and neutral grassland. This suggests that some types of landscapes maintain high species-richness, even as fertility increases.

Improved grassland

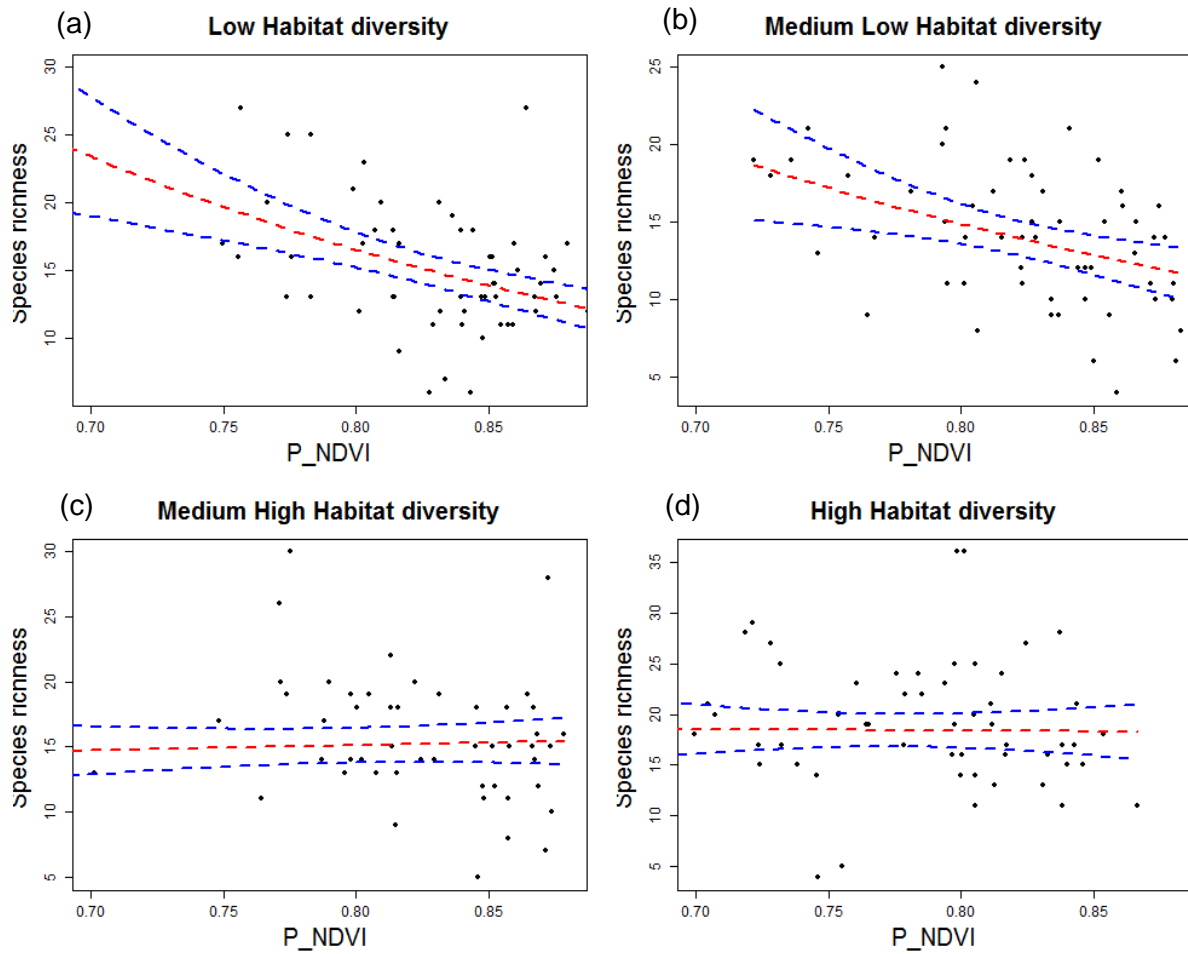


Figure 8.4.: Relationship between fertility (plot scale NDVI) and species richness in plots grouped by quantiles of habitat diversity a) Low, b) Medium-low, c) Medium-high, d) High, in Improved grassland.

Table 8.2: Results of dividing plots from previous analyses into four groups using quantiles from low to high habitat diversity. ‘-’ indicates a negative effect, ‘∩’ represents a unimodal effect. Note we did not find a significant interaction between P_NDVI and habitat diversity on neutral grassland (Table 8.1).

Habitat diversity	Improved		Neutral	
	Mean plot species-richness	Relationship with NDVI	Mean plot species-richness	Relationship with NDVI
Low	15.2	■ ***	20.1	■ ***
Medium Low	14.1	■ **	21.6	■ **
Medium high	15.3	ns	22.5	∩ **
High	18.9	ns	27.2	■ ***

Table 8.3 Results of dividing plots from previous analyses into four groups using quantiles from low to high species richness in a 1km square. ‘-’ indicates a negative effect, ‘∩’ represents a hump-backed effect.

Square species richness	Improved		Neutral	
	Mean plot species-richness	Relationship with NDVI	Mean plot species-richness	Relationship with NDVI
Low	13.7	- *	21.8	- **
Medium Low	15.1	ns	21.9	- *
Medium high	16.8	∩**	21.8	- ***
High	17.9	- ***	25.7	- ***

Table 8.4: Results from testing interactions between landscape context and fertility with species richness ***p<0.001, **p<0.01, ns not significant

Grassland type	Habitat diversity * fertility	Area semi-natural land * fertility	Species-richness in square * fertility
Improved grassland	***	**	ns
Neutral grassland	ns	**	ns

8.5 Discussion

Improved or semi-improved land will in most cases be the starting point for the creation of new semi-natural habitats on farmland, and it is important to understand how landscape context influences biodiversity status (Keenleyside et al. 2020). Agricultural intensification reduces the capacity of land to respond to alleviation of management intensity. Loss of semi-natural habitats as refugia for species, reduced species pools and persistence of nutrients make it more difficult to restore habitats and extend the time to reach a restored state (Critchley et al. 2000; 2004).

This work found that species richness was highest in grasslands where the surrounding habitat diversity, amount of semi-natural land or species richness of a 1km square was higher. Other research has found that species richness in agricultural fields increases from simple to complex landscapes, because semi-natural landscapes contain more diverse resources and dispersal corridors (Concepción et al. 2012, Benton et al. 2003). In simple landscapes there are few available species to colonise fields.

We also found that grassland richness trades off heavily with fertility. However, there may be a buffering effect within certain landscape contexts. Fields set in areas with high habitat diversity or an increased amount of semi-natural land are likely to have higher species richness. This was particularly true for improved grasslands. This result is not unprecedented and has been supported by other studies. However, there have also been studies that have shown that diversity increases in grasslands subject to interventions despite landscape context (e.g. Batary et al. 2011). Interestingly, though, we found that

total species richness in the square, as a measure of the landscape species pool, did not affect local responses to fertility.

These results suggest that in diverse landscapes high species richness can be sustained despite high fertility, so there may perhaps be an advantage in targeting interventions to areas that are not buffered by landscape diversity. However, if the species pool has been depleted by raised fertility and simplification then reducing fertility in a simple landscape may not elicit a response e.g Marris et al. 1996, particularly for specialised species associated with semi-natural habitats and lower fertility (Kleijn et al. 2011). In more intensively managed landscapes more active interventions may be required e.g. increasing plant species diversity through the addition of grass, forb and legume species by reseeded, oversowing, or slot seeding, or may also include introduction of plug plants or feeding animals with high quality hay containing seeds (from nearby sites). This will increase costs (Keenleyside et al. 2020, Torok et al. 2018).

This work also demonstrates that it is advantageous to consider implementing packages of several different interventions that increase the amount of semi-natural land and colonisation sources at the farm or landscape level as these can be helpful in sustaining diversity even where fertility is high.

9 ANNEX A: FURTHER DETAILS ON CASE STUDY 2

9.1 Detailed model results

Table 9.1. AIC values for models fitting different complexities of smooth function for the relationship between abundance and woody linear feature density. The results with no control are reported in the main text; the results here show that adding different landscape variables as simple controls did not affect the results (and this was supported by examination of the plot shapes, which are not shown because they did not differ from Figs 5.2 - 5.4). The lowest AIC among models with each control is shown in bold.

Group	AIC values with the specified control			
	1df	2df	3df	4df
<i>No control</i>				
Field & boundary	1920.8	1906.0	1894.9	1884.4
Open field	554.5	548.1	544.1	541.5
Woody	1751.7	1722.2	1698.6	1681.4
<i>Intensive farming area</i>				
Field & boundary	1889.0	1875.2	1864.4	1854.1
Open field	554.2	547.8	543.9	541.4
Woody	1747.4	1718.6	1695.4	1678.6
<i>Arable area</i>				
Field & boundary	1841.6	1829.6	1820.4	1811.7
Open field	523.3	516.2	511.2	507.3
Woody	1749.1	1718.9	1694.8	1677.2
<i>Small woody features</i>				
Field & boundary	1900.3	1886.1	1874.9	1864.1
Open field	498.4	490.9	487.2	485.0
Woody	1646.3	1620.8	1598.4	1581.2
<i>Landscape proportion broadleaf</i>				
Field & boundary	1919.1	1903.6	1892.3	1881.7
Open field	521.2	515.0	511.7	509.2
Woody	1670.2	1646.2	1625.5	1609.9

Table 9.2. Interaction effects in group models, assessed using AIC values. Models fitted with an intercept only (null), and linear and quadratic effects of woody linear feature density are compared, controlling for the four key landscape features, together with models fitting linear and quadratic effects and the interactions of those effects with the main effect of the landscape control in each case. For each species and control scenario, the best model (identified by having the lowest AIC, or the simplest model with a $\Delta AIC < 2$ relative to the minimum value) is indicated by “Best”: L = linear main effect only, Q = quadratic main effect only, IL = linear interaction model, IQ = quadratic interaction model.

Control	Group	Main effects			Interactions		Best
		Null	Lin	Quad	Lin	Quad	
No control	Field & boundary	3240.0	2994.3	2916.6	-	-	Q
	Open field	782.5	766.2	757.6	-	-	Q
	Woody	3423.3	2821.7	2714.1	-	-	Q
Intensive area	Field & boundary	3192.4	2957.3	2887.9	2958.8	2889.5	Q
	Open field	783.9	768.1	759.2	767.8	750.3	IQ
	Woody	3409.8	2816.2	2712.5	2817.5	2716.2	Q
Arable Area	Field & boundary	3153.4	2903.7	2840.9	2905.4	2840.5	Q
	Open field	751.5	734.8	729.2	716.7	705.9	IQ
	Woody	3424.0	2823.1	2713.0	2822.7	2710.2	IQ
Small woody features	Field & boundary	3174.1	2990.3	2917.7	2977.5	2905.8	IQ
	Open field	760.8	756.4	745.4	756.2	747.7	Q
	Woody	3059.1	2709.6	2636.2	2692.8	2620.2	IQ
Broadleaf	Field & boundary	3229.7	2996.3	2916.2	2986.4	2911.4	IQ
	Open field	740.5	737.6	725.4	723.7	713.1	IQ
	Woody	3199.9	2716.1	2640.4	2695.7	2616.4	IQ

9.2 Species-level results

At the species level, all species showed some evidence of non-linear responses to the density of woody linear features, as assessed using GAM fits (Fig. 9.1a-y), although the strength of statistical support for these patterns varied (Table 9.3). The predominant function shape tended to show abundance peaking at intermediate densities of woody linear features, and being lower at higher and/or lower densities (Fig. 9.1a-y). Across species, more complex smooth functions were supported (lower AIC values) for most species, with the exception of Lesser Whitethroat and Song Thrush, while there was no clearly better model fit for Blackcap, Skylark and Whitethroat (Table 9.3). However, it was also common for the differences in AIC between models with more complex smooths to be marginal, e.g. for Wren, Reed Bunting and Bullfinch (Table 9.3). There was also little evidence that the addition or choice of a landscape control affected the shape of the function that was identified: the complexity of the smooth fit with the strongest support changed with different controls for only one species, Dunnock, and the differences in AIC involved were very marginal (Table 9.3). This occurred despite AIC values indicating that the inclusion of one or more of the controls almost always improved overall model fit (Table 9.3).

Among individual species, the patterns revealed by the smooth functions showed the peaking pattern described above in most cases, with little evidence that greater fit complexity revealed biologically significant variation, even when it was strongly supported statistically, e.g. for Blackbird, Chaffinch and Chiffchaff: the more complex functions identified detail within a broad peak of abundance across intermediate woody linear feature densities (Figs. 9.1a, 9.1e and 9.1f). Clear patterns for abundance to increase from low to intermediate woody linear feature densities were *not* apparent for Lesser Whitethroat, Reed Bunting, Whitethroat, Willow Warbler, Greenfinch, Linnet, Yellowhammer, Lapwing and Skylark (Figs. 9.1o, 9.1r, 9.1u, 9.1x, 9.1i, 9.1m, 9.1y, 9.1l & 9.1s). Patterns for decreases from intermediate to high woody linear feature densities were *not* apparent for Dunnock, Lesser Whitethroat, Linnet, Song Thrush, Yellowhammer and Skylark (Fig. 9.1g, 9.1o, 9.1m, 9.1t, 9.1y & 9.1s). These sets of species do not align with the groups that were determined a priori, suggesting that unpredicted factors drove the associations with linear features. These could include subtle features of land-use or landscape context that are not accounted for by the controls that were applied here, or variation within the woody linear features themselves, such that they have different effects on species in areas where they are relatively common or relatively rare. Further, in cases such as that of Skylark, which is well-known to have an aversion to woody boundary structures, the failure to find such a pattern could indicate that woody features effectively replace other features that make habitat less suitable anyway, such as walls, within the sample.

Fig 9.1a-y are GAM fits with no landscape control for individual species. Each graph shows the best smoothed fit (as identified in Table 9.3, except for Lapwing (Fig 9.1l), which showed statistical artefacts associated with a small sample size, so the fit for 2df is shown) as a dark red line, with the 95% confidence interval for the smooth shown by pale red lines and the raw data by blue points (note that all y-axes have been truncated to show the smooth lines better; outlier raw data points are therefore not shown):

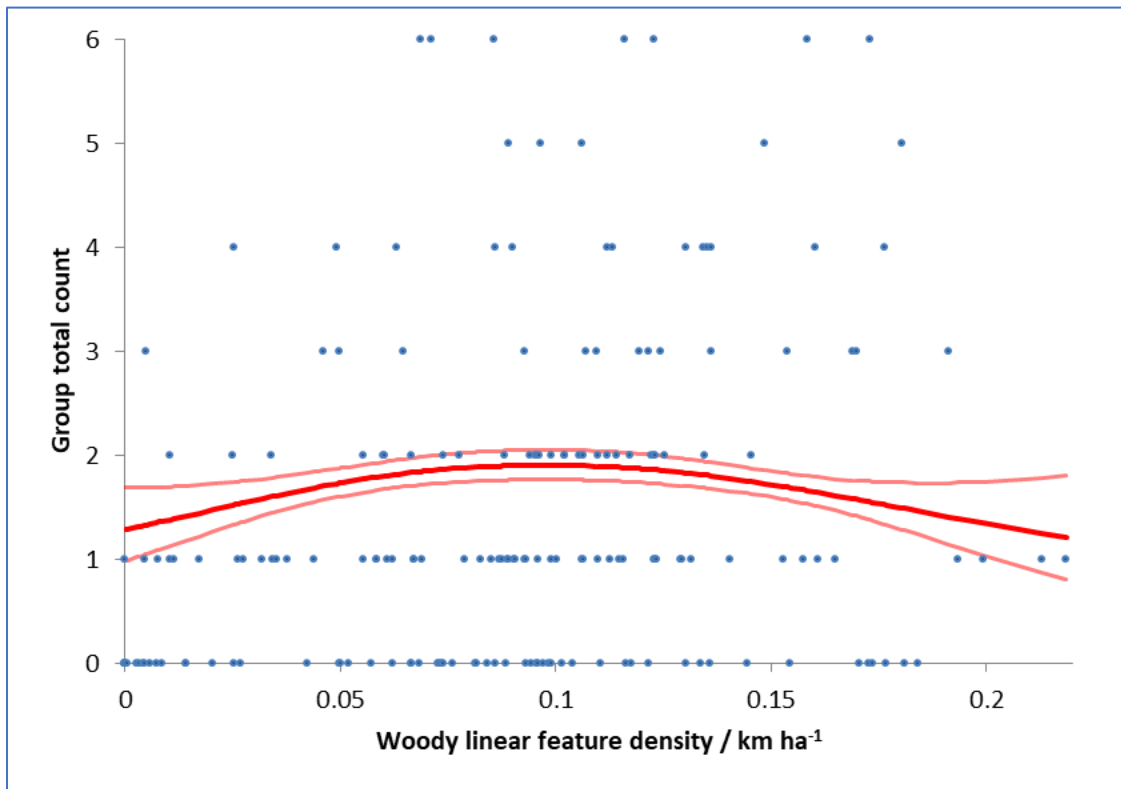


Fig. 9.1a GAM fit with no landscape control for individual species: Blackbird

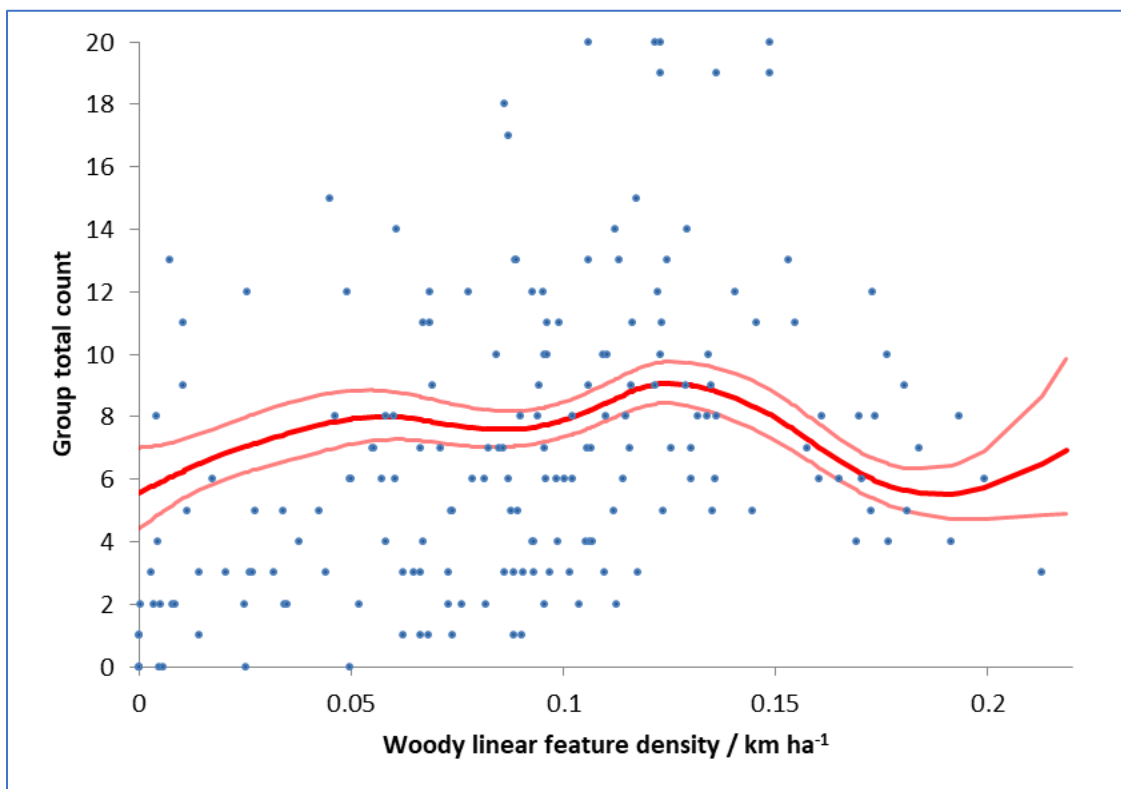


Fig. 9.1b GAM fit with no landscape control for individual species: Blackcap

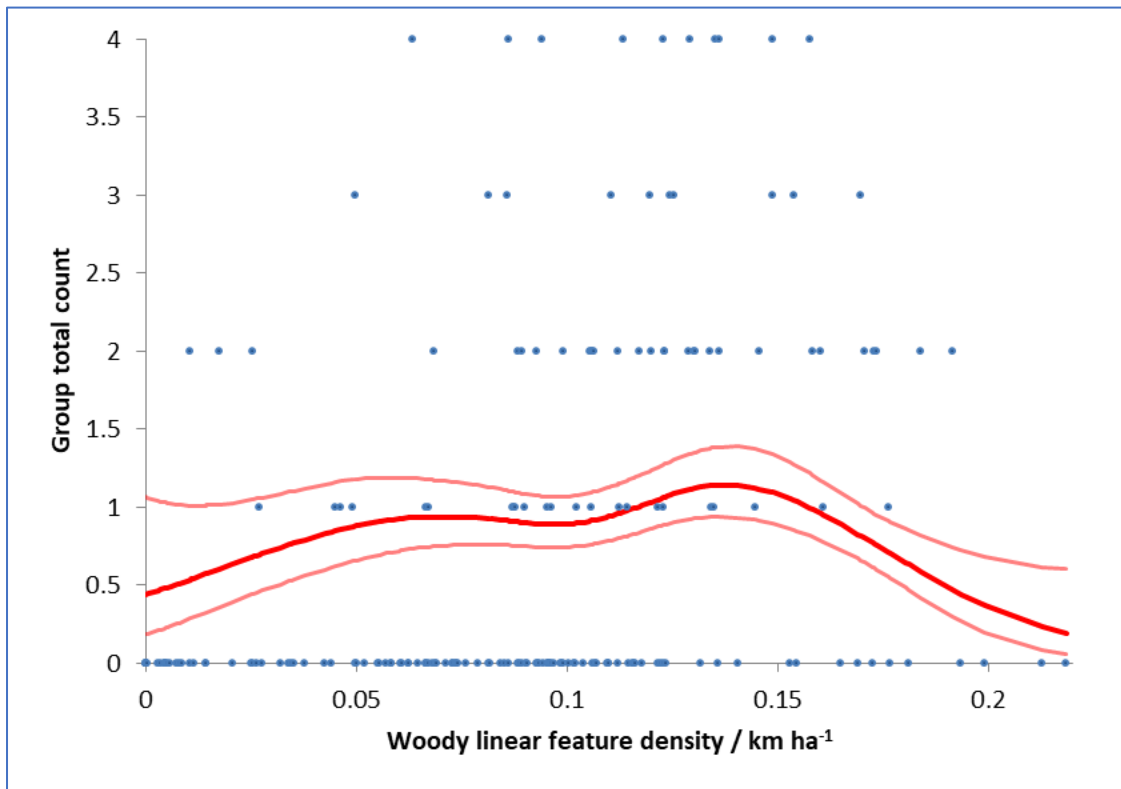


Fig. 9.1c GAM fit with no landscape control for individual species: Bullfinch

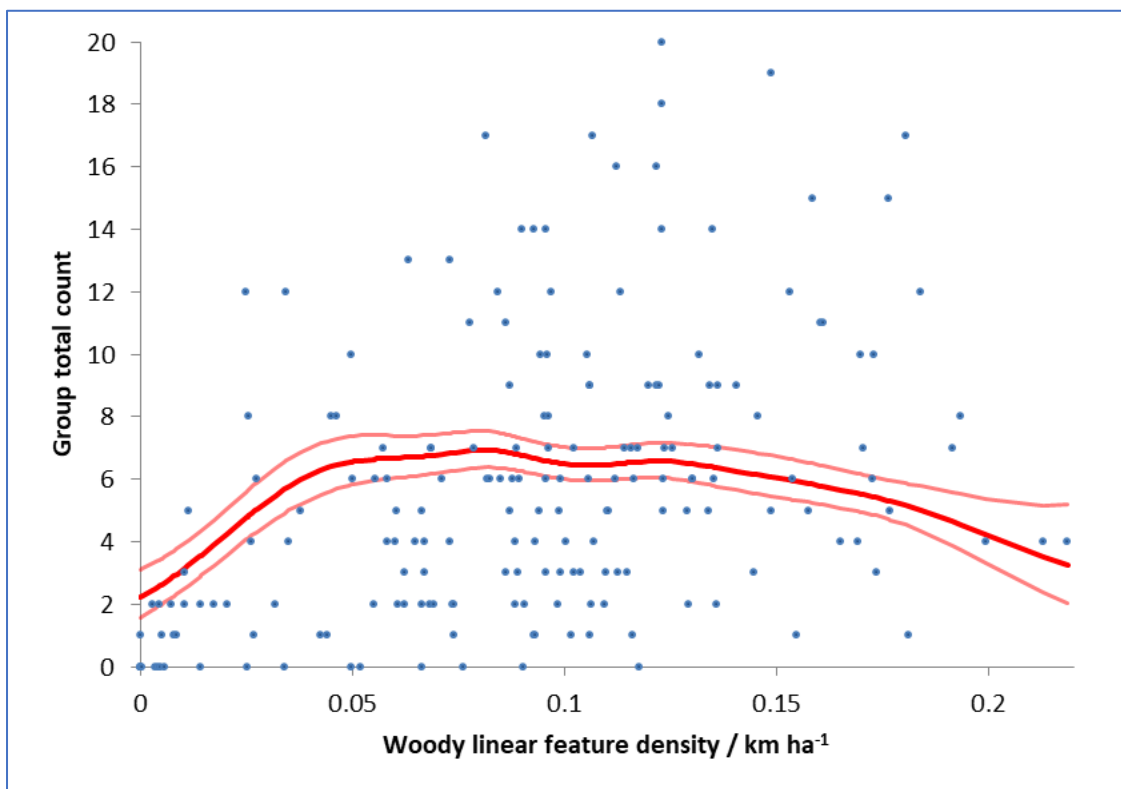


Fig. 9.1d GAM fit with no landscape control for individual species: Blue Tit

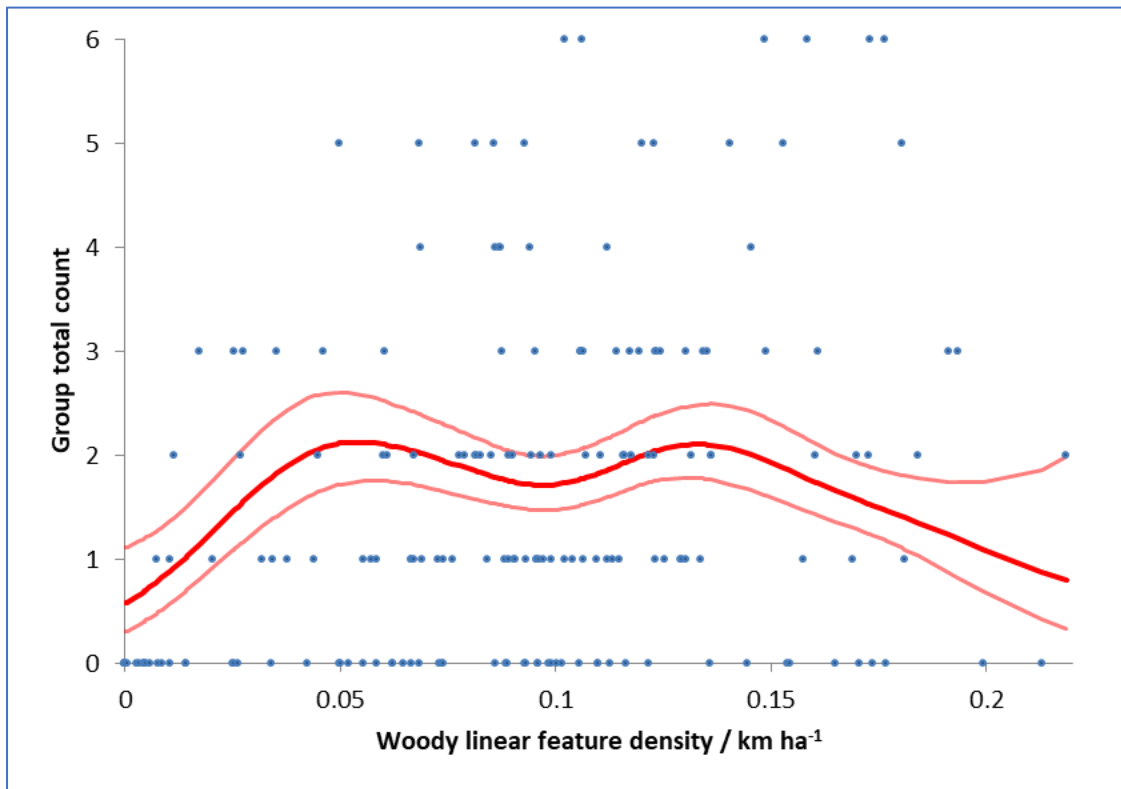


Fig. 9.1e GAM fit with no landscape control for individual species: Chiffchaff

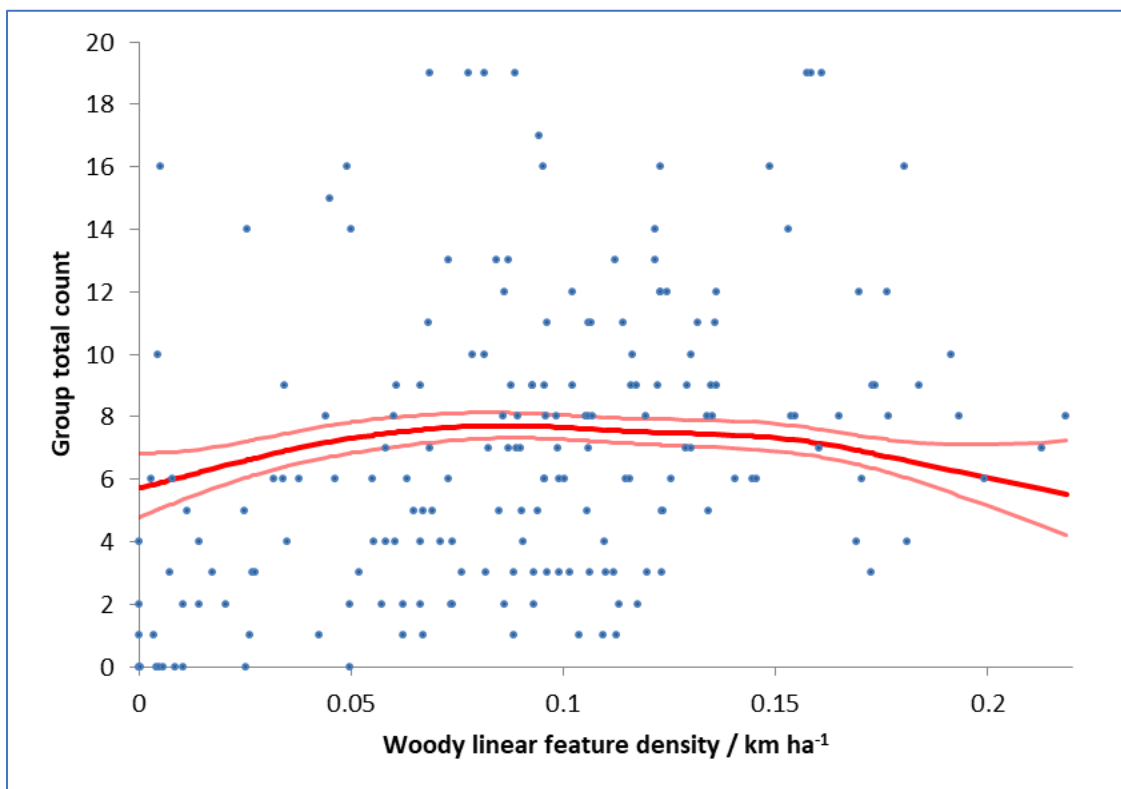


Fig. 9.1f GAM fit with no landscape control for individual species: Chaffinch

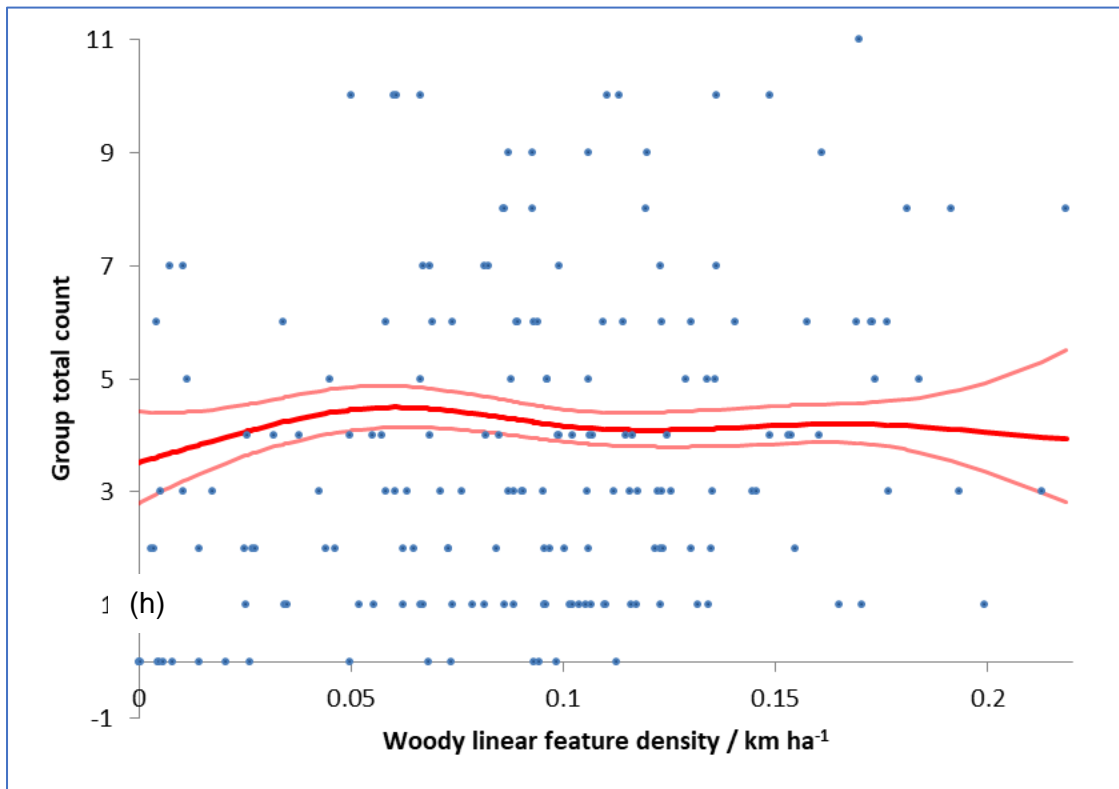


Fig. 9.1g GAM fit with no landscape control for individual species: Dunnock

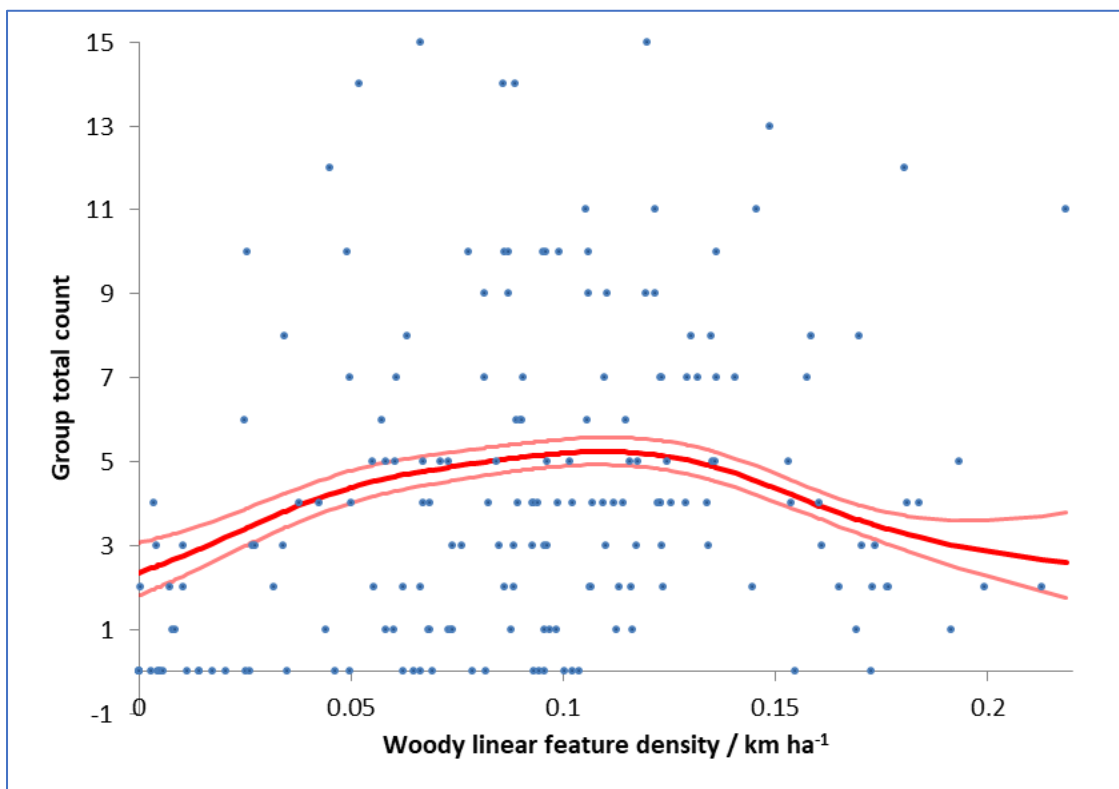


Fig. 9.1h GAM fit with no landscape control for individual species: Goldfinch

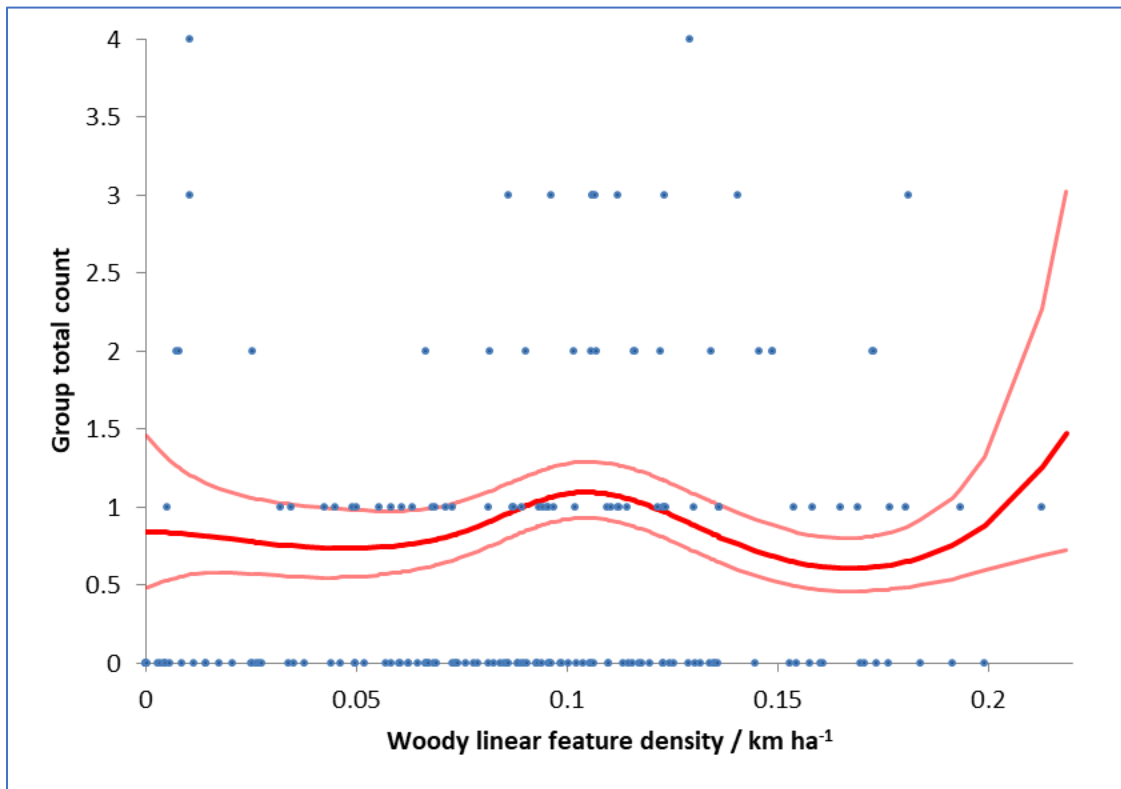


Fig. 9.1i GAM fit with no landscape control for individual species: Greenfinch

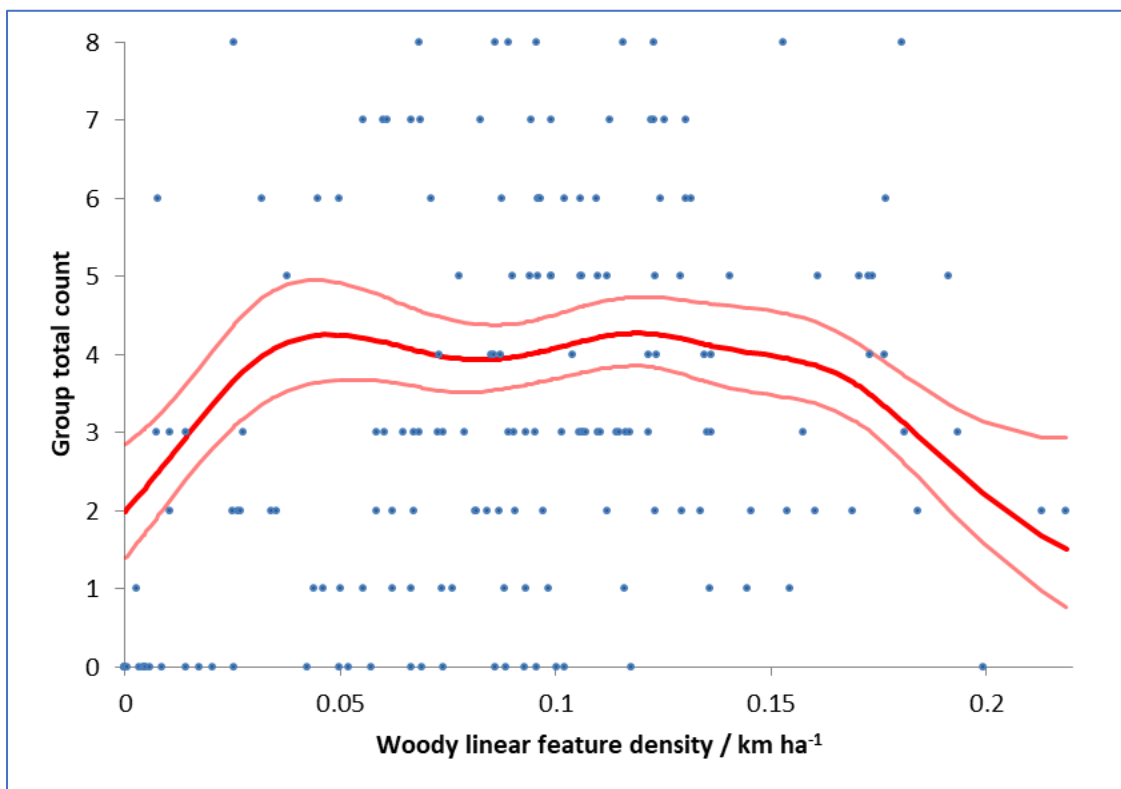


Fig. 9.1j GAM fit with no landscape control for individual species: Great Tit

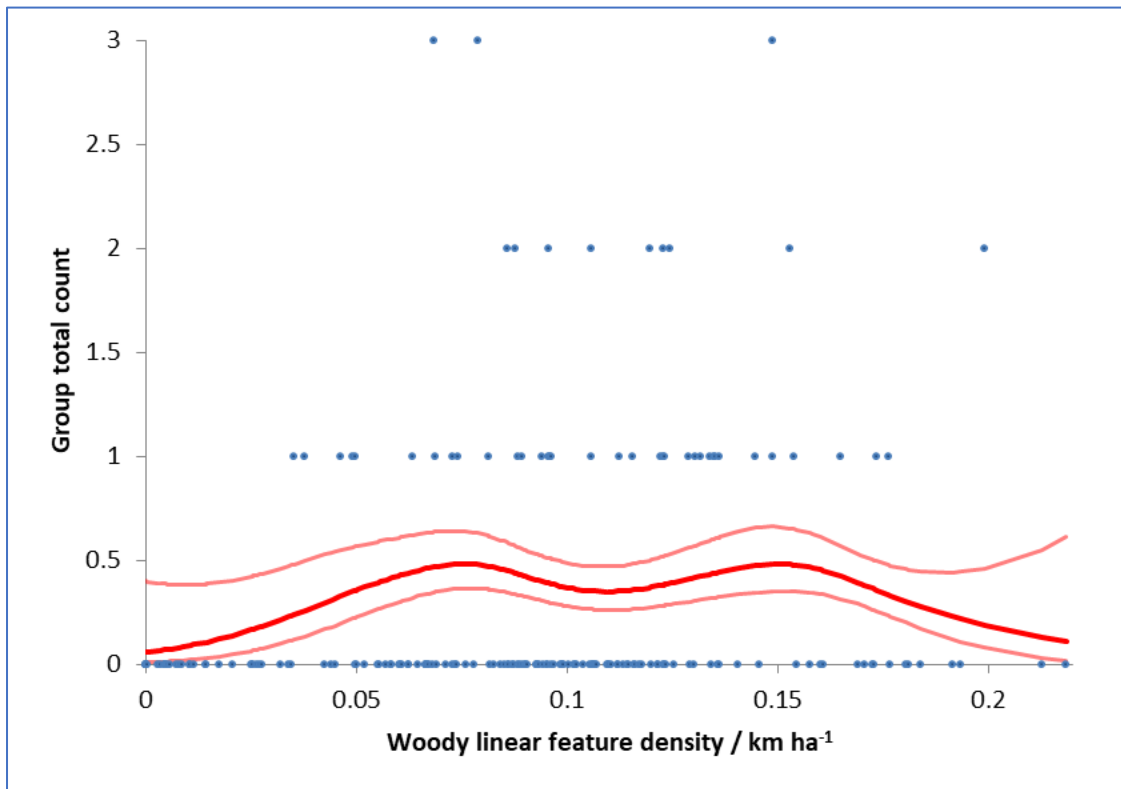


Fig. 9.1k GAM fit with no landscape control for individual species: Garden Warbler

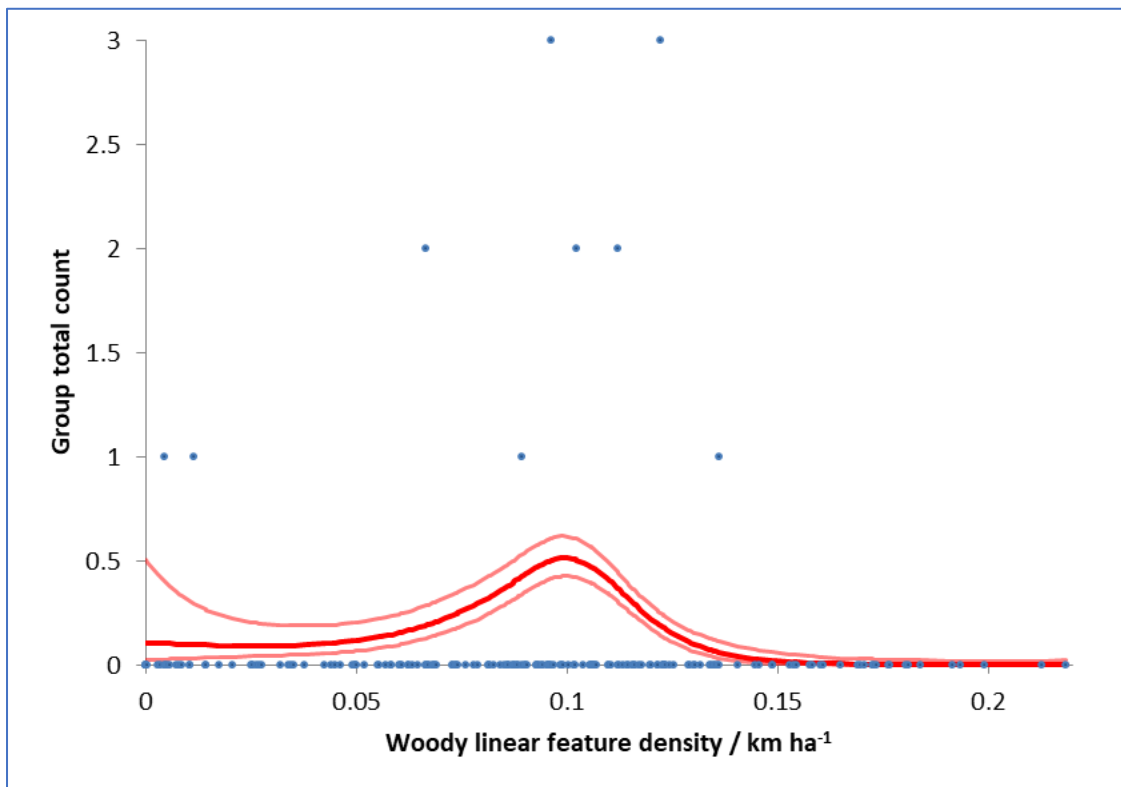


Fig. 9.1l GAM fit with no landscape control for individual species: Lapwing

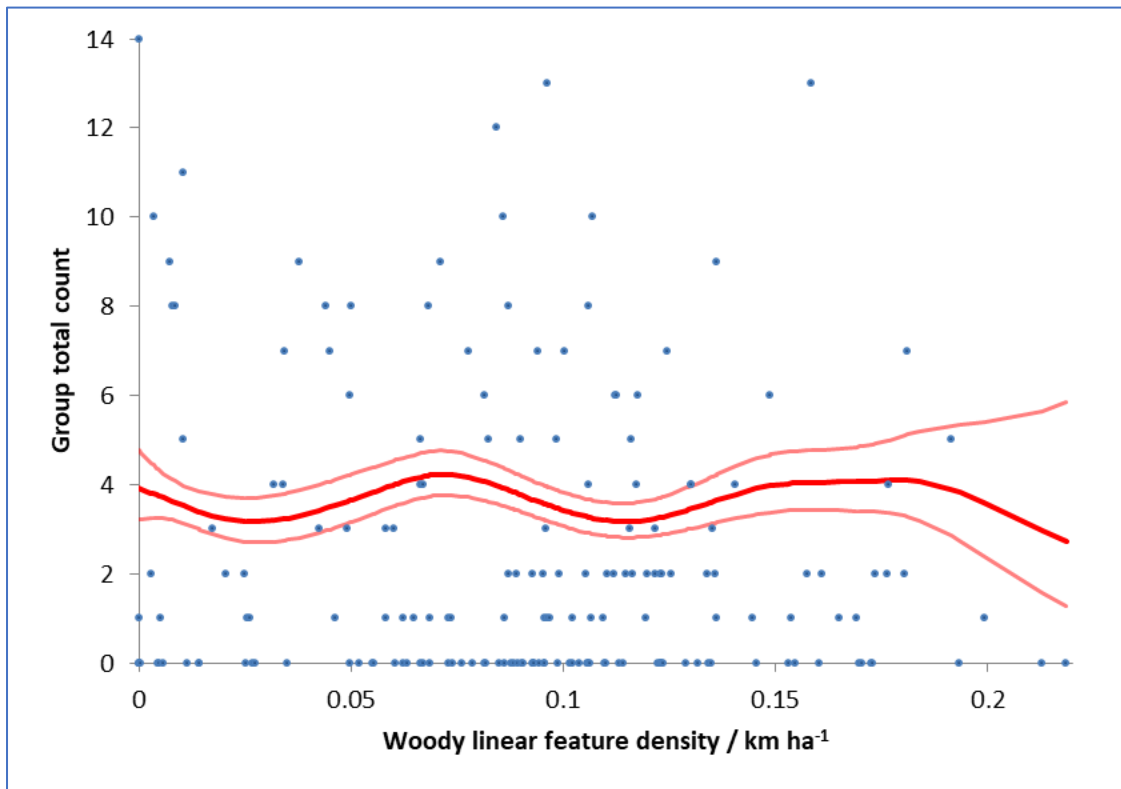


Fig. 9.1m GAM fit with no landscape control for individual species: Linnets

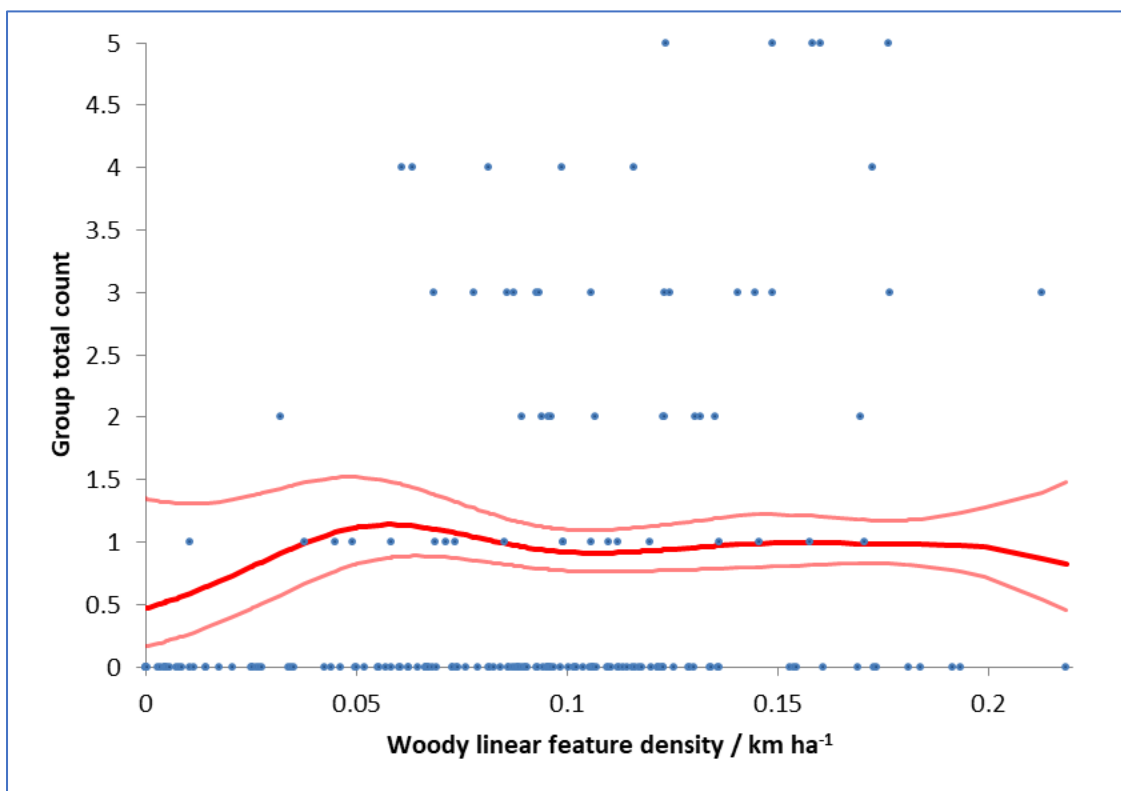


Fig. 9.1n GAM fit with no landscape control for individual species: Long-tailed Tit

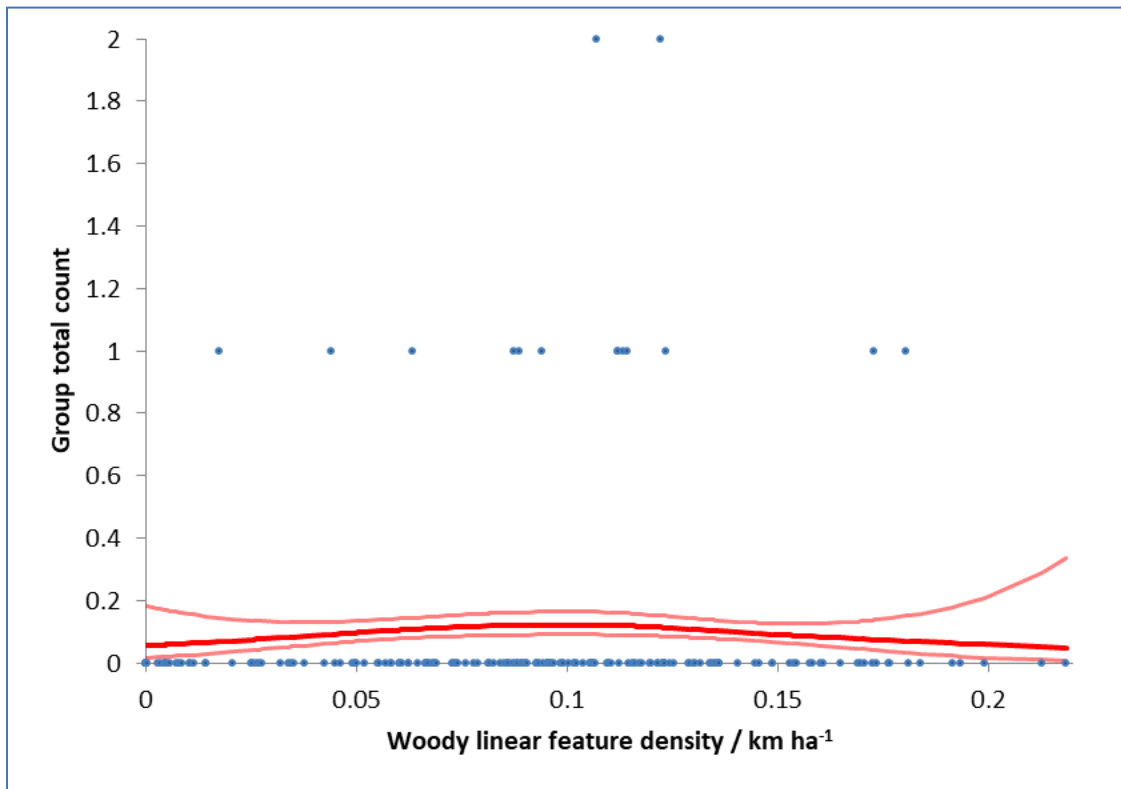


Fig. 9.1o GAM fit with no landscape control for individual species: Lesser Whitethroat

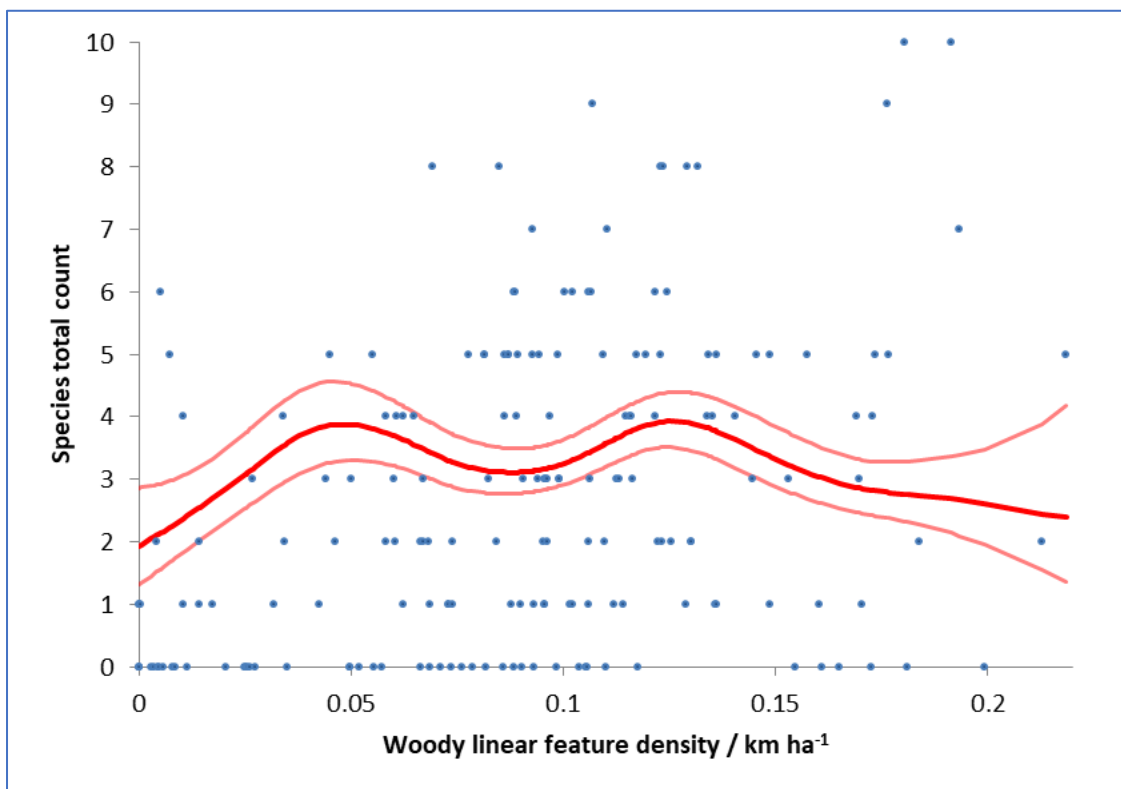


Fig. 9.1p GAM fit with no landscape control for individual species: Magpie

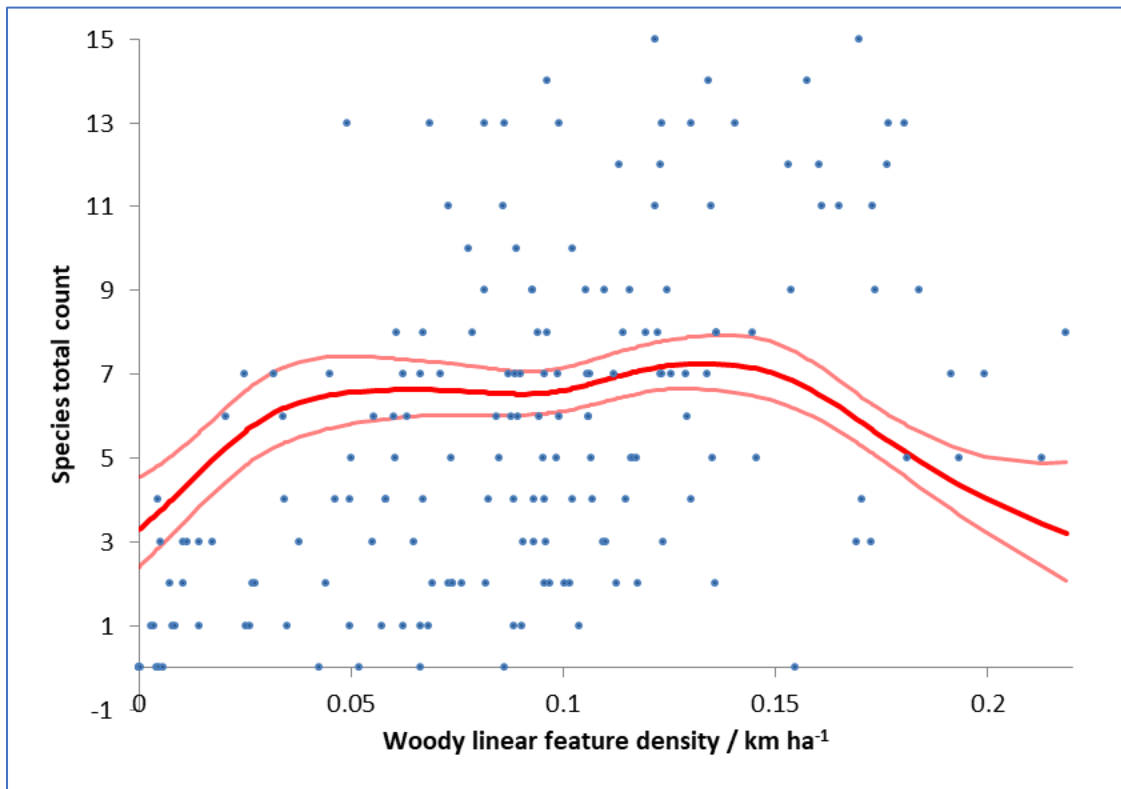


Fig. 9.1q GAM fit with no landscape control for individual species: Robin

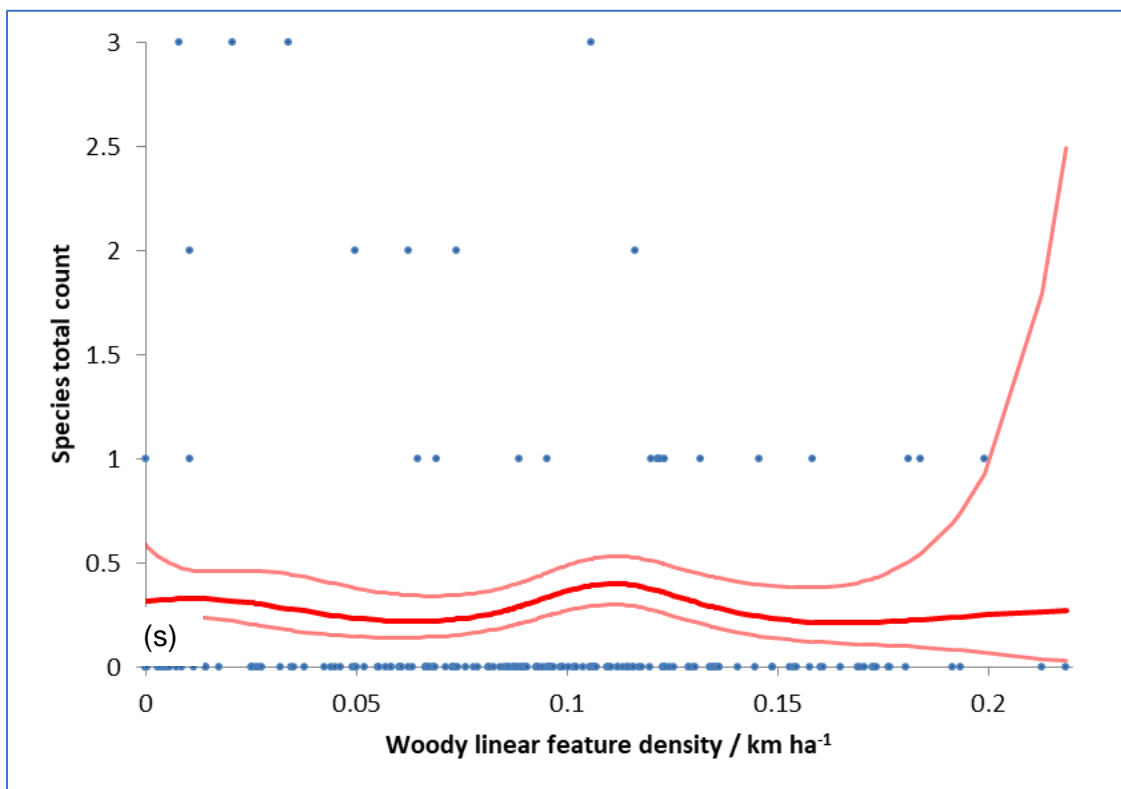


Fig. 9.1r GAM fit with no landscape control for individual species: Reed Bunting

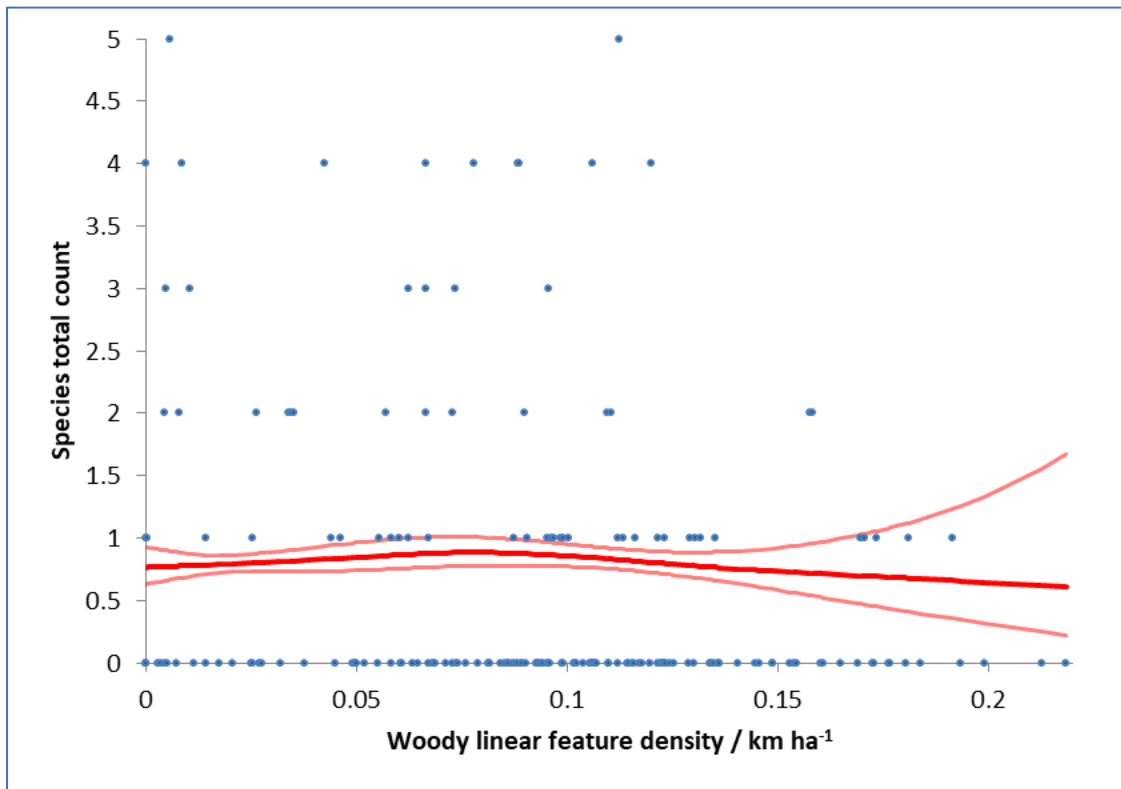


Fig. 9.1s GAM fit with no landscape control for individual species: Skylark

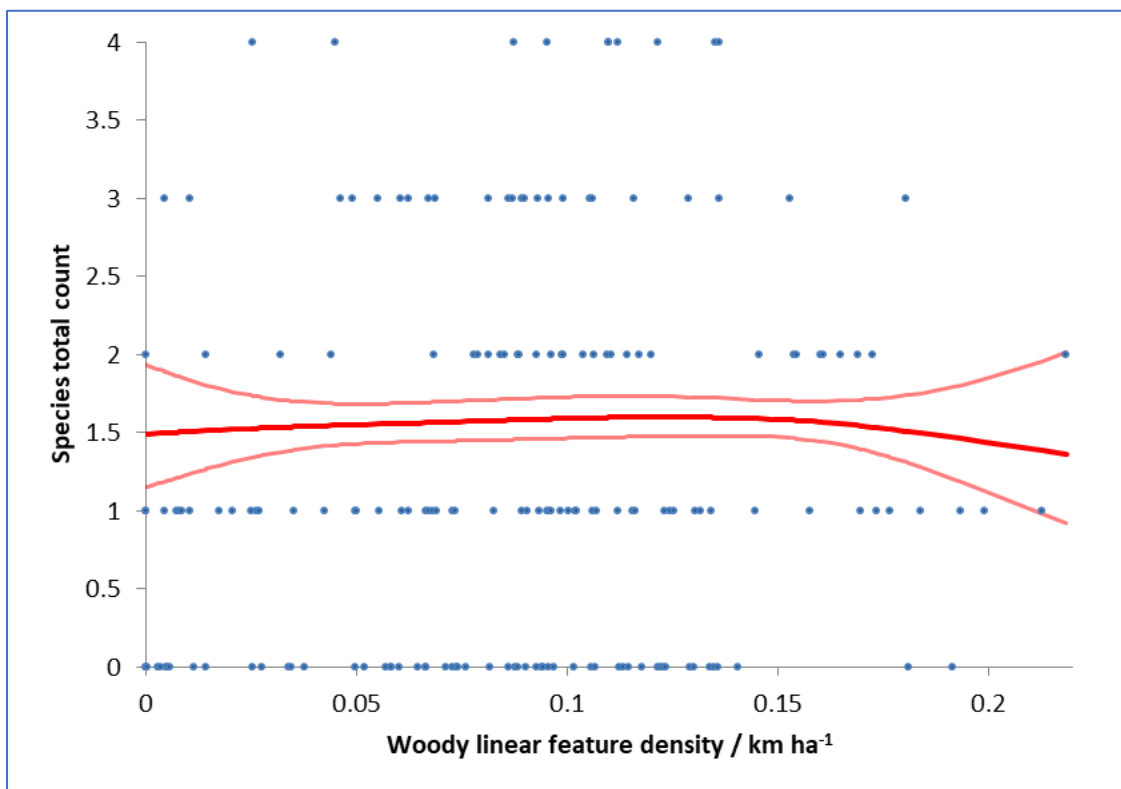


Fig. 9.1t GAM fit with no landscape control for individual species: Song Thrush

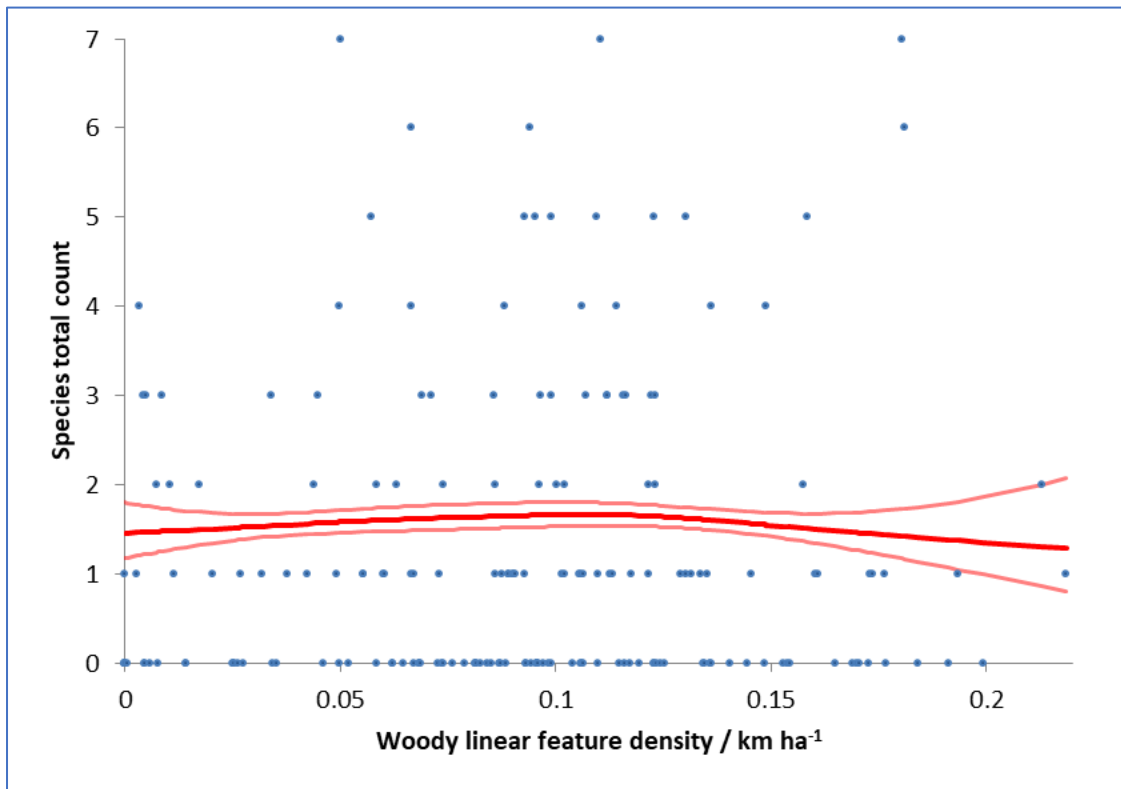


Fig. 9.1u GAM fit with no landscape control for individual species: Whitethroat

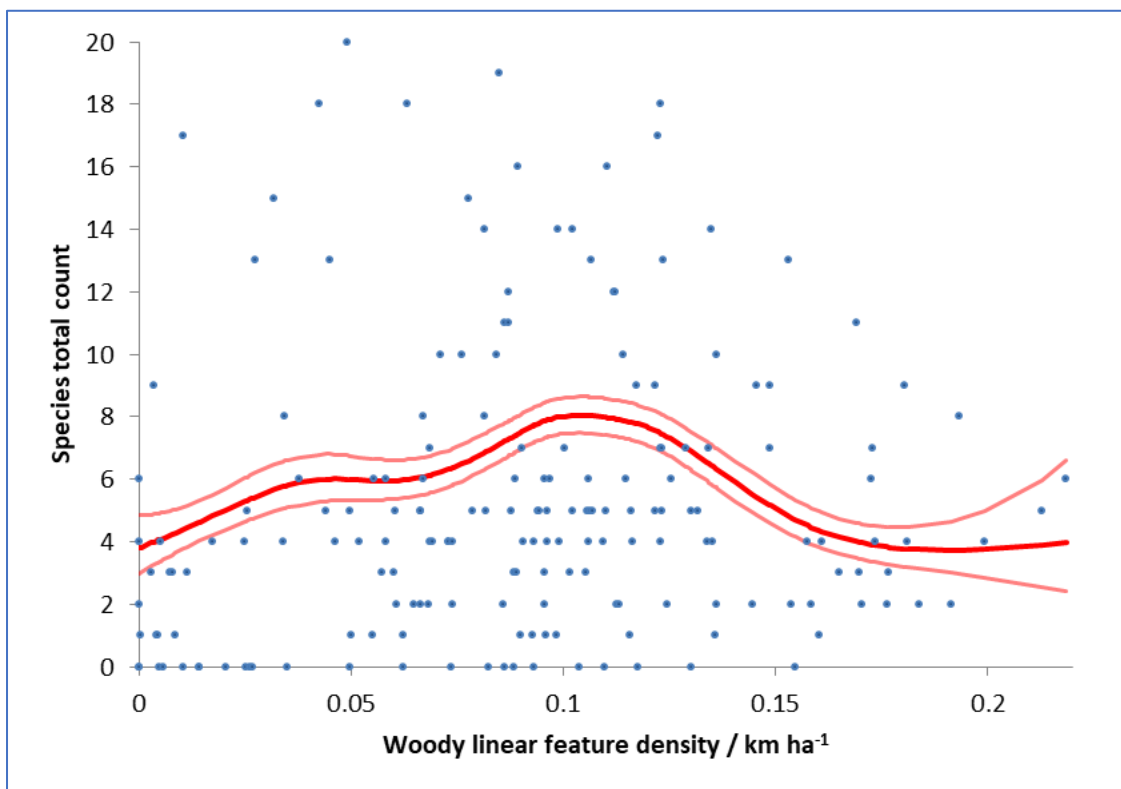


Fig. 9.1v GAM fit with no landscape control for individual species: Woodpigeon

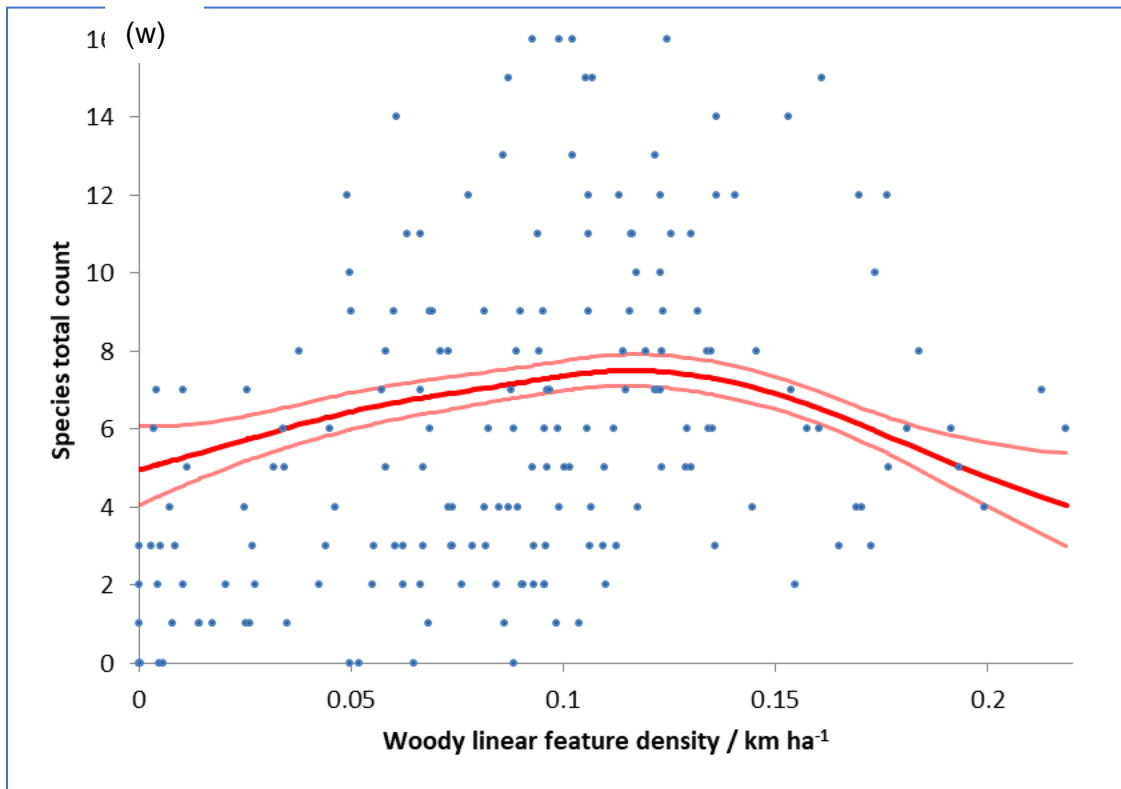


Fig. 9.1w GAM fit with no landscape control for individual species: Wren

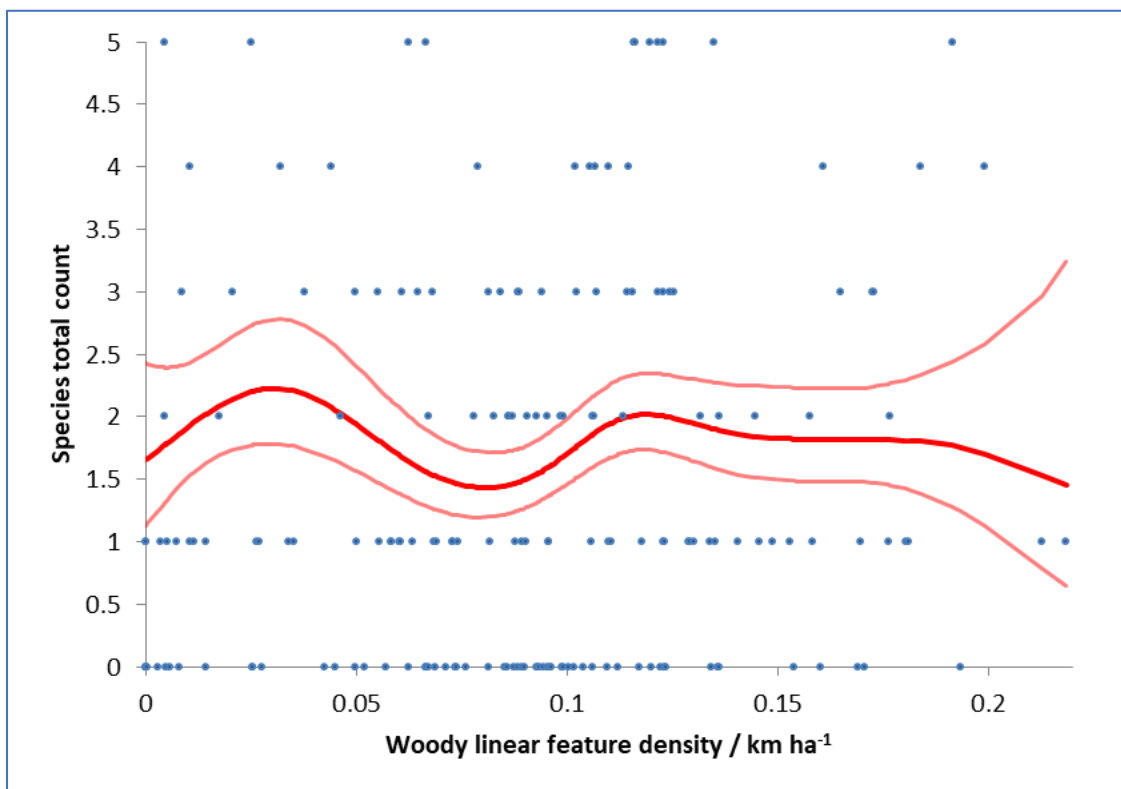


Fig. 9.1x GAM fit with no landscape control for individual species: Willow Warbler

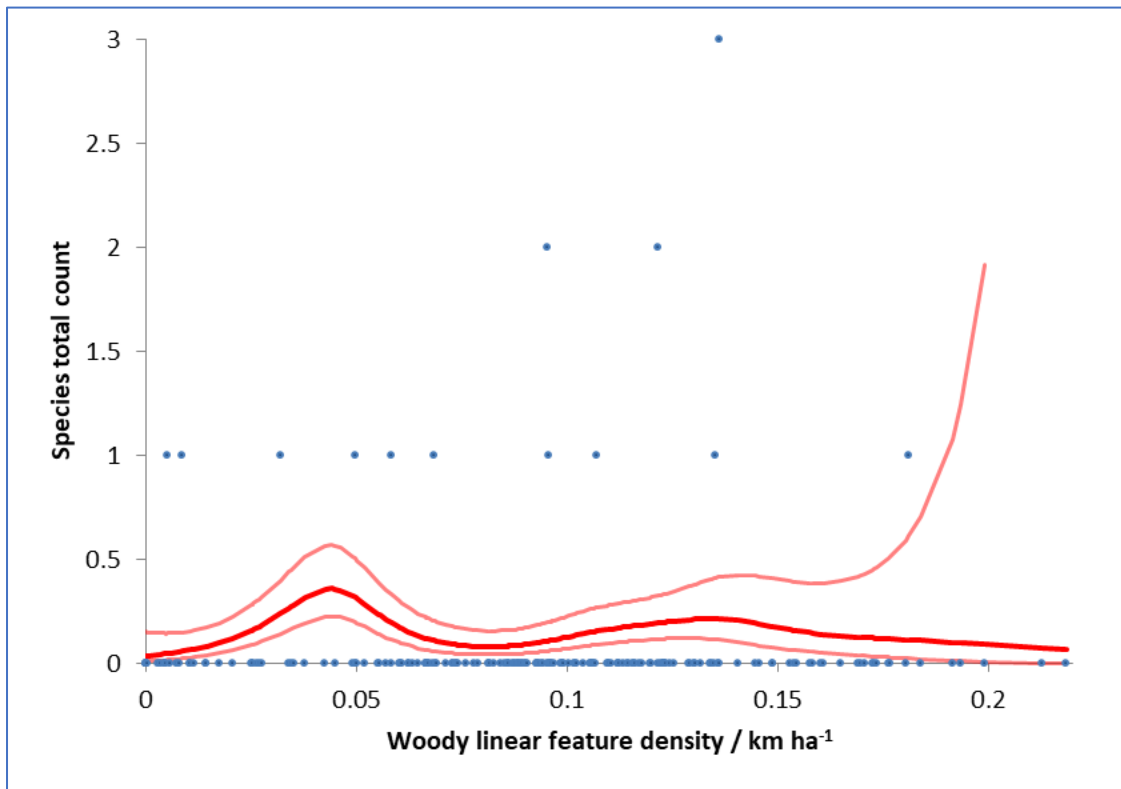


Fig. 9.1y GAM fit with no landscape control for individual species: Yellowhammer

Table 9.3. AIC values for models fitting different complexities of smooth function for the relationship between species-specific abundance and woody linear feature density, and with different landscape controls. The AIC for the simplest model with an AIC value within two units of the model with the lowest AIC among models with each control is shown in bold.

SPECIES	AIC values with the specified control																			
	No control				Intensive farming area				Arable area				Small woody features				Landscape proportion broadleaf			
	1df	2df	3df	4df	1df	2df	3df	4df	1df	2df	3df	4df	1df	2df	3df	4df	1df	2df	3df	4df
Blackbird	615.1	608.5	599.9	591.3	613.1	606.6	598.1	589.5	614.3	607.8	599.3	590.7	601.5	595.4	586.7	578.0	587.1	581.5	573.0	564.5
Blackcap	377.8	376.9	376.8	377.3	377.3	376.4	376.2	376.6	374.9	374.2	374.2	374.7	374.4	373.6	373.5	373.9	363.0	362.5	362.6	363.1
Bullfinch	321.2	318.5	316.8	316.2	321.2	318.5	316.8	316.1	320.7	318.1	316.4	315.9	312.6	310.7	309.4	309.0	300.1	298.7	297.8	297.6
Blue Tit	645.3	636.5	630.5	624.5	645.3	636.5	630.5	624.5	638.3	629.0	622.5	616.0	616.3	608.0	601.8	595.4	596.9	589.2	583.9	578.8
Chiffchaff	356.9	353.2	349.7	347.6	354.1	350.6	347.2	345.3	356.8	353.2	349.7	347.6	350.8	347.4	343.9	341.8	350.0	346.8	343.5	341.6
Chaffinch	500.9	499.6	498.6	497.7	499.7	498.2	497.1	496.2	499.9	498.7	497.7	496.8	494.2	493.1	492.1	491.1	497.2	496.2	495.5	494.8
Dunnock	455.0	453.3	452.2	452.3	414.9	413.5	412.7	412.9	445.3	443.7	442.7	442.8	454.5	452.7	451.6	451.7	453.0	451.3	450.0	449.9
Goldfinch	611.2	602.4	594.4	586.7	607.8	599.3	591.4	583.8	610.6	602.0	594.1	586.6	610.5	601.5	593.6	586.1	608.4	600.0	592.0	584.4
Greenfinch	343.1	338.8	334.5	332.5	341.5	337.2	332.9	330.9	329.9	325.7	321.5	319.6	340.2	336.0	331.9	330.0	340.9	336.9	332.8	330.8
Great Tit	442.7	439.0	435.6	432.7	441.5	437.7	434.2	431.2	441.4	437.5	433.9	430.8	434.6	431.4	428.0	424.9	412.7	410.4	407.8	405.4
Garden Warbler	200.3	198.0	195.7	194.4	194.0	191.5	188.9	187.6	198.3	196.0	193.6	192.3	195.4	193.4	191.2	190.1	188.5	186.6	184.5	183.5
Lapwing	323.4	303.3	295.6	292.7	320.8	300.3	291.8	288.3	276.2	258.8	250.6	246.4	289.3	269.6	262.4	259.7	266.3	248.3	242.0	240.0
Linnet	1326.9	1324.4	1319.0	1313.0	1314.5	1311.9	1306.4	1300.3	1305.8	1302.8	1296.5	1289.4	1302.5	1299.7	1293.3	1286.1	1249.0	1246.7	1241.5	1235.6
Long-tailed Tit	435.2	435.0	433.9	432.9	434.2	433.9	432.9	431.8	421.4	421.0	419.7	418.4	435.2	434.9	433.9	432.9	430.3	430.1	429.0	427.7
Lesser Whitethroat	104.6	105.8	106.6	106.9	98.8	100.0	100.8	101.2	103.2	104.4	105.2	105.5	104.6	105.8	106.6	106.9	101.6	102.7	103.7	104.1
Magpie	580.4	576.9	571.9	567.5	566.2	563.1	558.4	554.2	576.2	572.4	566.9	562.0	560.5	557.4	552.0	547.1	575.2	571.2	566.0	561.6
Robin	487.3	481.7	478.0	475.0	487.2	481.7	478.0	475.0	486.6	480.9	477.0	474.0	469.4	465.1	461.5	458.3	440.3	437.2	434.5	432.3
Reed Bunting	254.5	253.5	251.8	250.2	240.5	239.7	238.0	236.4	252.1	251.2	249.6	248.2	254.1	253.1	251.4	249.8	249.6	248.5	246.8	245.1
Skylark	386.6	386.5	386.0	385.6	384.1	384.1	383.7	383.3	383.5	383.2	382.3	381.4	386.2	386.1	385.5	384.9	380.5	380.7	380.4	379.8
Song Thrush	307.0	307.9	308.7	309.3	305.3	306.2	306.9	307.6	305.8	306.6	307.4	308.0	306.4	307.4	308.2	308.9	283.6	285.0	286.1	287.0
Whitethroat	534.7	534.9	534.2	532.9	522.7	523.0	522.3	521.0	507.6	508.1	507.7	506.6	533.0	533.1	532.4	531.1	512.5	512.3	511.7	510.7
Woodpigeon	1168.5	1157.4	1150.4	1144.2	1142.5	1131.9	1125.0	1118.9	1036.6	1028.2	1023.2	1019.3	1165.7	1154.1	1147.5	1141.6	1157.2	1145.3	1138.5	1132.1
Wren	474.1	471.3	471.1	471.3	465.6	463.0	462.9	463.2	474.0	471.2	471.1	471.3	459.8	458.2	458.1	458.3	470.4	466.7	466.3	466.5
Willow Warbler	403.3	402.0	399.2	396.1	395.7	394.2	391.2	387.8	384.0	382.4	379.3	376.0	389.3	388.1	385.0	381.4	403.2	402.0	399.2	396.1
Yellowhammer	166.7	163.2	158.6	154.8	163.6	159.8	154.9	150.9	165.3	162.2	158.1	154.7	160.7	157.6	153.3	149.6	153.9	149.8	144.3	140.2

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