A regional-scale study of associations between farmland birds and linear woody networks of hedgerows and trees

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Abstract

Farmland birds have declined throughout Europe over recent decades. Many farmland songbirds are associated with linear woody features on field boundaries, such as hedgerows and tree lines. Previous studies have assessed songbird associations with specific hedgerow and tree characteristics, and their landscape context, but large-scale assessments have been limited by difficulties in mapping linear woody networks over large extents, particularly their height structure. We used a high-resolution lidar model of the complete network of linear woody features in southwest England (9,424 km^2), summarising linear feature lengths by height class. Associations were tested between heights of linear woody features and the abundance of 22 farmland birds, using bird survey data summarised for 1446 near-contiguous tetrads, and a weighted version of the phi coefficient of association. Land cover mapping defined tetrads as grassland, mixed or arable farmland.

Results showed that the linear woody network was dominated by features corresponding to managed hedgerows (1.5-2.9 m tall, 42-47% of the network by land cover type), followed by tree lines (≥ 6.0 m, 28-35%). All songbird species had statistically significant, but weak, associations with combinations of land cover and height class of linear woody features, although land cover appeared to be the dominant factor. Many species showed more positive associations with linear woody features on arable farmland than on grassland, particularly for taller hedgerows and tree lines. The results suggest that land-use diversification may benefit some farmland songbirds, such as introducing pockets of arable farming in landscapes dominated by intensively managed grassland. Diverse heights in the linear woody network, incorporating tall hedgerows and trees, would also likely benefit a range of songbird species. The study demonstrates the significant potential of lidar in characterising the structure of linear woody features at the landscape scale, facilitating detailed analyses of wildlife habitat associations and landscape ecology.

Keywords: lidar, farmland biodiversity, habitat selection, landscape ecology, phi coefficient of association, remote sensing

1. Introduction

The loss of farmland biodiversity since the mid 20th Century is well documented, particularly in Europe, with substantial declines in the populations of plants, invertebrates and birds (Sotherton and Self, 2000; Benton et al., 2002; Donald et al., 2006; Kleijn et al., 2011). These declines have largely resulted from agricultural intensification, primarily the destruction of semi-natural habitats and the increasing use and efficacy of pesticides (Wilson et al., 1999; Botías et al., 2019).

Field boundaries provide key habitats and refuges for much of the remaining farmland biodiversity, being uncropped and receiving no direct inputs of agrochemicals (Dover, 2019; but see Gove et al., 2007 for diffuse effects). Hedgerows are the dominant field boundary feature across lowland farmed landscapes in Western Europe and parts of North America, and also occur in South America, Australia and China (Baudry et al., 2000). Hedgerows, or hedges, are broadly defined as linear rows of woody shrubs and/or trees of several metres in height, enclosing fields of arable crops or grassland livestock, and are typically managed by regular cutting to maintain their shape and function as boundary features (Pollard et al., 1974; Baudry et al., 2000). Other linear woody features include unmanaged rows of shrubs and lines of mature trees.

Whether originating as remnants of forest clearance, by deliberate planting or natural growth, linear woody features are recognised as highly valuable biodiverse habitats and landscape features, often protected by environmental legislation (Pollard et al., 1974; Dover, 2019). However, the original function of hedgerows as boundaries and a means of enclosing livestock became less important in the 20th Century, due to the availability of inexpensive wire fencing and a desire to increase field sizes to maximise the efficiency of mechanised farming. As such, hedgerow conservation has increasingly relied on agri-environment schemes to subsidise regular maintenance to prevent their deterioration (Pollard et al., 1974; Dover, 2019).

In landscapes such as the UK and western France, networks of hedgerows and other linear woody features have existed for centuries, with modern hedgerow densities of up to 17 km/km^2 (Fuller et al., 2001; Michel et al., 2006). The total length of Britain's linear woody features in 2007 was 705,000 km, which incorporated 477,000 km of managed hedgerows, representing one of the most significant semi-natural habitats in the farmed landscape (Carey et al., 2008).

Species associated with UK linear woody features include approximately 600 wild plants, 1500 insects and 90 vertebrates (Pollard et al., 1974; UK Biodiversity Steering Group, 1995). Linear woody features can also act as important dispersal and foraging corridors for species crossing agricultural landscapes (Davies and Pullin, 2007; Alderman et al., 2011; Finch et al., 2020). In addition to this intrinsic ecological value, hedgerows and tree lines provide important ecosystem services such as habitats for pollinators and predators of crop pests (Morandin and Kremen, 2013), carbon storage (Black et al., 2014) and buffers against erosion and flooding (Mérot, 1999).

Approximately five million pairs of farmland birds breed in hedgerows in Britain, with 20-30 species being strongly associated with linear woody features for feeding and nesting, and these have received particular attention due to substantial declines in many of their populations (Newton, 2017). Suitable surrounding habitat is also important for some species that breed in hedgerows but predominantly forage in nearby open habitats, whereas open-field species may be negatively associated with hedgerows (Green et al., 1994; Newton, 2017). The UK farmland bird index of 19 indicator species showed an overall decline in abundance of 55% between 1970 and 2018 (Defra, 2019). These bird declines overlapped with a 24% loss in the length of managed hedgerows between 1984 and 2007 (Carey et al., 2008). However, the overall decline in linear woody features was only 1% during this period, because many managed hedgerows had developed into unmanaged shrubs and tree lines. It is unclear how changes in hedgerow density and management have impacted farmland bird communities, but some population declines may be directly related to this (e.g. Cornulier et al., 2011).

Studies to date have indicated that farmland bird species richness and abundance is related to several key variables of linear woody features, including their density in the landscape, their structure (e.g. height), the frequency of mature trees in the hedge, and the adjacent crop type (Burgess et al., 2015; Newton, 2017; Hinsley and Bellamy, 2019). Agri-environment scheme options for enhancing management of linear woody features for biodiversity, including birds, focus on the cutting regime (Staley et al., 2012). Most bird species appear to benefit from moderate to low intensity cutting to create a range of heights, carried out late in the winter after berries and seeds have been exploited (Hinsley and Bellamy, 2000). However, associations between linear woody features and farmland bird communities have not been assessed over large extents or on the regional scale.

A barrier to such analyses is that consistent and repeatable large-scale mapping and characterising of linear woody features can be problematic, due to the extent of their networks in the landscape and complex three-dimensional structure. Typically, hedgerows and tree lines have been mapped using a combination of labour-intensive field surveys and examination of aerial photography (Burel and Baudry, 1990; Defra, 2007), followed by manual digitisation in a geographical information system (GIS). These methods can be impractical for mapping large areas. Consequently, mapping linear woody features and the associated birds (or other taxa) has largely been restricted to the localised sampling of transects or squares of 1 km^2 or less (Arnold, 1983; Barr and Gillespie, 2000; Fuller et al., 2001; Heath et al., 2017). These limitations have constrained the scale and/or detail of hedgerow inventories and analyses (Graham et al., 2019).

Remote sensing can overcome the mapping limitations of scale and detail, enabling complete coverage of high-resolution linear woody feature maps at the landscape-scale (Graham et al., 2019). In the UK and Ireland, remote sensing methods have been employed for comprehensive regional and national mapping of hedgerows (Black et al., 2014; Tebbs and Rowland, 2014; Scholefield et al., 2016). Lidar (light detection and ranging) imagery perhaps has the greatest potential and additionally provides information on height (and potentially width), using laser scanning to produce three-dimensional models of vegetation and linear woody networks across entire landscapes (Redhead et al., 2013; Hill et al., 2014). Matching remotely-sensed linear woody feature models to survey data for bird distributions and abundance, which have been collected extensively at a range of spatial scales (e.g. Bibby et al., 2000; Balmer et al., 2013), enables powerful analyses at a resolution and extent that have previously been impractical (Sullivan et al., 2017).

In this study, we demonstrate a novel approach to examining associations between farmland birds and the structure of linear woody features across an entire regional landscape in south-west England. We use a large-scale, lidar-derived model of a complete network of linear woody features, classified by height, and combined with high-resolution land cover data and surveys of the breeding bird community at the tetrad level. Associations are tested with a modification to the standard phi coefficient of association typically employed in ecology/botanical studies (De Cáceres and Legendre, 2009), using a weighted version of the method to gauge species-habitat associations (Chetcuti et al., 2019).

The study provides a useful contribution to the understanding of farmland birds in relation to linear woody features and their land use context, at a very large spatial scale, and the results can inform management prescriptions aimed at enhancing farmland biodiversity. The study also provides a case study for integrating large-scale remote sensing and field survey datasets to characterize species-habitat associations, which can have wider applications in landscape ecology.

2. Methods

2.1 Study area

England's south-western peninsula contains the counties of Devon and Cornwall (10,269 km^2; Fig. 1). This area has a generally rural, undulating landscape dominated by arable farming and permanent grassland grazed by sheep, cattle and horses, with open moorland on the higher ground (up to 621 m). The landscape is largely characterised by small, irregular fields bounded by hedges, with some field systems dating to the Iron Age (Pollard et al., 1974). The hedges consist of mixed shrubs and trees, typically including Common

Hawthorn *Crataegus monogyna*, Common Hazel *Corylus avellana*, Common Gorse *Ulex europaeus*, Sycamore *Acer pseudoplatanus*, Pedunculate Oak *Quercus robur*, Common Ash *Fraxinus excelsior* and Common Beech *Fagus sylvatica*. Some hedges contain linear earthbanks and stone walls of between 1-1.5 m in height, which are often, but not always, encapsulated within the woody vegetation (Pollard et al., 1974).

2.2 Mapping the linear woody network

The landscape-scale mapping of linear woody features, including hedgerows and boundary trees, was achieved using publicly accessible datasets and a masking and filtering approach within a desktop GIS (ArcGIS 10.4, Esri, Redlands, California). The primary dataset was a complete lidar coverage of 9,424 km^2 of Cornwall and Devon (all land west of approximately 3° 21' W), collected by the Tellus South West project (Ferraccioli et al., 2014). Tellus is a collaboration between academic and research institutes to provide data to facilitate regional environmental and economic sustainability (British Geological Survey, 2017).

The Tellus lidar data product is a 1 m resolution digital terrain model (DTM) and digital surface model (DSM) derived from airborne lidar acquired during leaf-on conditions during July-August 2013. The lidar has an average sampling density of 1 point per m^2 and a vertical accuracy of ±0.1 m (see Ferraccioli et al., 2014 for full details of lidar acquisition and processing). These data provide elevation values for the ground (DTM) and also the tallest feature above it (DSM), such as buildings, trees or hedgerows, for every 1 m^2 pixel.

The DTM was subtracted from the DSM to create a canopy height model (CHM) depicting relative height values of features on a flat plane, including woody vegetation and buildings. All features other than hedgerows were removed by a stepwise masking (deleting) process. First, all pixels with a height value below 1 m in height were deleted, to remove ground-layer herbaceous vegetation. Woodland blocks of 0.5 ha or larger were then masked using vector polygons from the National Forest Inventory for England (Forestry Commission, 2020). Buildings, such as houses and retail, were masked using vector polygons available from national mapping products (Ordnance Survey, 2016, 2017), applying a 5 m buffer to each building to capture ancillary structures such as temporary outbuildings.

The resulting raster output contained pixels mostly depicting field boundary hedgerows and non-woodland trees. These pixels were classified into four height bins (class 1-4) based on their value, to represent broad categories of hedgerow and other woody feature, broadly based on information in Defra (2007). Class 1 of vegetation 1.0-1.49 m tall identifies low hedgerows that have recently been planted or cut to regrow. Bare stone walls and banks were also included in this category, as they could not be distinguished from vegetation in the lidar data. Class 2 of 1.5-2.9 m tall vegetation reflects typical managed farmland hedgerows that were likely to dominate the landscape. Class 3 of 3.0-5.9 m vegetation includes unmanaged and outgrown hedgerows, semi-mature shrubs and young trees. Finally, class 4 of ≥ 6.0 m vegetation reflects larger non-woodland trees and tree-lines.

The raster data were then converted to a smoothed polygon vector coverage. A manual check of output removed any in-field crop vegetation or non-linear scrub, and any remaining glasshouses, caravan parks and solar farms that were not present in the masking data but were clearly identifiable by their geometry. Features in classes 1-3 with an area < 20 m^2, or in class 4 with an area < 10 m^2, were assigned to surrounding dominant values (i.e. reclassified to the same values as adjacent polygons where these were greater than these thresholds) to reduce small scale variability. Non-contiguous polygons of < 10 m^2 were removed, giving a minimum length of classified hedgerow of approximately 3 m.

The linear polygons were converted to polylines based on the longitudinal central axis of each polygon, using ET GeoWizards version 11.2 software (ET SpatialTechniques, Pretoria, South Africa). This linear polyline network formed the final linear woody habitat model. The total length of features in each height class were generated for each of 2371 individual 2 x 2 km tetrads throughout the study area, based on the British National Grid (Fig. 1). Hedgerow width was not included as a variable, due to its poor representation in 1 m^2 resolution lidar; hedgerow width is strongly correlated with height (MacDonald and Johnson, 1995; Hinsley and Bellamy, 2000), but we were unable to assess the independent importance of width or other characteristics. Tetrads were used as the sampling unit to match the bird data (see below). The accuracy of the woody habitat model in assigning features to the correct height class was assessed as 73.2% by ground truthing (see Broughton et al., 2017).

2.3 Land cover

To characterise the landscape composition of each tetrad, and to determine the land use context of hedgerows and other linear woody features, we used the UK Centre for Ecology & Hydrology's Land Cover Map for 2015 (LCM2015), which is a 25 m resolution classified raster coverage derived from satellite multispectral imagery (Rowland et al., 2017). The 21 land cover classes in LCM2015 were generalised into broad categories of grassland, urbanised, arable, woodland, freshwater and marine (including all coastal habitats). The broad land cover coverages were summarised as the proportional coverage in each tetrad.

2.4 Bird surveys

Comprehensive bird survey data for spring-summer were available for every tetrad, reflecting the breeding bird community. Survey periods differed due to separate county bird atlas projects, taking place during 2000-2009 in Cornwall (CBWPS, 2013) and 2008-2011 in Devon (Beavan and Lock, 2016). Due to the longevity and stability of the linear woody network in this region (Pollard et al., 1974), the mismatch in timings between the bird and habitat data were considered acceptable. Bird surveys in both counties used a timed tetrad visit (TTV) methodology during the spring and summer breeding seasons of April-July. The TTV method involved a transect survey by an experienced observer through major habitats in each tetrad to characterise the full breeding bird community. Each tetrad was surveyed in a single year on a minimum of two visits of 1 h duration, or one visit of 2 h, with a maximum of two 2 h visits.

Counts of all birds were recorded to species during each transect survey. The counts were standardised to a mean hourly count that was generated from all visits. The standardised count was then used as the abundance value for each tetrad. Twenty-two songbird species that are associated with farmland hedgerows and trees were selected for analysis (Table 1). Nine species are on the UK amber or red lists of species of conservation concern after showing long-term declines (Eaton et al. 2015). Birds were grouped into three broad 'guilds' based on their diet and feeding behaviour, comprising a) granivores that feed extensively on seeds, but with some insects in summer; b) ground-feeders that feed extensively on terrestrial invertebrates; c) foliage-gleaners that largely feed on insects in tree and hedgerow vegetation (Table 1).

2.5 Statistical Analysis

2.5.1 Tetrad summary

The data for birds, land cover and linear woody features were combined to give values for each tetrad. To focus on the dominant associations between linear woody features and birds on farmland, we discarded tetrads where the land area totalled less than 3.75 km^2, to only retain complete or near-complete tetrads. We also discarded tetrads where the land cover totalled < 75% of grassland or arable classes combined to exclude extensive woodland and urban areas, and where the hedgerow density was < 5 km/km^2. This gave 1446 tetrads for analysis, covering 5774.6 km^2, which only contained significant networks of hedgerows or other linear woody features in a primarily rural context (Fig. 1). Only five tetrads were not contiguous with others, separated a maximum of two tetrads apart.

To compare linear woody features in arable versus grassland or mixed habitats, which may influence bird associations with linear woody features due to the wider habitat context (Hinsley and Bellamy 2019), tetrads were coded by arable land coverage, where code 0 = 0-29.9% arable cover, code 1 = 30-49.9%, and code 2 = 50-86.8% (the maximum). Accordingly, tetrads assigned to code 0 were dominated by grassland (non-arable), code 1 by mixed arable/grassland, and code 2 by arable farmland (Table 2). The median proportions of these and other land cover types in tetrads, and linear woody feature densities, were compared using non-parametric Kruskal-Wallis tests. These tests compare land-use variation between classifications of arable, mixed or grassland, which may influence bird communities, such as the coverage of urban or woodland habitat. Comparing the linear woody feature densities would show if combined or different height classes varied with land cover type.

2.5.2 Habitat association

To test habitat associations we used the group-equalised weighted version of the phi coefficient of association (Chetcuti et al., 2019). The phi coefficient method is a standard analysis for simultaneously comparing the relative association of species between multiple groupings of habitat variables (Chytrý et al., 2002; De Cáceres and Legendre, 2009). The phi coefficient of association between a species and groups of habitat features can indicate a negative (avoidance) as well as a positive (preference) association, it is independent for different species and habitats, and it can accommodate spatial autocorrelation and small sample sizes (De Cáceres and Legendre, 2009; Chetcuti et al., 2019).

For each species the analysis produces either a positive or negative association for a group (typically a land cover or feature type), which can be equalised (i.e. standardised) by the numerical sizes of all groups (see Tichý and Chytrý, 2006; Chetcuti et al., 2019). The phi coefficient method uses a binary presence/absence value for species occurrence, which in this case was simplified count data for birds, where we created a weighted 0/1 score of relative abundance for each bird species.

The bird data were simplified to accommodate the phi coefficient of association, and to also minimise any limitations of the bird survey data, which were low intensity counts that may contain observer effects (e.g. observer skill, or choice of productive survey routes in the tetrad). This generally justified the loss of information in simplifying the count data. Bird counts for each species were reclassified according to their individual mean abundance across all tetrads, with a score of 0 = a count of less than the species' mean abundance, and 1 = a count equal to or greater than the mean abundance. The zero values, where a species' abundance is below the mean, are used to increase information on association in the phi coefficient analysis (De Cáceres and Legendre, 2009). Thirteen of the 21 species occupied at least 87% of tetrads; by weighting bird presence (score of 1) only to those tetrads where a species was relatively abundant, this should reveal the strongest habitat associations.

The phi coefficient of association assigns presence-absence to a location of one particular group (De Cáceres and Legendre, 2009). The group-equalised weighted version allows for a weighting of different groups within each location. The groups in our case are the combined linear woody feature class and coded arable proportion. The weighting applied was the proportion of each class of the total length of woody feature in each tetrad; for example, in a grassland-dominated tetrad with 20 km of linear woody features, the weighting for 2 km in class 1 (low hedges) would be 0.1, and weightings of the remaining groups in this tetrad would total 0.9. There were 12 groups in total combining the four hedge classes and the three arable classes.

The phi coefficient (*R*) was calculated for each of the 22 bird species using the R statistical package version 3. 5 (R Core Team, 2018), the R package 'PhiCor' (Chetcuti, 2020) and JASMIN HPC cluster LOTUS (Lawrence et al., 2013). For the 12 groups, a phi coefficient value of *R* was calculated between -1 and +1 (negative and positive association, as with a standard Pearson correlation) as well as *P* values of statistical significance (alpha level $P < 0.05$) from toroidal permutation. This toroidal permutation, using random shifts of observations, also addressed any potential spatial autocorrelation in the data (Fortin and Jacquez, 2000).

3. Results

3.1 Linear woody network and land cover characteristics

The modelled coverage of hedgerows and other linear woody features reveal densities ranging from the imposed minimum of 5 km/km^2 up to 21 km/km^2 in each tetrad. Kruskal-Wallis tests indicated that median densities of linear woody features varied significantly across arable, mixed and grassland dominated landscapes, but the differences were insubstantial (Table 2). The dominant woody feature type in all landscapes (height class 2) corresponded to typical managed hedgerows of 1-5-3.0 m tall, which accounted for 42-47%

of the total length of the linear woody network by land cover type. Trees and tree lines (height class 4) accounted for approximately one third (28-35%) of the linear woody network, whereas features less than 1.5 m tall (class 1) were only a minor component (3-4%). The woody feature classes were weakly inter-correlated, with maximum values (Pearson coefficient) of ±0.3 in a correlation matrix. Kruskal-Wallis tests showed that woodland was significantly less abundant in arable-dominated tetrads, but urbanised land cover was similarly distributed between arable, grassland and mixed tetrads (Table 2). Freshwater bodies occurred in 8% of tetrads, with a maximum coverage of 4.5% and medians of 0 across all tetrad types, so this category was not considered further.

3.2 Bird-habitat association

The *R* values for the phi coefficients of association between birds, woody features and land cover groupings were very low, with a range of only -0.13 to +0.14. However, statistically significant ($P < 0.05$) associations were detected for all species across the three guilds of granivores, insectivorous ground-feeders and foliage-gleaners.

The eight granivores generally showed significant positive associations with arable landscapes (seven species, excluding Common Reed Bunting) and negative associations with grassland (six species, excluding Common Reed Bunting and Eurasian Bullfinch). However, the granivores showed little or no discrimination between linear woody classifications, with most species having multiple significant associations with many or all height classes (Fig. 2). By contrast, the Common Reed Bunting and Eurasian Bullfinch each had only a single significant (positive) association with any hedgerow class and land cover combination.

All four ground-feeding species showed positive associations with arable and mixed landscapes, and particularly for medium or taller hedgerows and tree-lines in these landscapes (Fig. 3). In grassland, the ground-feeding species all showed significant negative associations with all hedgerow height classifications.

Among the ten foliage-gleaners, seven species showed a significant positive association with taller hedgerows and/or trees in mixed landscapes: Eurasian Blackcap, Common Chiffchaff, European Nuthatch, Marsh Tit, Blue Tit, Great Tit and Long-tailed Tit (Fig. 4). Six species showed a negative association for most or all hedgerow classes on grassland, comprising Common Whitethroat, Winter Wren, Eurasian Blackcap, Common Chiffchaff, Blue Tit and Great Tit. However, Willow Warbler, Marsh Tit and Eurasian Nuthatch had contrasting positive associations with woody features on grassland and negative associations with arable. In particular, Marsh Tit and Eurasian Nuthatch both had positive associations with the taller hedgerows and/or trees in the grassland and mixed tetrads.

4. Discussion

4.1 Associations between birds and linear woody features

This regional-scale study, combining large-scale datasets derived from field surveys and remote sensing, highlights patterns of association between farmland birds and linear woody habitat (i.e. hedgerows and tree lines) in the breeding season, at a spatial extent and resolution that have previously been unattainable. The study is the first to use a lidar-derived model of a continuous linear woody network for a whole region in relation to animal distributions. The approach shows how the increasing availability of lidar and other remote sensing datasets can enable novel analyses of species distributions over entire landscapes, particularly by utilising the heights of linear woody features.

Our analysis found significant positive and negative associations between the farmland birds examined and linear woody features, and also land cover types, although the magnitude of these associations is small and is based on a simplified categorisation of abundance. Despite the bird-habitat associations being modest, they are nevertheless ecologically meaningful. The granivorous birds are positively associated with hedgerows and tree lines in arable landscapes, where crop and weed seeds are available. Negative associations with grassland-dominated landscapes likely reflect the limited seed resource for over-winter survival of these species (Newton, 2017). Two species with few significant associations

(Common Reed Bunting and Eurasian Bullfinch) were possibly more influenced by crop type, ditches and scrub in the tetrad than the hedgerows (Hinsley and Bellamy, 2019).

Ground-feeding insectivores also show negative associations with grassland, involving all woody height classes. This is surprising, as grassland may be expected to have plentiful earthworms and beetle larvae for foraging birds (Newton, 2017). However, intensively managed grassland can be poor foraging habitat with reduced invertebrate abundance and access to bare ground (Atkinson et al., 2004; McCracken and Tallowin, 2004). The positive associations between ground-feeding birds and the arable and mixed tetrads, including for taller hedgerows and trees, may reflect preferences for habitats with a more diverse structure and composition (Hinsley and Bellamy, 2019).

Six of the ten foliage-gleaning birds also show negative associations with most or all woody feature heights in grassland-dominated tetrads, but positive associations in arable tetrads, despite only small differences in overall densities and composition of the hedgerow and tree networks. Affiliations with taller hedgerows and tree lines were to be expected for generalists of woodland and scrub habitats, such as Blue Tits, Great Tits and Winter Wrens (Fuller et al., 2001; Hinsley and Bellamy, 2019). However, for these species, and also Common Whitethroat, it’s unclear why positive associations with woody features are prevalent in arable and mixed habitats but not grassland. These species typically feed and nest within the tree and hedgerow vegetation, rather than within the surrounding fields (Newton, 2017), and so differing associations between grassland and arable may reflect other variables in these habitats, such as hedgerow tree/shrub species or field margin vegetation.

In contrast to other foliage-gleaners, associations of Marsh Tit, European Nuthatch and Willow Warbler likely reflect their stronger preference for woodland habitats (Fuller et al., 2001). Willow Warblers prefer young woodland and scrub (Bellamy et al., 2009), whereas Marsh Tits and European Nuthatches prefer mature woodland in well-wooded landscapes (Bellamy et al., 1998; Broughton et al., 2013). All three species have positive associations with linear woody features in grassland tetrads, and some in mixed areas, where woodland was more abundant than in arable. This suggests that these birds are using hedgerows in relatively wooded landscapes (MacDonald and Johnson, 1995), which may facilitate dispersal between woodland patches (Broughton et al., 2010; Alderman et al., 2011).

Many studies have investigated bird abundance and diversity in relation to hedgerow characteristics and adjacent habitats, as reviewed by Hinsley and Bellamy (2000, 2019) and Newton (2017). Our results largely agree with these syntheses, in that most of the positive associations between birds and linear woody features were for taller hedgerows and tree lines. As such, a regime of moderate or low intensity cutting that produces a range of medium to tall hedgerows and trees in the landscape, rather than intensive annual cutting, would be beneficial for more farmland bird species.

However, a major result from our study is the dominance of land cover in the significant associations, which largely override the importance of all the height classes of the hedgerows and trees in the linear woody network. Siriwardena et al. (2012) also showed that for many farmland species the landscape variation was a stronger influence on bird abundance that boundary variables. Variable effects of landscape context on farmland hedgerow birds are frequent in the literature (e.g. Green et al., 1994; MacDonald and Johnson, 1995), largely reflecting the preferences of individual species and groups (Parish et al., 1995; Siriwardena et al., 2000).

Fine-scale landscape features, such as the crop type in arable fields or the presence of wet habitat or suburban gardens, can be important determining factors for species richness and abundance (Green et al., 1994; Mason and Macdonald, 2000; Whittingham et al., 2009; Siriwardena et al. 2012). However, our results indicate that the proportion of arable land cover, or an associated variable, is perhaps the most significant factor driving farmland bird abundance in networks of linear woody features. A similar dominance of land use over vegetation structure influencing bird abundance was reported by Parish et al. (1995).

Hedgerow structure and the amount of woodland in the landscape may contribute to bird abundance, but associations in our study were overwhelmingly driven by the distinction between arable, mixed and grassland, with the latter being the most negative.

The possible reasons for negative associations between farmland bird abundance with grassland need further consideration. Intensively managed productive grassland typically contains fewer or less accessible seed and invertebrate food resources than mixed arable farmland, and generally lacks conservation field margins or headlands to promote insects and wild plants (Wilson et al., 1999; Atkinson et al., 2005). Batáry et al. (2010) found that arable and particularly mixed landscapes may offer more diverse habitats than grassland, and Westbury et al. (2011) showed that areas of barley on pastoral farms were important for supporting farmland birds. Sullivan et al. (2017) found that positive effects of hedgerow length on bird abundance were greater in arable than grassland landscapes.

The weakness of the bird-habitat associations in our study echoes those of Sullivan et al. (2017), who also found weak explanatory power of habitat variables in modelled relationships with bird abundance. This suggests that bird abundance might perhaps be related more to habitat quality than habitat type. Weak or modest associations may have resulted from broad classification or error in defining hedgerow and other habitat features, or high abundance of birds across the habitats, which masked specific preferences (Batáry et al., 2010; Siriwardena et al., 2000).

The lidar model was based only on height distributions, and may have omitted other variables that could be important for bird abundance, such as hedgerow width or the presence of ditches (Hinsley and Bellamy, 2019). Other limitations of our data and analyses include the low-intensity bird surveys, which may not have adequately reflected their abundance in relation to hedgerows. For example, observers could be biased to more 'productive' habitats in the tetrad, where more bird species could be expected to be observed. Furthermore, the bird survey protocol aimed to maximise the habitats sampled in a tetrad, not necessarily survey them representatively.

However, limiting the study to the suite of relatively common hedgerow birds, simplifying the count data and using a large number of tetrads surveyed in the region should have largely countered observer effects and major sources of 'noise' in the surveys. Nevertheless, any small counting errors around the mean would have been propagated into an incorrect 0/1 categorisation during data simplification, and this was an unavoidable source of potential error in analysis.

Other studies of birds, hedgerows and land use report relationships of varying strength, and it is the significance and direction (positive or negative) of the association that can be considered as more meaningful (Hinsley and Bellamy, 2000, 2019). However, our study only considered bird abundance in the breeding season, and habitat associations may differ in winter due to different populations utilising different resources (Hinsley and Bellamy, 2019). Overall, our results for farmland birds in the breeding season indicate that diversifying grassland habitats in the landscape context may be more important for species abundance than hedgerow management regimes. Nevertheless, sympathetic hedgerow management is still important for supporting farmland birds and other wildlife (Staley et al., 2012). Agri-environmental schemes directed at enhancing populations of farmland songbirds and other taxa tend to focus on arable habitat (e.g. Broughton et al., 2014; Redhead et al., 2018), but applying more of this resource to landscapes dominated by grassland may also benefit birds and other species associated with field boundaries, and help to reverse population declines (Woodcock et al., 2009, 2013, 2014; Peach et al., 2011).

4.2 Remote sensing for analysing species-habitat associations

Until recently, studies of relationships between hedgerows and tree lines, land cover and farmland plants and animals have only been possible with limited sampling up to the scale of individual farms or tetrads (reviewed in Feber et al., 2019; Hinsley and Bellamy, 2019; Staley et al., 2019). Studies at larger spatial extents were limited to only land cover effects, due to the difficulty of mapping the structure of complete hedgerow networks (Siriwardena et al., 2000; Fuller et al., 2005; Graham et al., 2019). Sullivan et al. (2017) used a national model of British linear woody feature lengths (Scholefield et al., 2016) alongside land cover mapping to investigate the abundance of 18 bird and 24 butterfly species. Although the linear features improved modelled predictions of species-habitat associations, this analysis was limited to the discontinuous sampling of 1 km^2 squares (totalling 3723 km^2) for birds and 2-4 km transects for butterflies, and contained no height information for woody features. Our study extends this approach by utilising a lidar model of a continuous linear woody network, combined with comprehensive land cover and bird atlas data. This demonstrates how the structural characteristics of linear woody features can be considered alongside land cover and species abundance over an entire landscape (in this case 5775 km^2) and at high spatial resolution (1 m^2 for woody features, tetrad level for species abundance). The weighted version of the phi coefficient of association provides an adaptable framework for testing relationships between the species abundance and habitat variables (Chetcuti et al., 2019), and has wide applicability for exploiting other species and habitat distribution data. The increasing availability of high-resolution lidar and other remote sensing datasets, often at no cost from public repositories, and open source software tools to manipulate such data, provides equitable opportunities for substantially more detailed analyses of ecological data than has previously been possible (Hill et al., 2014; Graham et al., 2019; Rocchini et al., 2017). The increasing availability of high performance computing facilities also extends the capability of analysing such data (e.g. Chetcuti et al. 2019). The resolution of national habitat feature mapping, typically at 1 m for lidar (Environment Agency, 2020), is now finer than that of plant or animal taxa data, which may only attain 1 km resolution (Preston, 2013). Nevertheless, resolutions of e.g. 1 km may be appropriate for assessing habitat and species associations, depending on the ecological processes in question. The use of high-resolution lidar for mapping linear woody networks also has a much broader potential for producing detailed inventories of hedgerow distribution and structure, which can be used to model carbon sequestration, woodfuel availability or cultural landscapes of traditional hedgerow management (Pollard et al., 1974; Graham et al., 2019).

4.3 Conclusions

In summary, combining very large and high-resolution remote sensing and biological recording datasets can enable powerful analyses of species-habitat relationships at an unprecedented scale, which are primarily limited only by the data quality. Our study employed such data to indicate that landscape context is potentially a more important factor for determining breeding farmland bird abundance than the height structure of the network of linear woody features. Most bird species had negative associations with linear woody features in grassland areas and positive associations in arable, particularly with taller hedgerows and tree-lines. Diversifying non-arable farmland, for example by introducing small patches of arable cropping, may, therefore, achieve greater benefits for hedgerow birds than focussing only on management regimes of the hedges themselves. Case studies such as ours are valuable in demonstrating novel approaches for utilising lidar and other remote sensing datasets alongside standard biological recording data.

Acknowledgements

We are grateful to Mike Lock, Stella Beavan and the late Mike Hounsome from Devon Birds (www.devonbirds.org), Mark Grantham at Cornwall Bird Watching and Preservation Society, and the volunteer surveyors for collection, collation and access to the bird atlas data. The study used spatial data supplied by the Forestry Commission and Ordnance Survey © Crown copyright and database right 2015, licensed under the Open Government Licence v3.0. The work used the JASMIN at RAL STFC (http://jasmin.ac.uk), operated jointly by the centre of environmental data analysis and the scientific computing department. This facility was funded by NERC.

Funding - This research was funded by the Natural Environment Research Council (NERC) and the Biotechnology and Biological Sciences Research Council (BBSRC) under research programme NE/N018125/1 LTS-M ASSIST – Achieving Sustainable Agricultural Systems www.assist.ceh.ac.uk. JC was funded by a studentship from the NERC SPHERES Doctoral Training Partnership (NE/L002574/1).

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Table 1. Farmland bird species used in the analyses, classified by their foraging guild, and their listing in the Birds of Conservation Concern 4 (Eaton et al. 2015) as Red (severe long-term population decline), Amber (moderate decline) or Green (stable or increasing population).

Species		BoCC4 list	Guild
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Amber	Granivore
Common Chaffinch	*Fringilla coelebs*	Green	Granivore
European Goldfinch	*Carduelis carduelis*	Green	Granivore
European Greenfinch	*Chloris chloris*	Green	Granivore
House Sparrow	*Passer domesticus*	Red	Granivore
Common Linnet	*Carduelis cannabina*	Red	Granivore
Common Reed Bunting	*Emberiza schoeniclus*	Amber	Granivore
Yellowhammer	*Emberiza citrinella*	Red	Granivore
Common Blackbird	*Turdus merula*	Green	Ground-feeder
Dunnock	*Prunella modularis*	Amber	Ground-feeder
Song Thrush	*Turdus philomelos*	Red	Ground-feeder
European Robin	*Erithacus rubecula*	Green	Ground-feeder
Eurasian Blackcap	*Sylvia atricapilla*	Green	Foliage-gleaner
Blue Tit	*Cyanistes caeruleus*	Green	Foliage-gleaner
Great Tit	*Parus major*	Green	Foliage-gleaner
Marsh Tit	*Poecile palustris*	Red	Foliage-gleaner
Long-tailed Tit	*Aegithalos caudatus*	Green	Foliage-gleaner
Eurasian Nuthatch	*Sitta europaea*	Green	Foliage-gleaner
Common Whitethroat	*Sylvia communis*	Green	Foliage-gleaner
Willow Warbler	*Phylloscopus trochilus*	Amber	Foliage-gleaner
Common Chiffchaff	*Phylloscopus collybita*	Green	Foliage-gleaner
Winter Wren	*Troglodytes troglodytes*	Green	Foliage-gleaner

Table 2. Median and minimum-maximum values of habitat features in tetrads categorised by arable coverage. Land cover classes refer to percentage cover. Freshwater coverage is omitted due to negligible values. LWF refers to density (km/km^2) of linear woody features, where features in class 1 = 1.0 -1.49 m tall, class 2 = 1.5-2.9 m, class 3 = 3.0-5.9 m and class 4 ≥ 6.0 m. The Kruskal-Wallis test compares land cover and LWF densities between the grassland, mixed and arable tetrads.

	Grassland (n = 388)			Mixed (n = 641)			Arable (n = 417)			All (n = 1446)			Kruskal-Wallis test for arable/mixed/grassland	
	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max	*W* (df = 2)	*P*
Arable	17.5	0.0	29.8	41.3	30.0	50.0	57.5	50.3	86.8	41.6	0.0	86.8	-	-
Grassland	70.0	47.0	95.3	45.8	25.5	66.5	31.3	8.8	47.0	45.8	8.8	95.3	-	-
Woodland	10.0	0.0	24.8	10.0	0.8	25.3	6.5	0.3	24.0	8.8	0.0	25.3	112.4	< 0.01
Urban	0.5	0.0	20.8	0.5	0.0	18.5	0.5	0.0	18.5	0.5	0.0	20.8	2.9	0.24
LWF class 1	0.3	0.1	2.2	0.3	0.0	3.0	0.3	0.1	3.2	0.3	0.0	3.2	35.5	< 0.01
LWF class 2	4.2	0.7	8.9	4.7	1.0	9.9	4.9	1.6	8.4	4.6	0.7	9.9	52.0	< 0.01
LWF class 3	1.8	0.5	5.5	2.0	0.4	7.2	2.1	0.5	6.6	2.0	0.4	7.2	9.4	0.01
LWF class 4	3.4	0.4	9.4	3.6	0.1	9.0	2.9	0.1	6.6	3.3	0.1	9.4	48.6	< 0.01
All LWF	10.0	5.1	17.3	10.9	5.1	21.0	10.4	5.0	18.5	10.4	5.0	21.0	27.7	< 0.01

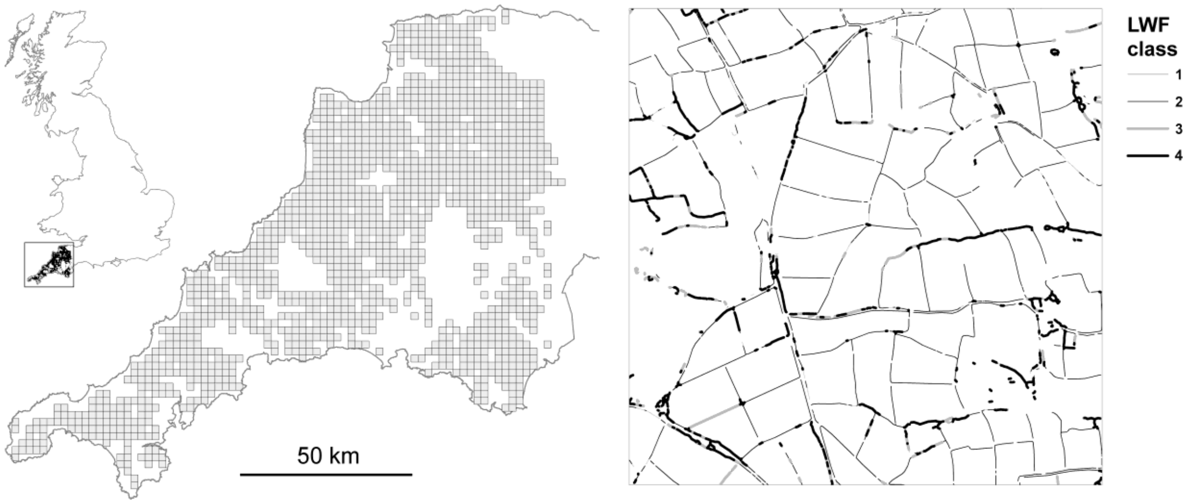

Figure 1. Study area location in southwest England (left), showing the distribution of 1446 tetrads used in analyses of associations between songbirds and linear woody features (LWF). An example tetrad (right) showing the lidar-derived model of the network of LWF classified by height, where 1 = 1.0-1.49 m tall, 2 = 1.5-2.9 m, 3 = 3.0-5.9 m and 4 ≥ 6.0 m.

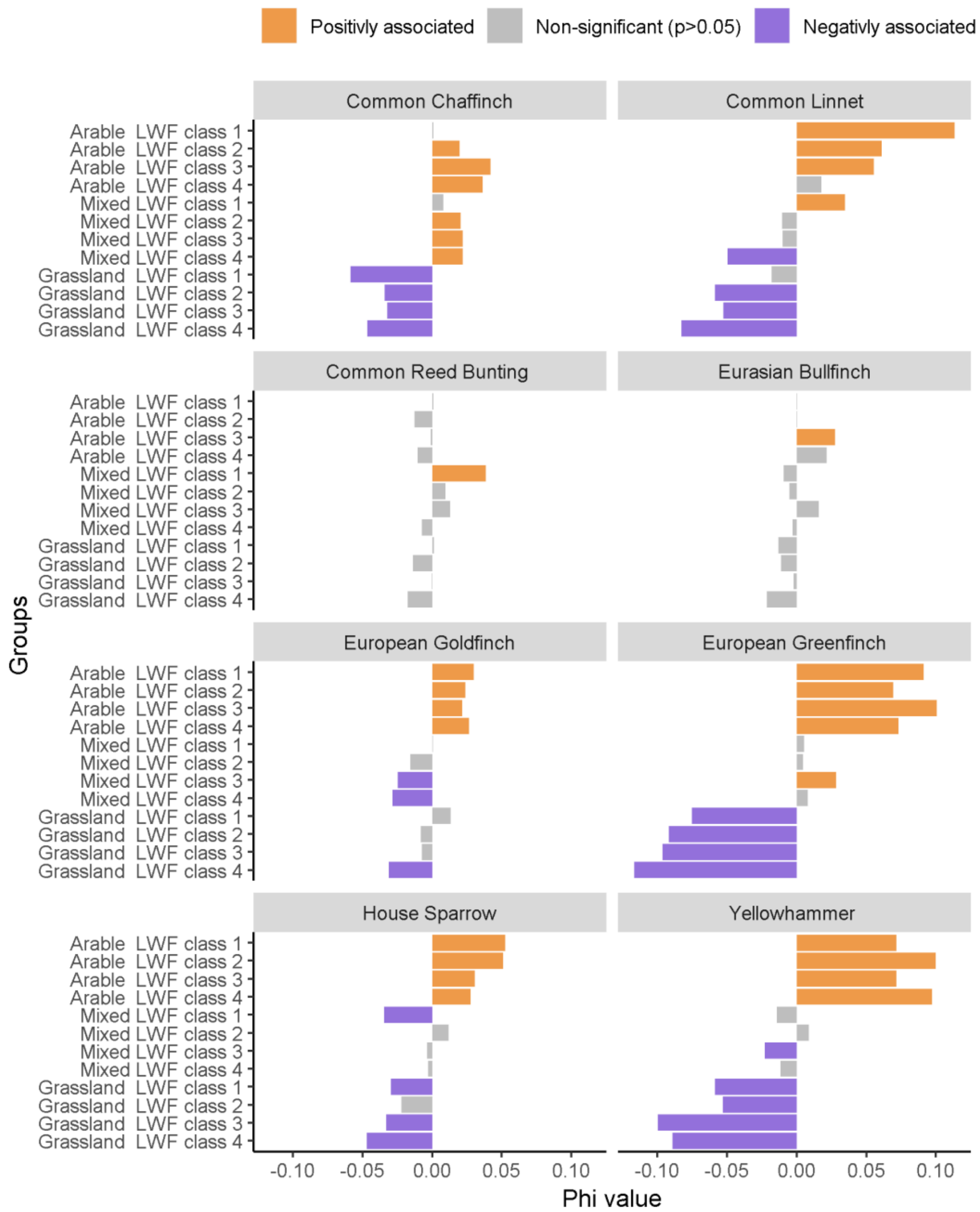

Figure 2. Phi coefficients of association between relative abundance of granivorous farmland songbirds and combinations of linear woody features (LWF) and land cover in 1446 tetrads. LWF are classed by height, where 1 = 1.0-1.49 m tall, 2 = 1.5-2.9 m, 3 = 3.0-5.9 m and 4 ≥ 6.0 m. Land cover in tetrads is defined as Arable (≥ 50% arable and < 29% grassland), Mixed (30-49% arable and 26-67% grassland) or Grassland (0-29% arable and ≥ 47% grassland). A group-equalised weighted version of the phi coefficient is used, based on groups of combined linear woody feature class and coded land cover, and weighted by the proportion of each class of the total length of woody feature in each tetrad.

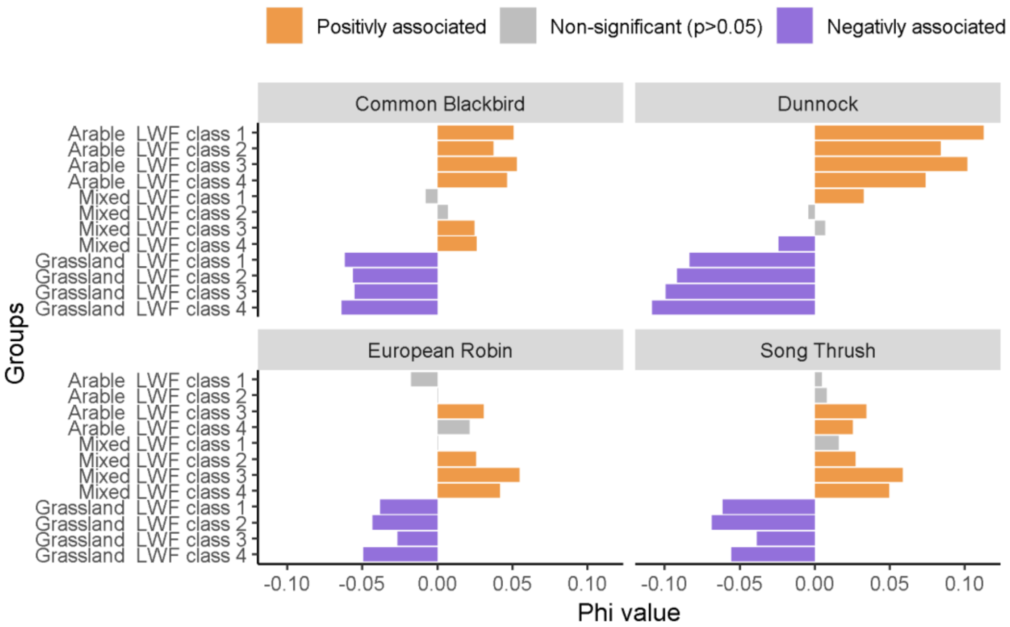

Figure 3. Phi coefficients of association between relative abundance of ground-feeding farmland songbirds and combinations of linear woody features (LWF) and land cover in 1446 tetrads. See Fig. 2 for axes labels and further detail.

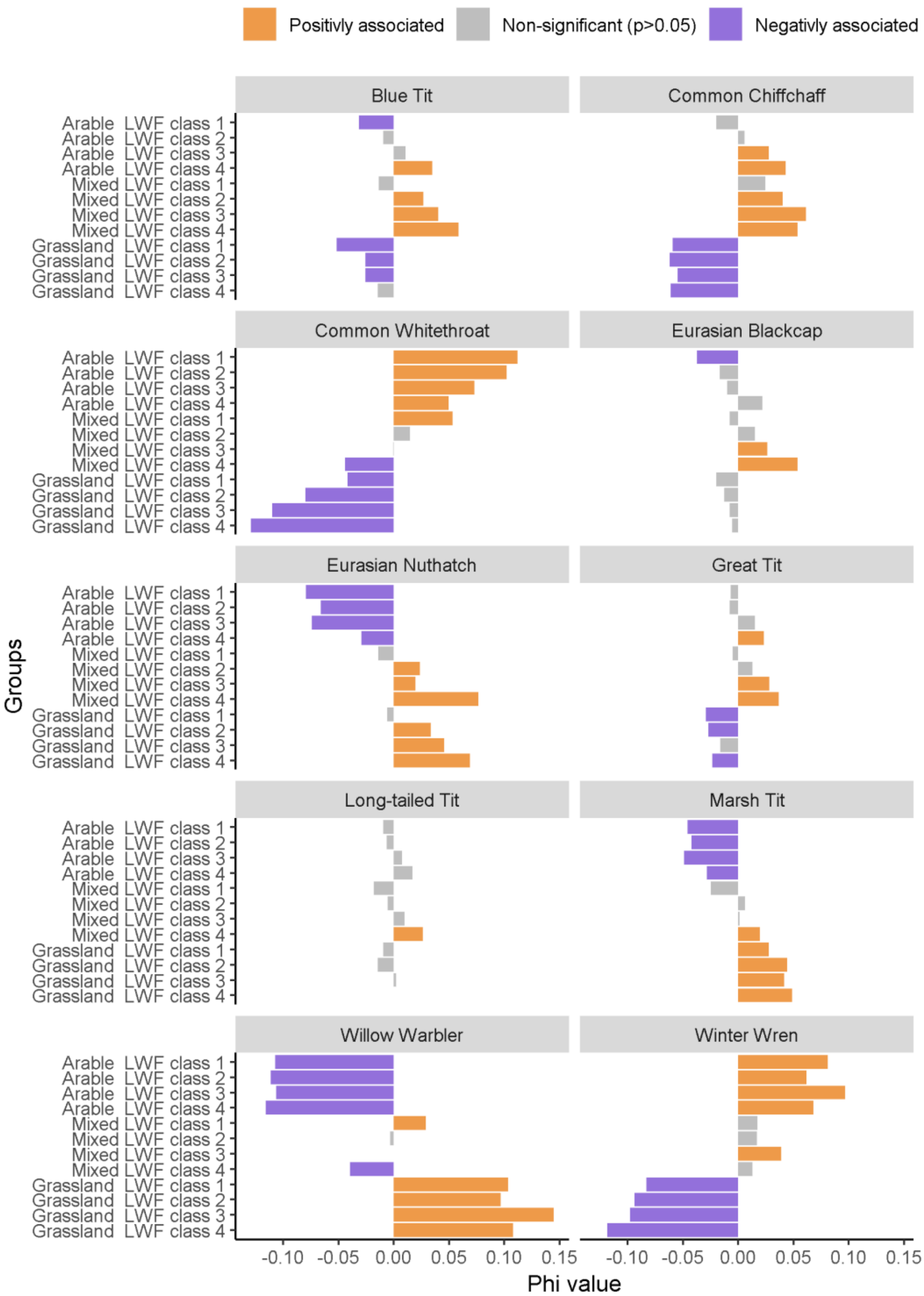

Figure 4. Phi coefficients of association between relative abundance of foliage-gleaning farmland songbirds and combinations of linear woody features (LWF) and land cover in 1446 tetrads. See Fig. 2 for axes labels and further detail.