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ORIGINAL ARTICLE

Habitat correlates of Eurasian Woodcock *Scolopax rusticola* abundance in a declining resident population

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Abstract

In Europe, woodland bird populations have been declining since at least the 1970s, and in Britain, around one third of woodland bird species have undergone declines over this period. Habitat change has been highlighted as a possible cause, but for some species clear evidence of this is lacking owing to an incomplete knowledge of the species' habitat requirements. Here, we analyse national data to explain the variation in abundance of a declining woodland bird, the Eurasian Woodcock. A nationwide, species-specific survey of breeding Woodcock was conducted in 2003 and 2013 at 807 and 823 randomly selected 1-km squares respectively. The counts were compared with a range of landscape-scale habitat variables as well as local habitat measures recorded by surveyors, using generalised linear mixed models. Habitat variables were measured at a variety of spatial scales using ring buffers, although our analyses show that strong collinearity between scales hinders interpretation. At large landscape scales, breeding Woodcock abundance was correlated with total woodland area and the way this interacted with woodland type. Woodcock were more abundant in woods containing a more heterogeneous mix of woodland habitat types and in woods further from urban areas. On a smaller spatial scale, Woodcock were less likely to be found at sites dominated by beech *Fagus* spp. and more likely to occur in woods containing birch *Betula* spp. The Woodcock's association with large, heterogeneous woods and the apparent attractiveness of certain woodland types present the most relevant topics for future research into the role of habitat change in long-term declines.

Keywords Breeding ecology · Spatial scale · Woodland bird · National survey · Ring buffers · Collinearity

Zusammenfassung

Habitatkorrelate der Abundanz der Waldschnepfe *Scolopax rusticola* in einer zurückgehenden Standvogelpopulation

In Europa haben Waldvogelpopulationen spätestens seit den 1970er Jahren abgenommen, und in Großbritannien hat etwa ein Drittel der Waldvogelarten in diesen Zeitraum Bestandsrückgänge erfahren. Als eine mögliche Ursache wurde Habitatveränderung hervorgehoben, aber für einige Arten fehlen hierfür klare Beweise, da das Wissen über ihre Habitatansprüche lückenhaft ist. Hier analysieren wir landesweite Daten, um die Variation in der Abundanz eines im Bestand abnehmenden Waldvogels, der Waldschnepfe, zu erklären. Eine landesweite artspezifische Zählung brütender Waldschnepfen wurde in den Jahren 2003 und 2013 in 807 bzw. 823 zufällig ausgewählten 1-km-Quadraten durchgeführt. Mit Hilfe generalisierter linearer gemischter Modelle wurden die gewonnenen Zahlen mit einer Reihe von Landschafts-Habitatvariablen sowie lokalen Habitatparametern, die von den Gutachtern vor Ort aufgenommen worden waren, verglichen. Habitatvariablen wurden auf mehreren räumlichen Skalen mit Hilfe von Ringpuffern gemessen, wobei unsere Analysen zeigen, dass eine starke Kollinearität zwischen den Skalen die Interpretation erschwert. Auf großräumigen Landschaftsskalen hing die Abundanz brütender Waldschnepfen mit der Gesamtwaldfläche sowie deren Interaktion mit dem

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Waldtyp zusammen. Waldschnepfen kamen häufiger in Wäldern vor, die eine heterogenere Mischung von Waldhabitattypen aufwiesen, sowie in Wäldern, die weiter von Stadtgebieten entfernt waren. Auf einer kleinräumigeren Skala waren Waldschnepfen an von Buchen *Fagus* spp dominierten Standorten seltener anzutreffen und häufiger in Wäldern mit Birken *Betula* spp. Die Assoziation von Waldschnepfen mit großen, heterogenen Wäldern und die offensichtliche Attraktivität gewisser Waldtypen stellen die relevantesten Themen für zukünftige Forschung zur Rolle von Habitatveränderungen bei langfristigen Bestandsrückgängen dar.

Introduction

Approximately one third of woodland bird species breeding in Britain have experienced population declines over the past 40 years (Hewson et al. 2007; DEFRA 2015). While there have been attempts to link declines to woodland habitat change occurring over the course of the last century (Amar et al. 2006; Hewson and Noble 2009), clear evidence of a direct effect remains scarce for most species.

Some declining species are associated with late-stage woodland [Pied Flycatcher *Ficedula hypoleuca,* Common Redstart *Phoenicurus phoenicurus,* Wood Warbler *Phylloscopus sibilatrix* (Smart et al. 2007; Mallord et al. 2012; Goodenough 2014)] while others require early successional deciduous woodlands with dense understoreys [Common Nightingale *Luscinia megarhynchos,* Willow Tit *Poecile montanus* (Fuller and Henderson 1992; Lewis et al. 2009; Holt et al. 2011)]. These types of woodland habitat are among those most threatened by changes to woodland management occurring during the last century (Fuller and Warren 1993; Hopkins and Kirby 2007), but isolating the effect of habitat change is hindered since most studies have focused on a narrow range of study sites, and because many of these species are long-distant migrants, making it difficult to separate the effects of breeding habitat from the unmeasured factors affecting overwinter survival and migration (Goodenough 2014; Mallord et al. 2016).

As a British and Irish breeding species, the Eurasian Woodcock *Scolopax rusticola* (hereafter Woodcock) has experienced a decline since at least 1970 and site occupancy, at the 10×10-km^2 scale, has declined by 56% between 1970 and 2010 (Heward et al. 2015). Similar declines have not been observed in the large, migratory populations that breed in northern Europe (Fokin and Blokhin 2013; Lindström et al. 2015) and overwinter in Britain and Ireland alongside locally breeding residents (Hoodless et al. 2013), suggesting that the causes of recent decline in the resident population are most likely taking effect during the breeding season.

Only a small number of studies have attempted to determine the habitats used by breeding Woodcock (Hirons and Johnson 1987; Hoodless and Hirons 2007; Machado et al. 2008). In the most comprehensive of these, Hoodless and Hirons (2007) used radiotelemetry to study habitat use at two contrasting sites in Derbyshire, central England and Angus, east Scotland. In Derbyshire, young stands of trees with dense ground vegetation were most commonly used for feeding and brood-rearing while more open ground vegetation was preferred for nesting. In Angus, Woodcock tended to use sapling-stage birch *Betula* spp. and birch thickets more frequently than older birch or coniferous woodland (Hoodless and Hirons 2007). Such studies offer an insight into the species' selectivity, but their findings vary depending upon the local characteristics of the chosen study area and cannot consider the full range of potential Woodcock habitats.

Assessing the potential role of habitat change in a species' decline is difficult for those species whose basic ecology is still poorly understood. A large-scale, multisite assessment of a species' abundance in relation to relevant habitat data provides a means of studying basic habitat associations which may be the first step towards identifying causes of decline. Here, we provide this by combining broad measures of woodland area, type and surrounding habitat at multiple spatial scales, with the results of two national, species-specific surveys of breeding Woodcock in Britain. We separately model habitat associations in 2003 and 2013 to assess how declines over this period may be shaping correlations with habitat. By identifying the habitat characteristics with which Woodcock are most commonly associated, and how this changes with time, this study provides a firmer basis for future research into the causes of recent population declines.

Methods

Woodcock surveys

In 2003, Woodcock abundance was assessed at 807 randomly selected 1×1-km British ('Ordnance Survey') national grid squares across Britain (England, Wales and Scotland), using counts of displaying ('roding') males (Hoodless et al. 2009). In 2013, identical surveys were conducted at 823 randomly selected (see below) 1×1-km survey squares, 544 of which were repeats of survey squares visited in 2003 (Heward et al. 2015).

All British national grid squares containing more than 10 ha of woodland were assigned to one of four woodland size classes based on their total wooded area (10–30, 31–50,

51–70, 71–100 ha) and one of 11 regions (Supplementary appendix, Fig. S1). These regions were delineated so that they each contained equal proportions of the four woodland size classes while maintaining logical geographic divisions. Survey squares were then randomly selected using a random number generator, with the number selected per region being based upon the number of potential surveyors (BTO members). Randomly selected squares had to be at least 3 km apart from centre to centre to maintain their independence (roding ranges are typically around 43–132 ha; Hirons et al. 1980). In this way, a list of 2677 random squares was generated, from which volunteer observers, consisting largely of non-professional birdwatchers, were able to select sites to survey. Because the number of squares available was adjusted for the number of potential observers, regional coverage was not biased towards areas that are densely populated.

Observers were provided with instructions to identify a suitable count point within their chosen square and if sites from the 2003 survey were repeated, the observer was given the grid reference for the original count point and asked to revisit it. Observers were permitted to deviate from the 2003 count point if changes to the surrounding vegetation meant that it no longer met the requirements specified above, or if access to the original count point could not be obtained.

Up to three dusk surveys, each 60 min in length and at least 7 days apart, were conducted in May–June when roding behaviour is at its peak (Hoodless et al. 2006). A small number of occupied sites were only visited once (8% in 2003, less than 1% in 2013) or twice (10% in 2003, 11% in 2013), and at sites where Woodcock were absent on the first two surveys, the third was not obligatory. Surveys were not conducted during persistent rain or if the wind exceeded Beaufort scale 3. For observers without prior experience of roding Woodcock, recordings of typical Woodcock calls were provided online (British Trust for Ornithology 2013). Each separate Woodcock seen or heard was noted. The survey methodology, interpretation and limitations are covered in greater detail in Hoodless et al. (2009) and Heward et al. (2015).

Observers also made a simple assessment of vegetation composition and structure within a 200-m radius of the count point during a visit made between 15th May and 15th June. A recording form, containing clear instructions and a worked example, was provided to yield consistent records. Observers were asked to estimate, with the help of a large-scale map or aerial photograph, the proportion of closed canopy woodland, open space within woodland (tracks/clearings) and non-woodland habitats (arable land/water bodies) within 200 m of their count point (to the nearest 5%). Observers were then asked to divide the area of closed canopy woodland into stands based upon tree age or type, and record the predominant tree type, the stand age [establishing (< 2 m height)/intermediate (2–5 m)/mature (> 5 m)] and the proportion of the 200-m buffer occupied by each stand. All observers were provided with online web resources for tree identification. A copy of the recording form can be viewed online (British Trust for Ornithology 2013).

Landscape-scale habitat variables

For each count point, three types of buffer were created: a circular buffer with a 1-km radius (3.1 km^2), a circular buffer with a 2-km radius (12.6 km^2) and a 2-km ring buffer (i.e. the 2-km radius circular buffer with the 1-km buffer removed from its centre, 9.4 km^2). A ring buffer was selected in an attempt to reduce the high levels of collinearity associated with concentric circular buffers and the repetition of their core area (Schneider et al. 2011), although the effectiveness of this measure was tested and is presented in the results.

The 1-km radius was selected on the basis of the movements of radio-tagged Woodcock described by Hoodless and Hirons (2007); the largest distances travelled in this study were to reach nocturnal foraging sites and averaged 1005 ± 612 m (1 sd). Hirons (1980) found that displaying males roded over areas between 0.34 and 1.32 km^2, around a quarter of the area covered by a 1-km buffer, but these roding areas averaged approximately 2250 m across their longest axis. Roding behaviour and flights to nocturnal foraging sites represent the largest movements made by Woodcock during the breeding season (Hirons 1980; Hoodless and Hirons 2007), so most individuals spend the entire breeding season within a range of these dimensions or smaller. The 2-km ring buffer was used to consider how relationships with habitat occurring within a 1-km buffer may be reflective of larger landscape-scale patterns. Buffers larger than 2 km could not be used because overlaps with buffers of neighbouring count points became more frequent and greater in area when they exceeded this size. The distribution of count points within selected survey squares meant that no 1-km buffers overlapped in 2003 and only one pair slightly overlapped in 2013. For 2-km ring buffers, 66% of buffers had no overlaps. Among those that did overlap, the average overlap between pairs of neighbours was 11.1 ± 8.3% (1 sd) in 2003 and 11.1 ± 8.2% (1 sd) in 2013. No pair overlapped by more than 26%.

Data relating to woodland area and type were extracted from the Forestry Commission's National Inventory of Woodland and Trees (NIWT) (2003) and the 2013 National Forest Inventory (NFI). At both buffer sizes, the total area of woodland was extracted along with areas of broadleaved, coniferous and mixed woodland and 'open space' within woodland. The last of these was a composite of bare ground, felled woodland, land prepared for planting, grass within woodland and 'young' trees i.e. those that are too small to be classified using the NFI's satellite photography classification

technique. The area of each woodland habitat was divided by the total wooded area to provide a proportional figure. Other habitat categories recorded by the NFI, such as coppiced woodland or shrubby cover, could not be included because of a low rate of occurrence at surveyed sites, but were incorporated into an index of woodland heterogeneity. For both buffer sizes, this measure of heterogeneity was calculated using an index comparable to Simpson's index of diversity (D):

$$D = 1 - \sum (n/N)^2$$

where n is the area of each woodland category and N is the total area of woodland within the buffer.

Broader measures of non-woodland land use were obtained from CEH Land Cover Map (LCM) 2000 (Fuller et al. 2002) for the 2003 count points and LCM 2007 (Morton et al. 2014) for the 2013 points. The LCM 2000 and LCM 2007 are raster maps that assign each 25 × 25-m cell a habitat type using satellite imagery.

Total 'urban' area was extracted at both buffer sizes using a combination of the urban and suburban LCM categories. We also measured distance to the nearest continuous 'urban' area greater than 50 ha, which was not confined by the limits of the buffer. The proportion of the buffer occupied by grassland was extracted at both buffer sizes using a composite of the improved, rough, neutral, calcareous and acid grassland LCM categories. The LCM was also used to calculate the area of the individual woodland block in which the survey was conducted (wood block size), by counting the number of contiguous 25 × 25-m cells containing woodland.

Deer have a significant effect on the structure and floristic composition of woodland habitats (Gill and Fuller 2007). Deer abundance data were obtained from the Game and Wildlife Conservation Trust's (GWCT) National Gamebag Census (NGC) (Aebischer et al. 2011). The NGC provides a measure of relative abundance for a range of mammals that are either hunted as game species or legally controlled as pests. Estimates of abundance are derived from annual bags for each species from 900 sites nationally and provide a reasonable proxy for the relative abundance of live animals (Noble et al. 2012).

The relative abundances of three deer species were extracted at each count point from a raster map that provided smoothed values based on all NGC submissions in the surrounding 35-km radius (Noble et al. 2012). The species considered were European Roe Deer *Capreolus capreolus*, Fallow Deer *Dama dama*, and Reeves' Muntjac *Muntiacus reevesi*. Red Deer *Cervus elaphus* and Sika Deer *Cervus nippon* were also initially considered, but because they were completely absent from more than 70% and more than 85% of squares respectively in 2003, models failed to converge. Deer data averaged over the periods 1995–1999 and 2005–2009 were used for surveys conducted in 2003 and 2013 respectively. More details of the NGC methodology can be found in Noble et al. (2012).

Analysis of Woodcock abundance in relation to landscape-scale habitat variables

Pearson's correlation tests were used to identify collinearity between the 1- and 2-km scales for variables measured with both buffer sizes. The 1-km circular buffers were compared to 2-km ring and 2-km circular buffers to assess how effective this measure was at reducing collinearity.

The data were analysed using four generalised linear mixed models (GLMMs), analysing each of the 2 years and two spatial scales separately. Different models were created for 2003 and 2013 because Woodcock declines in the intervening period were expected to affect habitat associations. It was hoped that analysing data from both survey years may reveal something about the causes of decline. Separately analysing each year, rather than directly analysing change in Woodcock abundance, was expected to produce fairer results; only 544 sites (of over 800) were surveyed in both years, so analysing change would have meant a large reduction in sample size. The 1- and 2-km scale data were analysed separately with the collinearity tests described above providing the rationale for this approach (see "Results"). Variables which did not vary with scale, such as the distance from urban area and deer abundance, were included in all four models.

Woodcock count data were analysed using GLMMs with a Poisson distribution and a logarithmic link function in R (R Development Core Team 2016). The glmmPQL function from the MASS package (Venables and Ripley 2002) was used, which fits GLMMs using penalised quasi-likelihood (PQL) estimation and accounts for overdispersion. Because of the underlying spatial nature of our data arising from the geographic distribution of woodland within Britain, an exponential correlation structure was specified on the basis of the latitude and longitude of each count point.

A preliminary Pearson's correlation test showed negative collinearity between the proportions of broadleaved and coniferous woodland ($r = -0.72$ in 2003 and $r = -0.91$ in 2013 for 1-km buffers and $r = -0.73$ in 2003 and $r = -0.90$ in 2013 for 2-km ring buffers) (Fig. 1). Because of this, only the proportion of broadleaf was included in the final model, but an equivalent model in which broadleaf was replaced by conifer was trialled, and is discussed.

The dependent variable was the total number of Woodcock registrations recorded across all visits, with the natural logarithm of the number of visits included as an offset to account for sites which did not receive three visits. Twelve fixed effects were considered (Supplementary appendix, Table S1) along with three pairwise interactions between the

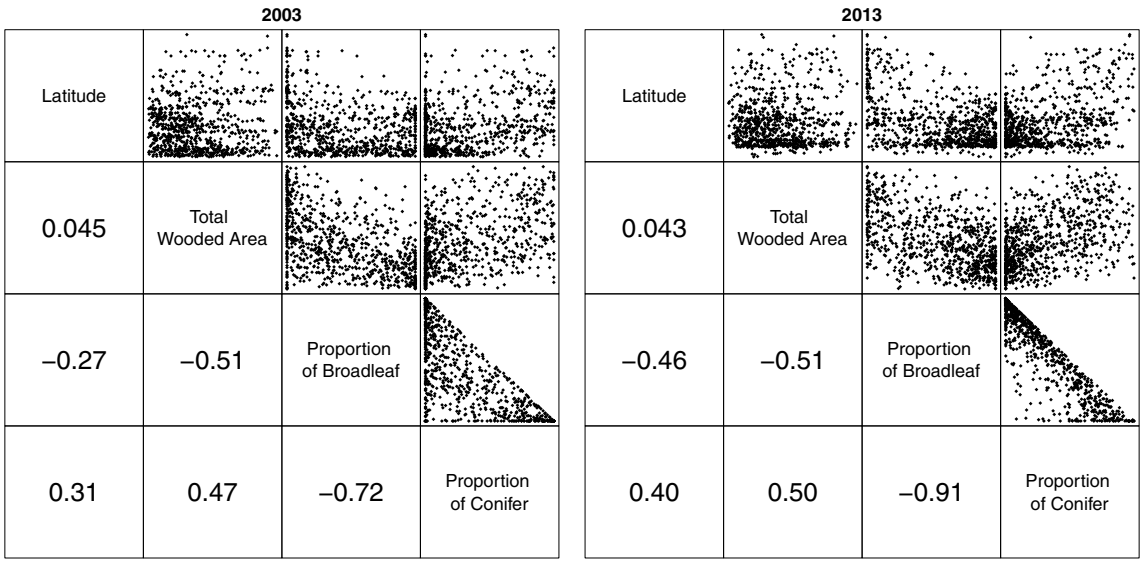

Fig. 1 Collinearity plots between three model variables measured across Britain at the 1-km buffer scale (total wooded area, proportion of broadleaved woodland, proportion of coniferous woodland) and latitude. Pearson's correlation values are provided in the lower panels. Figure produced in R

total wooded area, the proportion of broadleaved woodland and of open habitat within woodland. Region was included as a random effect and was defined by the 11 regions that are intrinsic to the Breeding Woodcock Survey stratification (Hoodless et al. 2009). We present results from the maximal models, as these account for the relative effect of all habitat variables tested.

Analysis of fine-scale survey site data

Using the habitat data gathered by observers, we created five explanatory variables for each count point: (1) the proportion of the 200-m buffer occupied by closed canopy woodland, (2) the proportion of the total wooded area occupied by open woodland habitats, (3) the proportion of closed canopy woodland in which stands contained establishing trees (those under 2 m), (4) a simplified 'predominant tree' type based on seven rudimentary groups (Table 1) and (5) a binary variable indicating the presence/absence of at least one birch-dominated stand. If a single dominant tree type made up more than 50% of the closed woodland within the buffer, this was considered the predominant tree type, which was otherwise classified as 'various'.

These data were analysed using a binomial GLMM in which Woodcock presence was the dependent variable, region was specified as a random effect and the five variables listed above were used as fixed effects. The log number of visits was included as an offset since some sites received fewer than the recommended three visits. The analysis was performed in R using the MASS package.

Table 1 Percentage of sites occupied by Woodcock in Britain (England, Scotland & Wales) in 2013 in relation to dominant tree type

	Surveyed	Occupied (%)	Estimate	SE	*P* value
Beech *Fagus* spp.	37	16.2	–	–	–
Oak *Quercus* spp. (inc. oak-birch)	158	32.9	0.899	0.428	0.036
Wet woodland	65	52.3	1.262	0.454	0.006
Other broadleaf	117	9.4	0.066	0.487	0.892
Sitka Spruce *Picea sitchensis*	54	44.4	1.335	0.460	0.004
Other conifer	141	45.4	1.200	0.339	0.005
Mixed woodland	81	29.6	1.003	0.446	0.025
Various	36	41.7	0.958	0.476	0.045
Total	689	33.4			

'Mixed woodland' refers to sites where an intimate mix of broadleaf and conifer dominate. 'Various' refers to sites where no single woodland type makes up at least 50% of the wooded area. Test statistics from the fine-scale vegetation GLMM compare predominant woodland type to Beech

Results

Collinearity across spatial scales

The Pearson's correlation tests showed strong collinearity between 1- and 2-km circular buffers for all habitat variables (r = between 0.81 and 0.94; Table 2). Using 2-km ring buffers did reduce collinearity (r = between 0.48 and 0.88), particularly for habitat variables that are less common (e.g. open space within woodland). However, this precaution was not effective enough to justify including data for 1- and 2-km ring buffers in the same GLMMs. In preliminary models where this was attempted, most woodland habitat variables were deemed non-significant at both scales, even those, such as total woodland area, that were highly significant when included singly. When tested in separate 1- and 2-km ring buffer models, woodland variables showed consistent relationships with Woodcock abundance, with the scale that variables were measured having little effect on correlation strength or standard errors.

Table 2 Collinearity between the two spatial scales for eight woodland habitat variables in Britain

		2003		2013	
		Circular 2-km buffer	Ring 2-km buffer	Circular 2-km buffer	Ring 2-km buffer
Broadleaf	1-km buffer	0.92	0.74	0.94	0.82
Conifer	1-km buffer	0.94	0.81	0.94	0.81
Mixed	1-km buffer	0.85	0.56	0.85	0.48
Open space	1-km buffer	0.9	0.68	0.85	0.61
Total woodland	1-km buffer	0.9	0.8	0.88	0.88
Heterogeneity	1-km buffer	0.81	0.81	0.82	0.57
Grassland	1-km buffer	0.9	0.85	0.87	0.81
Urban area	1-km buffer	0.9	0.84	0.86	0.78

The r values were produced using Pearson's correlation test and compare the area of each variable within 1-km radius buffers to 2-km circular buffers and 2-km ring buffers

Landscape-scale analysis of habitat data

Woodland variables

At the 1-km scale, Woodcock abundance was influenced by the interaction between total woodland area and the proportion of broadleaved woodland ($P < 0.001$ in 2003 and $P = 0.026$ in 2013; Table 3). This meant that Woodcock abundance showed a positive correlation with the proportion of broadleaved woodland when the total area of woodland within the buffer was high, but negative when total woodland area was low (Fig. 2). There appeared to be a positive association between woodland heterogeneity and Woodcock abundance in both years, although this was slightly outside of the 95% confidence interval in 2013 (2003: $P = 0.003$, 2013 and $P = 0.054$).

Broadly consistent results were recorded at the 2-km ring buffer scale. The same relationship with the interaction between total woodland area and the proportion of broadleaved woodland was observed in both years ($P < 0.005$) along with a positive relationship with woodland heterogeneity ($P = 0.036$ in 2003, $P = 0.002$ in 2013). In addition,

Table 3 Results of four GLMMs used to assess the relationship between Woodcock abundance in Britain and 15 variables (12 habitat characteristics and 3 interactions)

	2003 1-km buffer			2003 2-km ring buffer			2013 1-km buffer			2013 2-km ring buffer		
	Estimate	SE	P value	Estimate	SE	P value	Estimate	SE	P value	Estimate	SE	P value
Total woodland area	**0.5047**	**0.0587**	**< 0.001**	**0.5173**	**0.0750**	**< 0.001**	**0.5346**	**0.0836**	**< 0.001**	**0.5610**	**0.0860**	**< 0.001**
Woodland heterogeneity	**0.1780**	**0.0604**	**0.0033**	**0.1406**	**0.0670**	**0.0360**	0.1800	0.0931	0.0537	**0.3443**	**0.1078**	**0.0015**
Mixed woodland	0.0752	0.0524	0.1518	0.0537	0.0586	0.3602	−0.0533	0.0872	0.5410	**−0.2655**	**0.0965**	**0.0061**
Open woodland	−0.2267	0.1326	0.0877	−0.1815	0.1163	0.1189	−0.0960	0.1404	0.4942	**−0.3218**	**0.1353**	**0.0176**
Urban area	−0.0819	0.0621	0.1878	−0.1972	**0.0768**	**0.0104**	−0.0643	0.0918	0.4838	−0.1449	0.0947	0.1265
Broadleaf × total wood	**0.2594**	**0.0578**	**< 0.001**	**0.2153**	**0.0675**	**0.0015**	**0.1851**	**0.0832**	**0.0263**	**0.2560**	**0.0853**	**0.0028**
Distance from urban area	**0.1265**	**0.0620**	**0.0418**	0.1036	0.0677	0.1266	**0.2061**	**0.0639**	**0.0013**	**0.1635**	**0.0605**	**0.0070**
Roe Deer	**0.2685**	**0.0741**	**0.0003**	**0.2885**	**0.0759**	**0.0002**	0.1418	0.0924	0.1252	0.1549	0.0893	0.0833

Results are taken from maximal models, but only variables exhibiting a significant relationship with Woodcock abundance in one or more models are included in the table. Sections in bold indicate the models in which $P < 0.05$. For those that are not listed, see Supplementary Table S1. The five variables and one interaction in the upper sections of the table were measured at two different spatial scales. Variables which did not vary with scale (e.g. Roe deer / Distance to urban area) were included in both the 1- and 2-km ring models

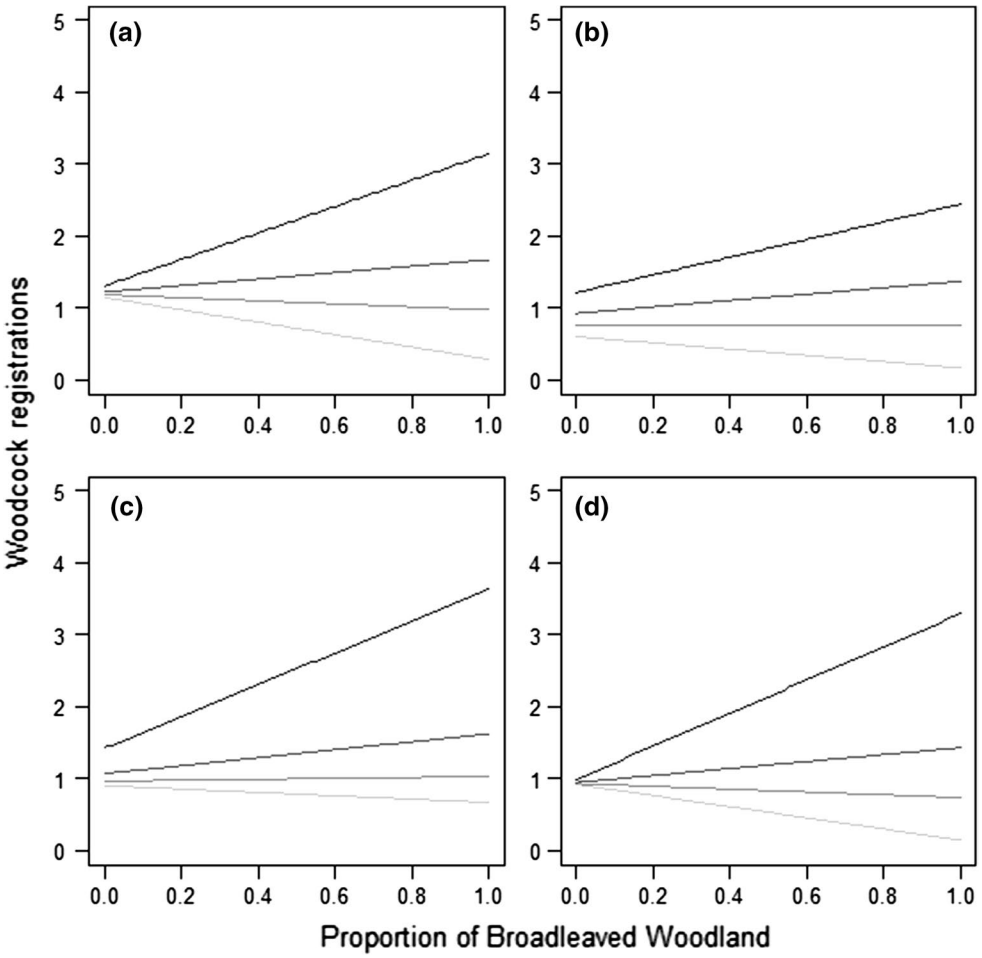

Fig. 2 Interaction between the proportion of broadleaved woodland and total wooded area in Britain plotted using model coefficients from the **a** 2003 1-km GLMM, **b** 2013 1-km GLMM, **c** 2003 2-km GLMM, **d** 2013 2-km GLMM. Woodland area is divided on the basis of sample quartiles and displayed as four separate lines (lightest grey = lowest wooded area, darkest grey = highest wooded area). Figure produced in R

the 2013 2-km ring buffer model found a negative relationship with the proportion of open habitat within woodland ($P = 0.018$) and with the proportion of mixed woodland ($P = 0.006$).

Substituting the broadleaved variable for the collinear coniferous variable made few qualitative differences to the models' outcomes regardless of scale. Similar interactions were observed between conifer and total woodland, but the slopes were mirrored versions of those seen for broadleaf.

Other habitat variables

In 2003, there was a significant negative relationship between Woodcock abundance and the proportion of the buffer occupied by urban habitat at the 2-km scale ($P = 0.010$). In the other three models, Woodcock abundance was greater in woods further from urban areas ($P < 0.05$ in all three, Table 3).

No relationship was observed with the grassland variable at any spatial scale. Woodcock abundance was positively correlated with Roe Deer abundance but only in the 2003 models ($P < 0.001$, Table 3).

Influence of fine-scale habitat on Woodcock occurrence

Among the fine-scale habitat variables measured within a 200-m buffer of the count point, four were identified as significantly related to Woodcock occurrence. Woodcock were more likely to be present at sites where a larger area was occupied by closed canopy woodland (slope = 0.021, $T = 4.281$, $P < 0.001$) and at sites where a proportionally greater area of open space was available within the buffer's woodland (slope = 2.051, $T = 3.226$, $P = 0.001$). Predominant tree type had a significant effect on Woodcock presence (Table 1). The lowest site occupancy was recorded in the Beech and the 'other broadleaf' categories (16% and 9% respectively), and was highest in wet woodland (52.3%), Sitka spruce (44.4%), other conifer (45.4%) and the 'various' category (41.7%) i.e. woodland in which a single tree type did not predominate. Woodcock occurred more frequently at sites where one or more woodland stand was dominated by birch (slope = 0.916, $T = 0.279$, $P = 0.001$).

Discussion

Interactions between woodland type and area

The most consistent correlates of Woodcock abundance were the proportion of broadleaf/coniferous woodland and total wooded area, and specifically the interaction between the two. A relationship with woodland size was to be expected; Woodcock declines recorded by the Bird Atlas (Balmer et al. 2013) show a retraction of the British breeding population towards more heavily wooded regions. We did not find a significant relationship with the size of the woodland block in which the survey was conducted, which suggests that wider availability of woodland within the landscape is more important.

Higher numbers of well-connected woodland patches in the landscape may allow male Woodcock to access larger or more efficient roding grounds. Woodcock density and roding activity are known to correlate in a non-linear fashion (Hoodless et al. 2008) suggesting that social interaction, which would be more common in larger woods, may be a stimulus for display. Ring recoveries of Woodcock show that natal dispersal distances are typically short [76% of Woodcock ringed as chicks were recovered within 10 km of their natal site (Hoodless and Coulson 1994)] and large inter-wood distances may reduce the ease of movement between isolated but otherwise suitable woods.

Given that the most heavily wooded landscapes in Britain tend to be dominated by conifer species, the interaction with the proportion of broadleaved woodland might at first appear to be an artefact of the strong relationship with woodland area. The collinearity plots (Fig. 1), however, suggest that our sample includes enough heavily wooded areas dominated by broadleaved trees for our model to separate the respective influence of each variable.

For most surveyed sites, both coniferous and broadleaved woods occurred within the 1-km buffer; and while many areas with extensive woodland cover are conifer-dominated, it may be that among these, abundances tend to be higher in areas where these conifers are frequently interspersed with stands of broadleaved trees. This observation appears to be supported by the Woodcock's association with more heterogenous woodlands and by an existing radio-tracking study (Hoodless and Hirons 2007) which found that Woodcock living in predominantly coniferous woods used home ranges with high proportions of young birch woodland relative to its availability.

The value of broadleaved woodlands likely depends on the exact species in question. Broadleaved species such as Beech were associated with low Woodcock occurrence in our fine-scale analysis, probably because Beech leaves are less palatable to detritivorous invertebrates (Hendriksen 1990), and because Beech typically occur in areas with dry soils and allow only sparse ground vegetation. Birch woods, on the other hand, provide increased soil penetrability owing to wetter soils and have leaves that decompose relatively quickly (Cornelissen 1996), potentially resulting in higher earthworm abundance under birch litter particularly compared to coniferous woods. Dense stands of young birch may also provide protection from predators for foraging or roosting Woodcock (Hoodless and Hirons 2007).

Landscape-scale associations: woodland type and heterogeneity

Increased heterogeneity of woodland habitats was generally associated with higher Woodcock abundance, despite the very broad woodland categories used to calculate this index. As described above, the association with heterogeneous woods may reflect the relative importance of broadleaf in conifer-dominated landscapes, but high heterogeneity should also provide more suitable breeding sites as a range of habitats are required through the different stages of the breeding cycle (Hoodless and Hirons 2007). Changes to woodland management practices over the course of the last century (e.g. reduction of coppicing, monocultural forestry) have reduced the areas of open and young woodland habitats and produced woods that are less heterogenous in terms of tree age and structure (Fuller and Warren 1993; Fuller et al. 2007; Hopkins and Kirby 2007). Open areas may be used as nocturnal feeding sites and are visited by roding male Woodcock when searching for females, while young woodlands, where trees are smaller and closer together, are used by females foraging with young (Hoodless and Hirons 2007). Young woodlands, with a high density of trees under a 7.6-cm diameter (1400–4500 per ha) are important breeding habitat for American Woodcock (*Scolopax minor*) (Dessecker and McAuley 2001) which have a similar ecology and diet to their Eurasian counterpart.

Our analysis does not include an accurate measure of young woodland at the landscape scale but the open space category, which includes areas prepared for planting and freshly planted trees, ought to indicate that the management required to maintain young woodlands is in place. This variable showed either no correlation, or, in one model, a negative correlation with Woodcock abundance. The establishing woodland variable included in the fine-scale analysis, which records the proportion of stands containing trees under 2 m in height, also showed no significant correlation. These findings may contradict what little information we already have about Woodcock breeding habitat but are based on crude measures of young and open woodland that may not be sensitive enough to reveal subtle relationships. Confirming any potential relationship with young woodlands will require

more accurate measures of woodland age than are currently available on a national scale.

Other factors influencing Woodcock abundance

Woodcock abundance showed a negative association with urban area or proximity to human settlements. Assuming this is correlated with human activity, disturbance is likely to be having a negative effect on Woodcock breeding success by increasing desertion or the risk of nest predation through more frequent flushing of adults, or directly through predation of nests by domestic pets (Langston et al. 2007; Coppes et al. 2017). It is sensible to assume that these factors could affect most ground-nesting species, but the effect of disturbance can be difficult to demonstrate explicitly without monitoring the fate of a large sample of nests.

The relative abundance of Roe Deer was positively correlated with Woodcock abundance in 2003, which seems to be at odds with existing research identifying a negative effect of unnaturally high deer densities upon woodland birds (Gill and Fuller 2007). It seems unlikely that this relationship was directly causal and is more likely to be the product of an underlying geographic covariate. Opposing population trends over the course of the next 10 years meant that this pattern was no longer apparent by 2013.

Suggestions for future research

Our analysis shows that the current distribution of breeding Woodcock in Britain correlates with several woodland habitat variables; chiefly the availability of large, well-connected and heterogeneous woods. The once widespread British distribution of the Woodcock shows that there is no inherent dependency upon large woods or particular woodland types, but that many smaller, particularly lowland, sites have apparently become unsuitable over the latter half of the twentieth century (Sharrock 1977; Balmer et al. 2013).

It is possible that there are underlying links between these variables and woodland management, whether it be the decline of active management in lowland deciduous woods or the management strategies associated with commercial forestry in the uplands. Investigating the role of management in the maintenance or creation of suitable habitat seems a logical next step. This should not only compare between areas where active management is present and absent, but also between different management techniques and stages within the timber rotation period. This line of enquiry should clarify whether young woodland is important to breeding Woodcock.

Changes to woodland habitats are not the only factors associated with Woodcock abundance and other variables may be having an equally large influence on recent declines: disturbance, nest and chick predation and increased severity of wet summers could all reduce breeding success while hunting and severe winter weather may affect overwinter survival. A comprehensive study that considers these additional factors alongside the habitat variables highlighted here would be required to fully understand the causes of recent Woodcock declines. This could be complemented by radio-tracking studies of resident British Woodcock that compare productivity and adult survival in woods supporting high and low Woodcock densities.

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