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DESCRIBING HABITAT OCCUPATION BY WOODLAND BIRDS WITH TERRITORY MAPPING AND REMOTELY SENSED DATA: AN EXAMPLE USING THE MARSH TIT (*POECILE PALUSTRIS*)

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Abstract. Changes in the structure of woodlands and forests, caused by shifts in management, stand maturity, and composition, have been implicated in the population decline of some bird species in Europe and North America. One such species is the Marsh Tit (*Poecile palustris*). We investigated relationships between Marsh Tit occupation (derived from territory mapping) and vegetation structure, tree species composition, and proximity to woodland edge in a British woodland, using a combination of 5 years of occupation data and high-resolution (0.5 and 1 m), large-scale (155 ha) habitat models derived from remote sensing. The results demonstrated that Marsh Tit occupation was linked to vegetation characteristics through the woodland's full vertical profile and related significantly and positively with overstory height, tree canopy closure, and the coverage of understory vegetation below the overstory. Marsh Tit occupation was lower within 50 m of the woodland perimeter, where habitat structure was less favorable than in the woodland interior. No preference was shown for areas rich in any particular prevalent tree species. Our results suggest that widespread changes in woodland structure resulting from abandonment by managers are unlikely to be responsible for the decline of the Marsh Tit in Britain and that reintroduction of active management that prevents woodland maturation could be detrimental to remaining populations. The study demonstrates a novel approach to integrating territory maps and remote-sensing data to permit highly detailed analyses of bird–habitat interactions and may have wider implications for woodland management and related bird species.

Key words: *habitat, LiDAR, Marsh Tit*, Poecile palustris, *remote sensing, woodland.*

Descripción de la Ocupación de Hábitat por Aves de Bosque a partir de Mapeo Territorial y Datos de Detección Remota: Un Ejemplo con Poecile palustris

Resumen. Los cambios en la estructura del bosque, causados por cambios en manejo, madurez del rodal y composición, han sido vinculados a la disminución de las poblaciones de algunas especies de aves de Europa y América del Norte. Una de estas especies es *Poecile palustris*. Investigamos la relación entre la ocupación de *P. palustris* (obtenida por mapeo territorial) y la estructura de la vegetación, la composición de especies de árboles y la proximidad al borde del bosque en un bosque británico, usando una combinación de datos de ocupación de cinco años y modelos de hábitat de alta resolución (0.5 y 1 m) y de gran escala (155 ha) derivados de detección remota. Los resultados demostraron que la ocupación de *P. palustris* estuvo ligada a las características de la vegetación a través de todo el perfil vertical del bosque y relacionada significativa y positivamente con la altura del estrato superior, la cobertura del dosel y la cobertura del sotobosque debajo del dosel. La ocupación de *P. palustris* fue menor dentro de los 50 m del perímetro del bosque, donde la estructura del hábitat fue menos favorable que en el interior del bosque. No se observó una preferencia por áreas dominadas por alguna especie de árbol en particular. Nuestros resultados sugieren que los cambios extendidos en la estructura del bosque que resultan de la falta de gestión probablemente no son responsables de la disminución de *P. palustris* en Gran Bretaña y que la reintroducción de un manejo activo que impida la maduración del bosque podría ser negativa para las poblaciones remanentes. Este estudio propone un enfoque novedoso para integrar mapas territoriales y datos de detección remota que permite realizar análisis muy detallados de interacciones entre aves y hábitat y que puede tener amplias implicancias para el manejo del bosque y las especies de aves correspondientes.

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INTRODUCTION

Habitat selection is a hierarchical process of behavioral responses that results in a use of resources out of proportion to their availability, influencing the fitness and survival of individuals (Jones 2001). The study of occupation patterns is a common approach to identify variation in habitat quality for birds (Johnson 2007) and typically involves the measurement or classification of vegetation structure or composition (e.g., Wilson et al. 2005, Arriero et al. 2006). Characterizing forest or woodland vegetation can be problematic, however, because of the strongly heterogeneous and three-dimensional environment (Hinsley et al. 2002, 2006). Data-collection methods for describing woodlands are often restricted to ground-based techniques of limited spatial extent (e.g., sample plots: Barg et al. 2006, Amar et al. 2010), or broad categorizations of tree species or age composition (Mazur et al. 1998, van Oort and Otter 2005), rather than the use of fine-grained, three-dimensional datasets at the landscape scale. In complex environments such as woodland, extrapolation of localized sampling and use of broad-scale categorization may not adequately describe habitat at a spatial resolution relevant to the individual birds or population concerned, and it may preclude detailed investigations of structural heterogeneity (Hinsley et al. 2008).

The use of remote sensing methods, such as light detection and ranging (LiDAR), can overcome some of these difficulties by providing landscape-scale data (>10 ha, Bradbury et al. 2005) at high spatial resolution (Vierling et al. 2008). LiDAR is particularly suitable for the detailed spatial modeling of woodlands, with the capacity to quantify the canopy surface and also the understory beneath (Hill and Broughton 2009, Martinuzzi et al. 2009). Optical imagery, derived from satellite or airborne multispectral scanners, has also been used to characterize broad-scale vegetation types (Laurent et al. 2005), yet there have been few attempts to integrate different sources of remote-sensing data for analyses of bird habitat (Goetz et al. 2010).

Populations of many forest and woodland birds have declined in the temperate and boreal regions of Europe and North America; the decline has been linked to habitat changes resulting from forest management (Holmes and Sherry 2001, Imbeau et al. 2001, Amar et al. 2006). Several species of forest-dwelling parids of the genus *Poecile* are included in this group, namely, the Gray-headed Chickadee (*P. cinctus*), Willow Tit (*P. montanus*), and Boreal Chickadee (*P. hudsonicus*), which have responded negatively to management such as logging and thinning (Virkkala 1990, Siffczyk et al. 2003, Hadley and Desrochers 2008). The Marsh Tit (*P. palustris*) has also declined throughout much of its European range, although the reasons for this are poorly understood (Burfield and van Bommel 2004, Fuller et al. 2005).

The Marsh Tit is a 10- to 12-g cavity-nesting passerine of deciduous woodland, feeding on seeds and invertebrates largely gleaned from trees and shrubs. Pairs are socially monogamous and sedentary within a home range throughout the year, in spring defending a large (average 4–6 ha) and exclusive breeding territory that is selected by males (Gosler and Clement 2007, Broughton et al. 2012). In Britain, where Marsh Tit abundance fell by 71% between 1967 and 2008 (Baillie et al. 2010), widespread abandonment of woodland management has been suggested as a possible factor in the species' decline, by allowing unfavorable changes in habitat structure through woodland maturation (Fuller 2005, Amar et al. 2006). Although the decline of the British Marsh Tit coincided with a reduction in woodland management (Mason 2007), previous work has variously identified increased woodland canopy height, canopy cover, and understory density as important factors influencing Marsh Tit occupation (Broughton et al. 2006, Hinsley et al. 2007, Carpenter et al. 2010), and some of these elements may have actually increased as a result of maturation (Mason 2007). However, previous studies have been inconsistent with regard to which habitat features they identified as important to the Marsh Tit, whether features of understory (Hinsley et al. 2007), tree canopy (Broughton et al. 2006), or both (Carpenter et al. 2010). This inconsistency may have resulted from limited spatial and/or temporal resolution, present in all studies, and sufficient detail in descriptions of occupation patterns and the structural complexity of habitat. Such uncertainty has implications for habitat management, because if Marsh Tits select for attributes of the understory rather than tree canopy, then active management of woodlands that arrests maturation through cropping or thinning of the canopy may benefit both understory vegetation and Marsh Tits (Fuller et al. 2005). Conversely, if Marsh Tits have an overriding preference for a mature canopy then such interventions may be counterproductive. Marsh Tits may also be sensitive to the proximity of woodland edge (Hewson and Fuller 2006), yet no study has attempted to investigate the combined roles of woodland canopy and understory structure and edge effects in relation to Marsh Tit occupation.

In this study, we use a novel combination of fine-scale, airborne LiDAR-derived models of an entire woodland canopy, overstory, and understory layers (Hill and Broughton 2009), airborne multi-spectral classification of the species composition of overstory trees (Hill et al. 2010), and 5 years of Marsh Tit occupation data, derived from territory mapping. Employing these comprehensive, high-resolution datasets, we aim to improve the understanding of the Marsh Tit's habitat preferences, inform conservation policy, and aid interpretation of the species' decline. The combined application of such detailed, long-term, landscape-scale datasets on occupation and vegetation is unprecedented in woodland bird research, and it serves as

a case study for the analysis of spatial data on a species and its habitat.

METHODS

STUDY AREA

The study site was 155 ha of woodland at the Monks Wood National Nature Reserve in Cambridgeshire, UK (52° 24′ N, 0° 14′ W). Monks Wood is a discrete patch of semi-natural lowland woodland, dominated by Common Ash (*Fraxinus excelsior*), English Oak (*Quercus robur*), and Field Maple (*Acer campestre*) in the overstory, with smaller amounts of Silver Birch (*Betula pendula*), European Aspen (*Populus tremula*), and elm (*Ulmus* spp.). The understory layer is composed of largely hawthorn (*Crataegus* spp.), Blackthorn (*Prunus spinosa*), and Common Hazel (*Corylus avellana*) (Gardiner and Sparks 2005). Monks Wood was historically managed as coppice, a traditional form of rotational cropping in which trees and shrubs are cut at the base and allowed to regenerate as multi-stemmed plants, leaving isolated mature trees (standards). This activity arrests woodland development at a dense, immature phase of shrubs and young tree stems, preventing development of a mature overstory (Fuller and Green 1998). Much of Monks Wood was clear-felled around 1918 and has been undergoing natural regeneration and maturation since that time (Steele and Welch 1973), but coppicing was reintroduced to 9% of the wood in 1961 on a 15- to 20-year rotation, predominantly in one 7.5-ha block (Fig 1a). The remainder of the woodland has received

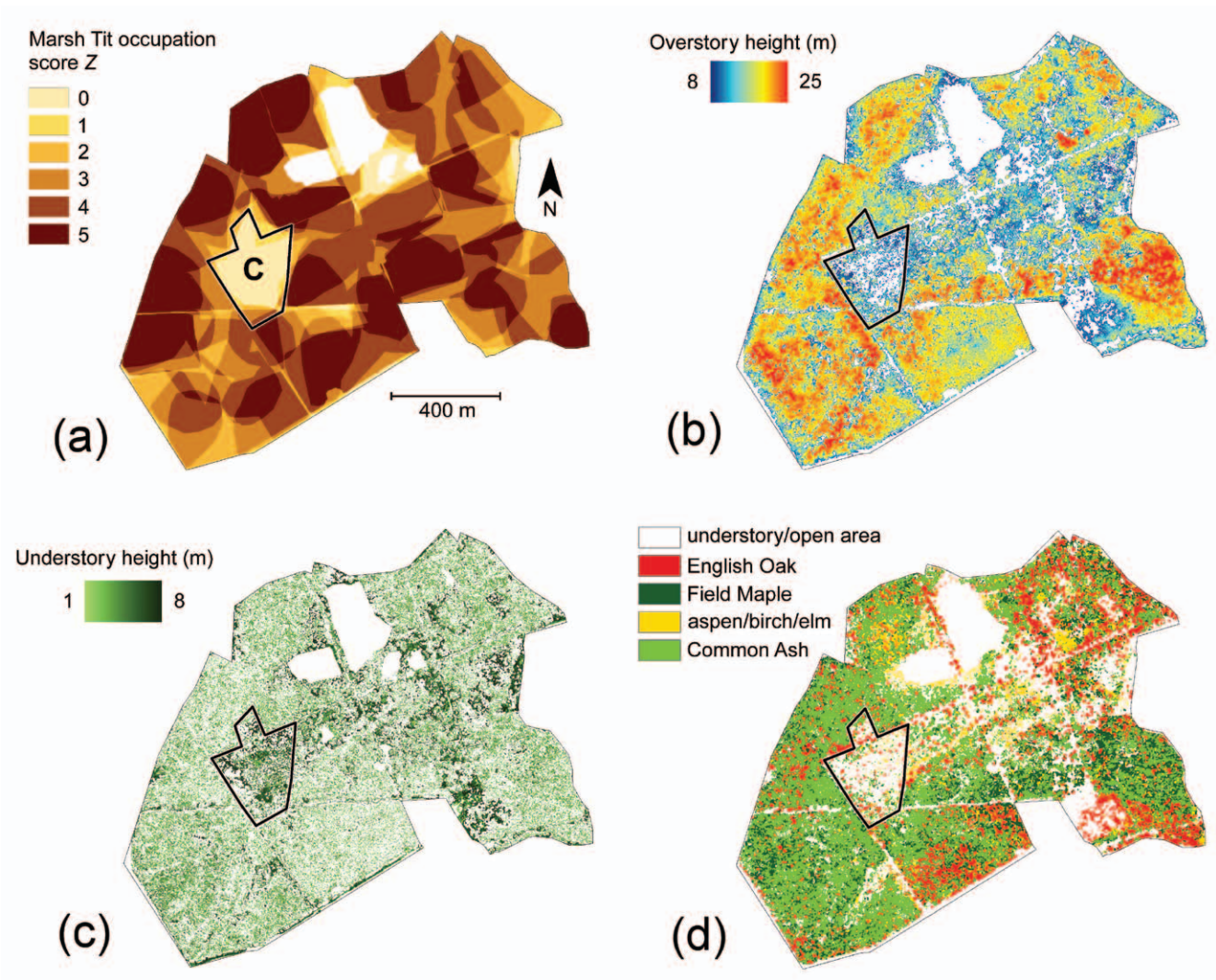

FIGURE 1. Models of Marsh Tit occupation and vegetation for Monks Wood: (a) cumulative territory map of Marsh Tit occupation, where score *Z* corresponds to the number of breeding seasons (out of 5) that Marsh Tits occupied a grid cell. Four open fields enclosed within the wood appear in white, and the outlined polygon marked "C" denotes a 7.5-ha block of coppice. (b) LiDAR model showing heights of vegetation in the woodland overstory, at the resolution of a 0.5-m cell. (c) LiDAR model showing heights of vegetation in the total understory, at the resolution of a 0.5-m cell. (d) Map of tree species distribution in the overstory, derived from optical imagery, at 1-m resolution. The coppice block denoted in (a) is also outlined in black in (b) to (d).

little or no management and consists of an overstory of mature or semi-mature trees (up to 25 m tall), with abundant standing dead wood, frequent tree falls, open or scrubby glades, and an extensive understory throughout (Broughton et al. 2006, 2011). Approximately 7 ha consists of younger woodland that has regenerated on adjoining arable land since the 1960s.

MARSH TIT OCCUPATION

The majority of Marsh Tits in Monks Wood have been individually marked with colored leg bands each year: 83% banded in 2004, 95–98% from 2005 to 2008. All 22 or 23 annual spring territories were delineated each year. We followed banded birds at least weekly for periods of up to 4 hr from March to May and generated territory maps of the maximum defended area from observations of movements and territorial behavior (for detailed description see Broughton et al. 2006, 2010). We defined occupation as defense of, or presence within, a territory for at least 2 weeks or until the bird was presumed killed. Territories were occupied by pairs or unpaired males (Broughton et al. 2011), the latter (0–5 per year) varying annually in location and not considered to represent a selection process differing from that of paired males. Approximately 2–3% of birds per year relocated to a new territory (Broughton et al. 2010), and 45–59% of all birds were replaced annually because of mortality. The extent of the territory of surviving birds differed from the previous year's by a mean of 26% (SD = 20%, $n = 44$), and 10–41% of the study area remained vacant each year (Broughton et al. 2006; unpubl. data). Thus turnover of birds was high, individuals could relocate their territories, vacant woodland was available should they select a new area, and the territories of birds that did not relocate in successive years varied in size.

We digitized territories in a geographic information system (GIS; ArcGIS version 9.3.1, ESRI 2009) and converted the polygons to grid-based raster representations (0.5 × 0.5-m-resolution grid cells). In order to use all information on territories while minimizing potential effects of philopatry, due to the same individuals establishing territories in consecutive years, which introduces non-independence, we did not use territories as sampling units. Instead, we gave each grid cell within a territory a value of 1 and each cell outside a territory a value of 0. We overlaid each year's territory maps for 2004–2008 cumulatively, so that a grid cell that was part of a territory in all 5 years accrued a value of 5 and a grid cell that was never occupied had a value of 0. The cumulative territory map therefore depicted frequency of Marsh Tit occupation across the study site over the 5-year period (Fig. 1a). We gave these categories a score Z on a scale of $Z = 0$ (never occupied) to $Z = 5$ (maximum occupation), then used grid cells with the same occupation score to group vegetation in corresponding areas into each of the six categories of Marsh Tit occupation. The structure and composition of vegetation could then be compared by areas with a different Marsh Tit occupation score.

MODELS OF WOODLAND STRUCTURE

We acquired LiDAR data in summer (June) 2005, when trees and shrubs were in full leaf, and from them generated a raster canopy-height model of Monks Wood at a resolution of 0.5 m (Hill and Broughton 2009). This model described the detailed structure of the woodland's full canopy surface, providing heights (to 1 cm) of the tallest vegetation in each 0.5-m grid cell. On the basis of field observations and frequency distributions of LiDAR-based heights of the vegetation of Monks Wood (Hill and Broughton 2009, Hill et al. 2010), we classified values of <1 m in the model as the field layer, values of 1–8 m as the understory layer of subdominant trees and shrubs, and values of >8 m as the overstory layer of the crowns of mature trees (Fig. 1b). Using a GIS, we calculated the mean overstory height and tree canopy closure (defined as the percentage cover of overstory) for each area categorized by Marsh Tit occupation score ($Z = 0$–5).

The summer LiDAR data contained information on the understory only where it was exposed by gaps in the overstory. To address this, we acquired additional LiDAR data of 0.5 m resolution in spring (April) 2003 (Hill and Broughton 2009), when understory shrubs were in leaf but the overstory trees were not. This provided information on understory shrubs lacking from the LiDAR data acquired during summer because of shrubs being screened beneath overstory trees in full leaf. We combined this spring model of "shaded" understory shrubs with the summer model of "exposed" understory vegetation to create a "total" model of understory height (Fig. 1c), representing all vegetation in the height range of 1–8 m. As with the overstory, we determined the mean height of vegetation in the three understory models (i.e., shaded, exposed, total), and the percentage of area covered by each, for each area categorized by a Marsh Tit occupation score ($Z = 0$–5). Full details of LiDAR data acquisition and processing are given in Hill and Broughton (2009). Previous analyses have revealed no apparent significant dynamic change in the vegetation structure of Monks Wood during the study period (Broughton et al. 2012), permitting the use of LiDAR and territory data acquired in different years.

We calculated the frequency of height values for all vegetation within each Marsh Tit occupation category by summing the number of cells in the models of the overstory and total understory height in 1-m height intervals ("bins") between 1 m and the maximum height of the canopy (25.4 m). A grid cell at a single geographical location would, therefore, contribute to two height bins if it contained both overstory and understory vegetation. This additive approach demonstrated the height distribution of trees and shrubs in each Marsh Tit occupation category.

OVERSTORY TREE SPECIES MODEL

We generated a 1-m-resolution raster map of the six tree species constituting the overstory from a supervised classification

of time-series Airborne Thematic Mapper data acquired in 2003 (Hill et al. 2010). The tree species model (Fig. 1d) had a surveyed overall accuracy of 88%, and we calculated the cover of each tree species in each category of Marsh Tit occupation as the proportion of overstory area.

WOODLAND EDGE EFFECTS

We looked for an edge effect on patterns of Marsh Tit occupation by delineating buffers of 50 m and 100 m inside the perimeter of Monks Wood and around the internal fields depicted in Fig. 1a, giving two measures of sensitivity for "edge" and "interior" habitat (Hewson and Fuller 2006). We assessed edge avoidance by calculating and comparing the percentage of each buffer and corresponding interior that was occupied by Marsh Tits in most or all years ($Z = 3$–5). For comparison of structural variables, we also used the 50-m and 100-m delineations of woodland edge and interior to subdivide the overstory and understory models.

STATISTICAL ANALYSES

Because areas of Monks Wood with the same frequency of Marsh Tit occupation were delineated according to the predefined scoring method (Fig. 1a), the occupation score within each scored area was, by definition, fixed. Therefore, we used the occupation score as a predictor of known, fixed value and the vegetation characteristics as random, continuous variables varying between such areas. The aim of this approach was to compare vegetation in areas defined by differing levels of Marsh Tit occupation.

We used linear regression to estimate characteristics of the overstory and understory as a function of Marsh Tit occupation score (Z) and Spearman's rank-order correlation to investigate relationships between occupation score and woodland structural variables. We tested the suggestion that Marsh Tits settled preferentially in areas rich in oak trees (Amann 2003), or any other tree species, by determining whether the proportion of any tree in the overstory of successive Marsh Tit occupation categories increased along with occupation at a rate greater than that of other species. The proportions of each tree species within the overstory of each occupation category were not independent, however, because of the mutually exclusive and exhaustive relationship between them. We therefore divided the proportion P_{SZ} of each tree species S by that of unclassified vegetation U_Z in the corresponding occupation category of score Z, denoting these standardized proportions by the ratios $Q_{SZ} = P_{SZ}/U_Z$. This procedure reduces the dimensionality of the data by one, in the manner of a compositional analysis (Aitchison 1986). Taking the natural logarithm of each ratio leaves the expected values unbounded above or below and allows the fitting of standard linear models by least squares. We initially fitted a model in which both intercepts α_S and slopes β_S representing the relationship with occupation score Z varied for each of the six tree species:

Equation 1. $$E[\log(Q_{SZ})] = \alpha_S + \beta_S Z, \quad S = 1, 2, \ldots 6; \quad Z = 0, 1, \ldots 5.$$

The intercepts α_S accommodate differences in the overall abundance of each species within the overstory. We then fitted additional models with various constraints imposed on the slopes β_S and used standard regression theory to compare and select between them. Obtaining estimates $\hat{\alpha}_s, \hat{\beta}_s$ of the coefficients in the selected model allows transformation to estimates $\hat{P}_{sz}$ and $\hat{U}_z$ of the original proportions, which sums to unity for each category, as the lack of independence requires. All statistical tests were carried out in R version 2.9.1 (R Foundation for Statistical Computing, 2009).

RESULTS

WOODLAND STRUCTURAL COMPOSITION

The mean height of the overstory increased significantly with Marsh Tit occupation score Z (overstory mean height = 11.9 + 0.9Z, $r^2 = 0.86$, $P = 0.008$, $n = 6$), as did tree canopy closure (percent tree canopy closure = 50.8 + 9.1Z, $r^2 = 0.87$, $P = 0.007$, $n = 6$), which was almost complete where Marsh Tit occupation was greatest (Table 1). The mean height and percentage cover of total understory declined significantly as Marsh Tit occupation increased (total understory mean height = 4.7 – 0.3Z, $r^2 = 0.90$, $P = 0.004$, $n = 6$; percent total understory coverage =

TABLE 1. Mean heights and standard deviations of overstory and understory vegetation and the percentage of tree canopy closure in areas categorized by Marsh Tit occupation score Z. Models were of 0.5 m spatial resolution.

Occupation score Z	Area (ha)	Overstory mean height (SD) (m)	Tree canopy closure (%)	Shaded understory mean height (SD) (m)	Exposed understory mean height (SD) (m)	Total understory[a] mean height (SD) (m)
0	8.2	11.6 (2.6)	51.2	2.4 (1.0)	5.2 (2.0)	4.8 (2.1)
1	5.1	12.1 (2.9)	50.1	2.5 (1.0)	5.3 (2.0)	4.6 (2.1)
2	13.1	14.6 (3.6)	77.3	2.7 (1.2)	5.3 (1.9)	3.7 (2.0)
3	34.3	15.1 (3.6)	83.3	2.7 (1.2)	5.6 (1.9)	3.6 (2.0)
4	44.9	15.2 (3.4)	87.3	2.6 (1.1)	5.6 (1.8)	3.5 (1.9)
5	49.8	15.7 (3.1)	91.1	2.6 (1.1)	5.5 (1.8)	3.2 (1.7)

[a]Total understory is a combination of shaded and exposed understory (see text).

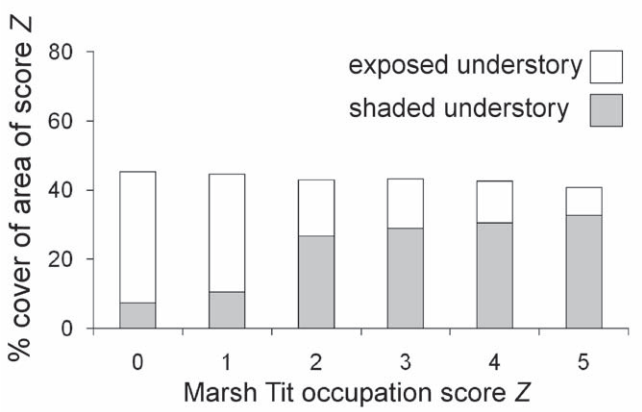

FIGURE 2. Relationship between Marsh Tit occupation score Z and cover of understory vegetation (as a percentage of the area of occupation score Z). Total understory is represented by the stacked column of its constituent parts (shaded and exposed understory).

45.3 – 0.8Z, r^2 = 0.91, P = 0.003, n = 6), but the overall change in cover was relatively minor (Fig. 2). Total understory broken down into its constituent parts, the mean height of shaded understory also changed little with Marsh Tit occupation (shaded understory mean height = 2.5 + 0.04Z, r^2 = 0.39, P = 0.19, n = 6), and exposed understory increased slightly (exposed understory mean height = 5.2 + 0.1Z, r^2 = 0.83, P = 0.01, n = 6). However, in terms of coverage, the proportions of each component changed substantially as Marsh Tit occupation increased (percent exposed understory coverage = 36.0 – 6.2Z, r^2 = 0.88, P = 0.006, n = 6; % shaded understory coverage = 9.3 + 5.4Z, r^2 = 0.85, P = 0.009, n = 6), so that the majority of total understory was exposed where occupation was low (Z = 0–1) and shaded where occupation was higher (Z = 2–5) (Fig. 2).

Significant correlation between overstory and understory variables showed that they were interrelated (Table 2), leading to difficulty in identifying which individual variable (if any) was most critical in territory selection. Tree canopy closure and overstory mean height were very strongly and positively correlated with each other and Marsh Tit occupation score, as was the coverage of shaded understory, but all were negatively correlated with the mean height and coverage of total understory (Table 2).

The vertical distribution of height values in the overstory and total understory models revealed a contrasting pattern between areas of low (Z = 0–1) and higher (Z = 2–5) Marsh Tit occupation (Fig. 3). Areas of higher Marsh Tit occupation were dominated by understory vegetation in height bins of 1–3 m and by overstory vegetation in height bins of 14–18 m, this effect being amplified as Marsh Tit occupation increased. Areas of low occupation were largely dominated by vegetation below 13 m, particularly at height bins of 7–8 m at the interface of the understory and overstory layers.

Over the entire study area, 8.2 ha of woodland remained unoccupied throughout the study period (occupation category Z = 0, Table 1). Compared to the other occupation categories, vegetation in these unoccupied areas had the shortest overstory, almost the lowest percentages of tree canopy closure, and the tallest total understory, but the least cover of shaded understory (Table 1, Fig. 2). The majority of unoccupied area (64%), which Marsh Tits largely avoided, was located in the 7.5-ha coppice block (Fig. 1a), 70% of which was never occupied in the 5 years of study.

OVERSTORY TREE SPECIES COMPOSITION

Common Ash and English Oak were the dominant tree species in the overstory of each Marsh Tit occupation category (Fig. 4a). Field Maple was the third most extensive species, except where Marsh Tit occupation was low (Z = 0–1). The contributions of European Aspen, Silver Birch, and elm to each category of Marsh Tit occupation were low (Fig. 4b). Fitting the regression

TABLE 2. Correlation matrix of variables derived from LiDAR models of the overstory and understory of Monks Wood. Values are Spearman's rank-order correlation statistic (r_s) where n = 6. Units of measurement for each variable are specified in the left column only. Asterisks denote statistical significance of P < 0.05.

	Marsh Tit occupation score Z	Overstory mean height	Tree canopy closure	Total understory[a] mean height	Shaded understory mean height	Exposed understory mean height	Total understory[a] coverage	Shaded understory coverage
Overstory mean height (m)	1.00*							
Tree canopy closure (%)	0.94*	0.94*						
Total understory[a] mean height (m)	–1.00*	–1.00*	–0.94*					
Shaded understory mean height (m)	0.43	0.43	0.37	–0.43				
Exposed understory mean height (m)	1.00*	1.00*	0.94*	–1.00*	0.43			
Total understory[a] coverage (%)	–0.94*	–0.94*	–0.87*	0.94*	–0.49	–0.94*		
Shaded understory coverage (%)	1.00*	1.00*	0.94*	–1.00*	0.43	1.00*	–0.94*	
Exposed understory coverage (%)	–1.00*	–1.00*	–0.94*	1.00*	–0.43	–1.00*	0.94*	–1.00*

[a]Total understory is a combination of shaded and exposed understory (see text).

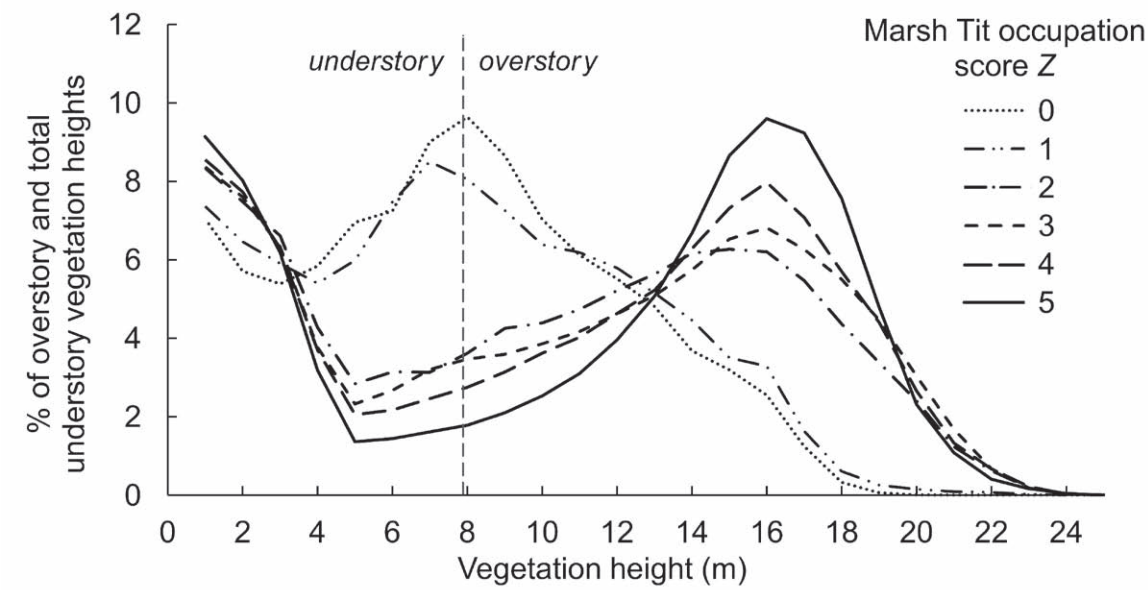

FIGURE 3. Distribution of vegetation-height surfaces in relation to areas defined by Marsh Tit occupation score *Z*. Vegetation surfaces are represented as a percentage of pooled values of total understory and overstory height.

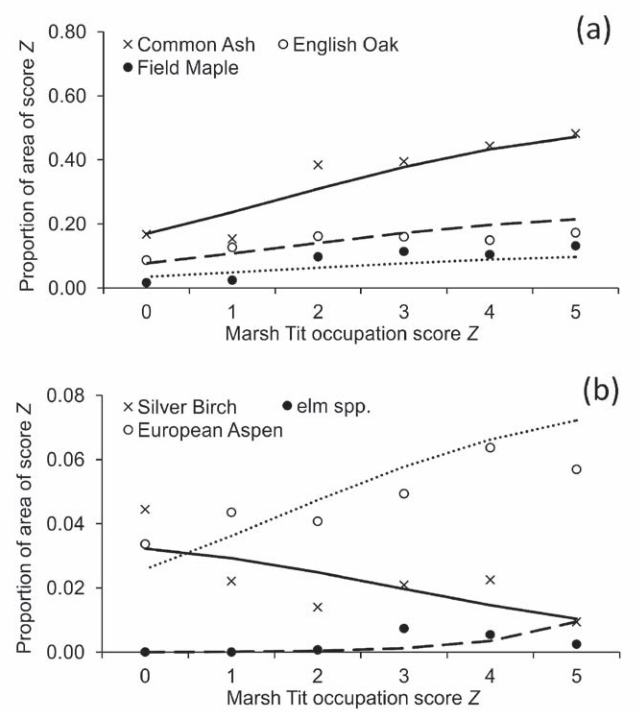

FIGURE 4. Proportion of the area categorized by each Marsh Tit occupation score *Z* that was occupied by each species of overstory tree. Lines estimated by regression of log ratios, where the model allowed different slopes for Silver Birch and elms while grouping remaining species in a constant ratio to one another. Plot (a): Common Ash (solid line), English Oak (dashed line), Field Maple (dotted line). Plot (b): Silver Birch (solid line), elm spp. (dashed line), European Aspen (dotted line). Note the differing vertical scales on the *y* axes.

model (Equation 1), imposing a constant slope, and then isolating and testing the slope of each tree species in turn gave a final selected model that had separate slopes each for elm and Silver Birch, but the other four tree species shared an identical slope. The fit of this final model (Fig. 4a and 4b) deteriorated significantly when the slope for Silver Birch ($F_{1,27} = 4.7$, $P = 0.04$) or elm ($F_{1,27} = 21.6$, $P = 0.004$) was set equal to that of the four remaining species. Addition of a separate slope for other species did not improve this reduced model, indicating that Marsh Tits were not preferentially selecting an overstory rich in any particular tree species (disregarding the negligible coverage of elm).

WOODLAND EDGE EFFECTS

Edge effects were more pronounced between the 50-m buffer of woodland edge and the interior than between the 100-m buffer and the interior. The percentage of area of high scores of Marsh Tit occupation ($Z = 3$–5) was 17% lower in the 50-m edge buffer than in the interior, but the difference between the 100-m edge buffer and its corresponding interior was only 4% (Table 3). This larger disparity in the 50-m delineation was also reflected in the vegetation; compared to that in the interior, vegetation within the 50-m edge buffer had a lower overstory mean height, less tree canopy closure, and more coverage of exposed understory but less of shaded understory, and these differences were much greater than those between the 100-m edge buffer and its interior (Table 3).

DISCUSSION

The approach of combining high-resolution remote-sensing data with overlays of bird territories accumulated over 5 years gave novel insights into the relationship between a woodland bird

TABLE 3. Comparison of heights and coverage of the overstory and understory and of tree canopy closure in edge and interior habitats in Monks Wood, woodland edge defined by buffers of 50 m and 100 m.

	50-m edge buffer		100-m edge buffer	
	Edge	Interior	Edge	Interior
Percentage with Marsh Tit occupation score (*Z*) of 3–5	70.6	87.5	81.3	87.7
Overstory mean height (SD) (m)	14.3 (3.2)	15.4 (3.4)	15.1 (3.4)	15.2 (3.5)
Shaded understory mean height (SD) (m)	2.6 (1.1)	2.6 (1.1)	2.6 (1.1)	2.6 (1.1)
Exposed understory mean height (SD) (m)	5.4 (1.9)	5.5 (1.9)	5.4 (1.9)	5.5 (1.9)
Total understory[a] mean height (SD) (m)	3.8 (2.0)	3.5 (1.9)	3.5 (1.9)	3.5 (1.9)
Tree canopy closure (%)	76.1	86.3	82.2	84.3
Area coverage of shaded understory (%)	25.7	31.1	29.8	29.6
Area coverage of exposed understory (%)	17.9	12.2	13.8	13.5
Area coverage of total understory[a] (%)	43.6	43.3	43.6	43.1

[a]Total understory is a combination of exposed and shaded understory (see text)

and its habitat. Previous studies of the Marsh Tit's habitat associations have been inconsistent; Hinsley et al. (2009) found a positive relationship between Marsh Tit occupation and tree canopy height, as did Broughton et al. (2006) with a subset of territories from the current study, but they found no association with characteristics of the understory. Hinsley et al. (2007), however, found that characteristics of the understory, rather than of the tree canopy, were the most consistent variables in which Marsh Tit territories differed. Carpenter et al. (2010), meanwhile, found significant associations between Marsh Tit presence and features of both the tree canopy and understory layers across England and Wales. Yet all of these studies employed data on Marsh Tit territories or presence from a single year only, or from small-scale, ground-based sampling of vegetation. By using comprehensive, high-resolution datasets on the vegetation of the entire study area, and complete data on Marsh Tit territories over 5 years, our analyses integrate and develop the findings of previous studies by showing that Marsh Tit occupation is strongly linked to the woodland's structure throughout its full vertical profile. The prominence of understory vegetation in the height range of 1–3 m at the highest levels of Marsh Tit occupation underlines the importance of understory at 2–4 m identified by Hinsley et al. (2007) and Carpenter et al. (2010). The relationships between Marsh Tit occupation, overstory height, and tree canopy closure in our results also reinforce the findings of Broughton et al. (2006) and Hinsley et al. (2009).

Our results also show that a substantial understory can persist under a mature, nearly closed tree canopy, which is important in demonstrating that the two structures are not necessarily incompatible in unmanaged woodland, as Fuller et al. (2005) hypothesized. Coppice management is therefore not always a prerequisite for maintaining a substantial woodland understory. Indeed, Marsh Tits largely avoided the large (7.5 ha) block of our study area that had been managed as coppice, which accounted for the majority of the area of Monks Wood that was permanently unoccupied. These unoccupied areas were characterized by less tree canopy cover and a shorter overstory than the rest of the wood. Marsh Tits may avoid such a structure because it constricts them within a shorter vertical layer of vegetation, reducing the diversity of opportunities for feeding that would otherwise be available in a wider range of vegetation strata. It may also heighten interspecific competition by decreasing the distance between birds and increase foraging pressure within a more limited spatial zone (Hartley 1953).

There were structural differences between the woodland interior and edge habitats within a 50-m buffer of the perimeter. The buffer had relatively less tree canopy closure, a lower overstory, and more exposed understory vegetation, all features Marsh Tits avoided in the study area, and indicating a lower, shrubbier habitat than that found in the interior. Marsh Tit occupation was correspondingly lower in the 50-m edge buffer than the woodland interior, although the effect became minor as the buffer increased to 100 m from the woodland edge, indicating the limit of influence. Although vegetation structure was likely to be a significant driver of the observed edge avoidance, greater exposure to predators, such as the European Sparrowhawk (*Accipiter nisus*), or inclement weather (Hadley and Desrochers 2008) may also have contributed, although we had no specific information on this.

On the basis of our results and the conclusions of previous studies (Broughton et al. 2006, Hinsley et al. 2007, Carpenter et al. 2010), it is possible to identify woodland-policy objectives aimed at providing high-quality habitat for breeding Marsh Tits. Maturity of woodland should be promoted, with a mean overstory height in excess of 15 m, tree canopy closure of at least 80%, and a minimum of 40% of the ground area covered by understory. Marsh Tits demonstrate a clear affinity with understory at heights of 1–4 m beneath a mature overstory, not as exposed shrubs and young trees, as in an active coppice regime. Because Marsh Tits avoid woodland edges, providing a pair with a territory of the minimum 1.5 ha (Broughton et al. 2012) of high-quality breeding habitat

requires a circular area of 4.5 ha of woodland to accommodate a 50-m buffer from the edge environment. Patch shape and core–to-edge ratio may partially explain why the probability of occupation is only ~20% for woods of this size in Britain (Hinsley et al. 1996), as long, narrow patches of woodland less than 100 m wide contain no interior that is buffered from edge effects.

We were unable to detect any selection for English Oak in the woodland overstory, or for other tree species (disregarding negligible amounts of elm), suggesting that tree species composition may be less important than structural variables (MacArthur and MacArthur 1961), at least for the species complement of Monks Wood. Similar results have been obtained in Britain for the closely related Willow Tit, which showed a preference for young deciduous woodland rather than tree species composition (Lewis et al. 2007, 2009). These differences between the Marsh Tit and Willow Tit in selection of habitat structure may reflect niche separation in Britain.

The decline of the Marsh Tit through the latter third of the 20th century is puzzling, as the condition of British woodlands appears to have changed to the species' advantage over that time. The area of broad-leaved woodland older than 50 years doubled from 1965 to 2000, while the area of active coppice management declined (Mason et al. 2007). There has been an increase in England in the numbers and range of deer, which may damage woodland vegetation, but Newson et al. (2011) found no relationship with Marsh Tit abundance. Furthermore, maturation of woodland coincided with a widespread and substantial increase in the cover of understory vegetation in the preferred height range of 2–4 m (and 4–10 m) from the 1980s to the early 2000s (Amar et al. 2010). We have shown that increased woodland maturation, understory coverage, and absence of coppice management can all have a positive influence on Marsh Tit occupation, yet the species' abundance in Britain fell by more than a third during the period in which these habitat changes were taking place (Baillie et al. 2010).

If results from our study site can be extrapolated to other areas of lowland Britain, they imply that widespread abandonment of woodland management and associated changes in vegetation structure have not contributed to the Marsh Tit's decline. The UK government's target to increase woodfuel production significantly (Forestry Commission England 2007) could, therefore, have a detrimental effect on remaining Marsh Tit populations by preventing or reversing maturation of woodlands. Forest management and commercial exploitation have been shown to have negative effects on other forest-dwelling, cavity-nesting species of *Poecile* in the Holarctic, such as the Gray-headed Chickadee (Siberian Tit) and Boreal Chickadee in the mature conifer forests of Finland and Quebec, Canada, respectively (Virkkala 1990, Hadley and Desrochers 2008), and on the Willow Tit in a mosaic of mixed forest habitats in Finland (Siffczyk et al. 2003). The Black-capped Chickadee (*P. atricapillus*), however, showed little response to localized logging or natural succession in the north-eastern USA (Loery and Nicholls 1985, Holmes and Sherry 2001). The Chestnut-backed Chickadee (*P. rufescens*) also adjusted to partial felling of mature forest in the Pacific Northwest of North America (Mahon et al. 2007) and may have even benefited from commercial forestry (Brennan and Morrison 1991). These varied responses within a single genus underline the importance of accurately defining detailed habitat associations of woodland and forest birds before conservation or commercial policies are implemented, so that the implications of management can be identified.

As high-resolution LiDAR and multispectral data become increasingly available and affordable (Vierling et al. 2008), alongside enhanced technologies for mapping birds' movements and distribution at greater spatial resolution (Fiedler 2009), analytical methods that can exploit the information produced are required increasingly. Our work provides a novel case study of how the integration of detailed spatial datasets of habitat and territory maps is an effective manner of achieving this aim and can have a broad application in the fields of population ecology and species conservation.

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