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Research Article

Larger native woods with less conifer plantation support greater populations of the marsh tit *Poecile palustris*, a declining forest specialist

Richard K. Broughton[1], **Paul E. Bellamy**[2], **Shelley A. Hinsley**[1] **and Marta Maziarz**[3]

[1]UK Centre for Ecology & Hydrology, Wallingford, UK
[2]RSPB Centre for Conservation Science, The Lodge, Sandy, UK
[3]Museum and Institute of Zoology Polish Academy of Sciences, Warsaw, Poland

Correspondence: Richard K. Broughton (rbrou@ceh.ac.uk)

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Many forest specialist birds are in widespread decline across Europe. In Britain, marsh tits are an indicator species of mature native woodlands, but have suffered an 81% population decline since the 1960s. We assessed whether habitat degradation during the mid 20th century, through the widespread conversion of native deciduous woodland to conifer plantations, could have impacted marsh tit populations. We surveyed the recent number of occupied marsh tit territories in 74 discrete woodland patches ('woods') of 1–296 ha in England, comprising purely native deciduous woodland or with varying coverages of conifer plantations (0–89%). We found that the number of marsh tit territories increased with the woods' size, but this increase was significantly greater for deciduous woods, and lower for woods with a greater proportion of conifer plantation. The area of woodland in the local landscape, reflecting a wood's isolation, had no significant effect on marsh tit abundance in a focal wood. The results indicated that the historical conversion of native deciduous woodland to conifer plantation likely degraded a substantial proportion of formerly high-quality habitat for marsh tits, affecting up to 37.3% of potentially suitable woods and possibly one-fifth of the former marsh tit population directly, likely contributing to the species' national decline. Many of the larger coniferized woodlands are in public/state ownership, which could facilitate habitat restoration for the conservation of woodland specialists, like marsh tits, via centralized policies, with additional incentives targeted at woodlands in private ownership. We cautiously estimated that restoration of native woodland could re-establish a median of 24 610 marsh tit territories in Britain, equivalent to an additional 86% of the current national population.

Keywords: biodiversity, forestry, habitat restoration, species conservation, woodland birds

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Introduction

The destruction, degradation and fragmentation of forest habitats through human exploitation and landscape change is a global phenomenon, and a major driver of biodiversity loss (Betts et al. 2017). Those regions with the longest history of industrialisation and intensive agriculture generally have a greater legacy of forest exploitation and the most severe deforestation and habitat fragmentation, such as Europe and North America (Williams 1989, Kirby and Watkins 2015). In deforested regions the patches of remaining woodland ('woods') are frequently small and poorly connected within an intensive agricultural landscape matrix; this represents a challenge for specialist forest species in sustaining viable populations due to dispersal barriers and limited habitat availability (Opdam et al. 1985, Fitzgibbon 1997, Gibbs 1998).

The influence of forest fragmentation and transformation on bird communities has been a frequent research subject (Opdam 1991, Rolstad 1991, Dolman et al. 2007, Gardner et al. 2019). Woodland birds are ideal as model organisms due to their diverse responses to forest fragmentation, resulting from differing requirements and tolerance between species to habitat change and configuration (Hinsley et al. 2015, Fuller and Robles 2018). Woodland patch size, isolation, composition and associated edge effects all have strong impacts on bird species richness in fragmented landscapes, determining the bird community and individual species' abundance (Opdam et al. 1985, Hinsley et al. 1995a, Melin et al. 2018, Porro et al. 2020).

Forest specialists appear more sensitive to habitat change and fragmentation than generalist woodland birds, and are less likely to occur in smaller, isolated woods or in plantations of non-native trees (van Dorp and Opdam 1987, Dolman et al. 2007, Sweeney et al. 2010, Gardner et al. 2019). One such forest specialist is the marsh tit *Poecile palustris*, a small (10–12 g) passerine of temperate Eurasian and East Asian forests, where it is an indicator species for mature woodland due its close association and greater frequency in this habitat (Broughton 2025). Marsh tits are socially monogamous, and pairs are resident and sedentary throughout the year in large home ranges averaging c. 30 ha in extent, based around a breeding territory of 4–6 ha that is strictly defended from conspecifics during the spring (Broughton 2025).

Like many other forest specialists, such as the willow tit *Poecile montanus*, wood warbler *Phylloscopus sibilatrix* and lesser spotted woodpecker *Dryobates minor*, populations of marsh tits are declining across Europe (PECBMS 2025). The marsh tit's decline is particularly acute in Britain, where its abundance fell by 81% between 1967 and 2023, and the species is on the national Red List of Birds of Conservation Concern (Stanbury et al. 2021, BTO 2025). The causes of the decline of marsh tits and other forest specialists in Europe are only partially understood (Fuller et al. 2007, Fuller and Robles 2018, Wade et al. 2013), although for some species and regions there are clear drivers of decline, such as habitat degradation (Lehikoinen et al. 2024). In Britain, population declines of several habitat specialists have been concentrated in regional landscapes with sparse woodland cover (Broughton et al. 2013). Generally, marsh tits are more likely to persist in woods with a larger patch size in well-wooded areas (Opdam et al. 1985, Hinsley et al. 1995a, Carpenter et al. 2010), reflecting the species' large home ranges and limited dispersal capabilities (Nilsson 1989, Broughton et al. 2010, 2012a). Marsh tits also appear sensitive to increased interspecific competition, such as from great tits *Parus major* or blue tits *Cyanistes caeruleus* (Maziarz et al. 2023, Broughton 2025).

Throughout Europe, marsh tits are most abundant in native deciduous forest, preferring mature or old-growth stands with a high species and structural diversity of trees and shrubs (Hinsley et al. 2007, Broughton et al. 2012b, 2014, Broughton 2025). Marsh tits avoid or occur at lower density in coniferous forest or plantations (Nilsson 1979, Hanzelka and Reif 2016, Porro et al. 2020, Wesołowski et al. 2022). However, in fragmented landscapes, where woodland patches are within an otherwise open matrix (such as farmland), plantations can increase the overall woodland cover in the landscape; this can have a positive effect on the presence or abundance of marsh tits and other forest specialists, probably by facilitating dispersal and habitat connectivity (Porro et al. 2020).

Natural or semi-natural forests generally support a richer avifauna than plantations, particularly those of non-native species (Nájera and Simonetti 2009, Sweeney et al. 2010). In England and Wales, where virtually all of Britain's marsh tits occur (Balmer et al. 2013, Broughton 2025), the total woodland cover is just 11% of the land area, but more than a quarter (27%) of this consists of non-native conifer plantations (Forest Research 2024). However, the coverage of native 'ancient woodland' (present since before 1600 AD) is just 2.8% of the land area in England and Wales, and is heavily fragmented (Woodland Trust 2018). Ancient woodland is considered the most important woodland habitat in Britain due to its high biodiversity and cultural value, and represents high-quality habitat for many woodland specialists, including marsh tits (Goldberg et al. 2007, Kimberley et al. 2013, Broughton 2025).

Of the small component of ancient woodland remaining in England and Wales, 62% consists of native, deciduous, ancient semi-natural woodland (ASNW), which is the closest descendent of the original forest vegetation for the region (Goldberg et al. 2007). The other 38% consists of planted ancient woodland sites (PAWS), which is former ASNW that was converted by forestry practices into (predominantly) non-native conifer plantations, largely between 1950 and 1985 (Rackham 1990, Spencer and Kirby 1992). This 'coniferization' of former ASNW was concentrated in larger woodland patches or clusters of woods (Spencer and Kirby 1992, Peterken 2015), and so may have destroyed or degraded large areas of formerly good habitat for marsh tits and other woodland species. However, despite its likely impact, studies are generally lacking for the effect of this woodland conversion on bird populations (Simms 1971, Fuller 1982, Avery and Leslie 1990). Importantly, there is no information for how an individual wood's area in addition to the degree of coniferization determines the population size of specialist woodland birds, like the marsh tit.

Understanding how a wood's conservation value for forest specialists may vary with patch size and coniferization would be valuable for assessing the potential impact of historical habitat loss or degradation. This could assist our interpretation of the population declines of species like the marsh tit, and could also indicate the possible conservation benefits from current ambitions in Britain to expand and restore coniferized sites back to native woodland (Fuller et al. 2007, Woodland Trust 2018, Forestry England 2022).

In this study we used the marsh tit as an example of a declining forest specialist in Britain to examine how a wood's patch size combined with its composition (proportion of conifers) influenced the number of territories that were supported. Larger woods were expected to support correspondingly more marsh tit territories (Opdam 1991, Hinsley et al. 1995a), but this would be mediated by a negative effect of an increasing proportion of coniferization. We also expected woods to support more marsh tit territories when surrounded by a greater area of woodland in the local landscape, to facilitate dispersal and colonisation (van Dorp and Opdam 1987, Nilsson 1989, Broughton et al. 2013). However, the positive effect of more woodland in the surrounding landscape was expected to be reduced if a study wood was small and/or contained a greater proportion of conifers. We also aimed to extrapolate our findings to estimate the population impact on British marsh tits from the historical conversion of ASNW to coniferized PAWS woodland at the national scale.

Besides our goals of determining the relationship between marsh tits and woods of varying size, proportion of non-native conifers, and isolation within the landscape, our results were used to aid interpretation of the factors driving the British marsh tit's decline and estimate the potential gains from future woodland restoration. Woodland ownership was also considered, to inform the ability of national policies to influence management. The results provide new evidence for conservationists, policymakers and stakeholders to support a landscape-scale strategy to maintain and potentially restore populations of marsh tits and other forest specialists that have similar requirements (Broughton et al. 2013).

Material and methods

Bird surveys

Marsh tit surveys were conducted in woodland patches in England following an established protocol outlined in Broughton et al. (2018), which was shown to detect almost all (96%) of the marsh tits present in a wood. English woods are generally well-defined habitat patches with sharp boundaries in an agricultural landscape. The survey methodology consisted of two survey visits to each wood between late February and early April, when marsh tits are highly territorial during the pre-nesting period of early spring. Surveys took place during calm weather and involved walking a route that took the observer within approximately 100 m of all parts of the wood. Playback of recorded songs and calls were broadcast at intervals of approximately 100 m, and responding birds were plotted on high-resolution maps. The plotted registrations from the two surveys were used to estimate the number of territories in each wood, which was based on the locations of observations and counter-singing between the birds and the playback, and against each other.

Marsh tit survey data were available for 74 woods of 1 ha or larger (Broughton et al. 2020), which is the minimum patch size found to be occupied by marsh tits in England by Hinsley et al. (1995a). Surveys took place between 2002 and 2019, with 93% of woods surveyed after 2010. Most woods (68%) were surveyed in a single spring only, with others surveyed for between two and 11 years (average of seven years) as part of long-term research involving more intensive studies of colour-marked individuals (Broughton et al. 2012a, Broughton 2025). For those woods with multiple annual surveys, the rounded mean number of territories across all years was taken as the single value for analyses. Survey years were excluded for some of these woods when they showed a consistent and significant population decline over time (generally after 2017), and so only time series of apparent population stability were included.

In almost all cases (72 of 74), we surveyed the entire woodland patch as defined by the standard protocol used in British state forestry (Forestry Commission 2024a), which considers discrete patches as being a minimum of 0.5 ha and separated from neighbouring woodland by a gap of at least 20 m or a strip of trees less than 20 m wide and 20 m long. However, for two large woods (Haughmond at 243 ha and Wytham Woods at 389 ha) surveying the entire woodland patch was not possible due to logistics or access restrictions, and the area surveyed constituted 70% and 61%, respectively, of the total wood.

Surveyed woods were selected from within 10 km squares that were mapped as being within the British range of the marsh tit during the most recent and contemporaneous national bird atlas survey in 2007–2011 (Balmer et al. 2013). The distribution of surveyed woods covered 14 of the 48 English ceremonial counties, within six of the eight larger English administrative regions, excluding the predominantly urbanised Greater London region where marsh tits are almost absent (Balmer et al. 2013, Fig. 1). However, 93% of surveyed woods were located within the two administrative regions of south-ast and eastern England, which respectively represented somewhat core and peripheral areas of the marsh tit's British range in 2007–2011 (Balmer et al. 2013). Apart from those woods for which data were available from previous or ongoing research, other sites were chosen opportunistically for their accessibility and to represent a variety of woodland types, sizes and ownerships. For all woods, their marsh tit population size was unknown before surveying began.

Woodland data

The area of each surveyed wood was derived from the GIS data of the 2017 National Forest Inventory (NFI) for England

Figure 1. The distribution of 74 surveyed woods in the administrative regions of England.

(Forestry Commission 2024a) and ranged in size from 1.1 ha to 295.7 ha, with a mean of 68.0 ha (Broughton et al. 2020). The NFI's spatial data comprised digitised woodland polygons with a minimum area of 0.5 ha and classified by type, including deciduous or conifer trees, or mixed. Surveyed woods could be composed of multiple adjacent polygons, representing their compartments. Where polygons were classed as mixed woodland in the NFI, this was reclassified as either deciduous or conifer depending on which was dominant in the NFI classification, or on field inspection during the marsh tit survey and on near-contemporary aerial imagery (Google Earth Pro © 2025 Google LLC). The proportion of coniferous coverage of each surveyed wood was then calculated. Spatial data handling and processing took place in a GIS.

According to the Ancient Woodland Inventory (AWI) for England (Natural England 2024), 42% of surveyed woods in our study were classed as ASNW, i.e. native deciduous woodland, and field visits found that these were mostly dominated by species such as pedunculate oak *Quercus robur*, common ash *Fraxinus excelsior*, common beech *Fagus sylvatica*, birches *Betula* spp., common hawthorn *Crataegus monogyna*, blackthorn *Prunus spinosa* and common hazel *Corylus avellana*. A further 39% of the woods were labelled as PAWS, where the native deciduous ancient woodland had been partially or wholly replaced by planted conifers. The conifers within these woods involved plantations of pines *Pinus* spp., larches *Larix* spp. and spruces *Picea* spp., which are not native to England but were widely planted for forestry during the 20th century (Rackham 1990, Sansum and Bannister 2018). The remaining 19% of woods were more recent woodland dating from after 1600, and could be native deciduous, non-native coniferous or contain areas of both.

To consider the reach of management policy, we determined ownership of the surveyed woods from public records and signage on site, classifying them as privately owned (e.g. a business or individuals, n = 35), owned by the public sector (i.e. the state Forestry Commission, local or national government, n = 16) or owned by a non-governmental organisation (NGO, e.g. a conservation charity, n = 23). Field visits found that 93% of PAWS woods, 57% of post-1600 woods and 55% of ASNW sites showed signs of management within the previous decade, such as cut tree-stumps, planting, coppicing or hunting (e.g. shooting platforms, or pens for rearing common pheasants *Phasianus colchicus*).

Landscape context

Marsh tit presence in a habitat patch can be sensitive to the amount of woodland in the surrounding landscape (Carpenter et al. 2010, Porro et al. 2020). To account for any influence of surrounding woodland area on the number of marsh tit territories in a surveyed wood, we included a variable of landscape woodland context in the analyses. Using the NFI for England spatial dataset (Forestry Commission 2024a), in a GIS we calculated the total area of woodland present within a 5 km radius of the boundary of each wood surveyed for marsh tits. All deciduous, coniferous or mixed woodland types were included in the total. The 5 km radius was informed by the typical maximum range of dispersing marsh tits in England and elsewhere in Europe (Nilsson 1989, Broughton et al. 2010, Broughton 2025). All woodland types were included in this assessment, as coniferous or mixed woodland could form lower-quality breeding habitat or act as important dispersal corridors and habitat connectivity (Porro et al. 2020, Broughton 2025).

National woodland change

For all of England and Wales (the countries containing almost all of Britain's marsh tits), we calculated the area of ASNW that had been converted to coniferized PAWS, and so represented the potential extent of historical degradation or loss of high-quality habitat for marsh tits; this area also represented the extent of woodland habitat of marsh tits that could be restored. The ASNW and PAWS data were derived from the ancient woodland inventories for England (Natural England 2024) and Wales (DataMapWales 2021).

To determine individual ASNW patches we aggregated the ancient woodland inventory features into single contiguous polygons if they were within a 20 m tolerance of each other. We then identified those ASNW patches that contained conifer (i.e. non-native) plantation, derived from the more recent 2023 NFI for England and Wales (Forestry Commission 2024b). This allowed an estimate of the area of formerly (presumed) good-quality marsh tit habitat in ASNW that was converted to conifer plantation (PAWS), mostly during the 20th century, including the mean and total area of coniferization across ASNW patches, and also the number of ASNW patches affected in England and Wales. From this estimate of the coniferized area of ancient woodland, predictions could made of the potential number of marsh tit territories that this impacted across England and Wales.

Statistical analyses

Statistical analyses were conducted in R ver. 4.4.0 (www.r-project.org). We used Poisson generalized linear mixed models (GLMM; package 'interplot'; Solt and Hu 2021) to examine the effect on the number of marsh tit territories of the wood's size (ha, log transformed), the proportion of conifers in the wood (arcsine transformed) and the total woodland coverage (ha, log transformed) within 5 km of each surveyed wood (the typical maximum dispersal distance of marsh tits, see above). In all models we included a random intercept of the county in which a wood was located to test for excessive geographical clustering that may have resulted from the opportunistic site selection.

To select the best model(s) to fit the data (with ΔAICc < 2) we performed automated model selection ('MuMIn' package; Bartoń 2023). Using the *dredge* function we generated a set of candidate models that tested alternative hypotheses and contained subsets of the terms that were included in the global model, i.e. the main effects and all combinations of the two-way interactions between the three predictors. To attain the minimum sample size of approximately 20 data points for each parameter, we limited the maximum number of parameters to four in the candidate models. We visualised and interpreted the effects of the two-way interaction term, retained in the top model, with the package 'interplot' (Solt and Hu 2021). For this purpose, the top Poisson GLMM model was executed.

A wood's ownership (private, public or NGO) could have implications for delivering conservation actions. Therefore, we evaluated the differences in patch size (log transformed) and the proportion of conifers (arcsine transformed) in private, public or NGO woods by setting contrasts and running GLMM models with a Gaussian distribution and a random intercept of the county (package 'glmmTMB', Brooks et al. 2017). The models contained a response of the wood size or the proportion of conifers, and a factor of the ownership class (private, public or NGO). The overdispersion of all models was tested with the package 'performance' (Lüdecke et al. 2021) and appeared insignificant (dispersion ratio ≤ 1.03, $p \geq 0.623$).

To assess the potential impact of woodland habitat change on marsh tits at the national scale, we estimated the number of marsh tit territories likely associated with coniferization of ASNW across England and Wales, derived from the national woodland inventory data. The top GLMM used for the 74 surveyed woods (including the parameters of wood size, proportion of conifers and the interaction between them) was employed to predict the total marsh tit territories in all ancient woodlands across England and Wales, including those containing coniferized PAWS. We then compared this total with a second prediction of marsh tit territories where the proportion of coniferized PAWS was set to zero for all woods, to replicate the situation before historical coniferization of ASNW, or after potential future restoration back to ASNW. The difference between the two estimates would represent the number of marsh tit territories in all ancient woodlands that we inferred to have been potentially lost during coniferization of ASNW.

For these predictions, the *predictInterval* function in the 'merTools' package (Knowles and Frederick 2025) was used to account for uncertainty in the fixed coefficients (wood size and proportion of conifers) and the uncertainty in the variance parameters for the grouping factors (counties of England and Wales in which the woods were located). We excluded the residual (observation level) variance and used the 'probability' prediction tool to obtain the median estimate of marsh tit territories and the upper and lower bounds ≥ 0. We set a 0.95 width of the prediction interval and used 1000 simulation samples. For counties in which no woods were surveyed for marsh tit territories in our fieldwork sample, the predictions were based only on the fixed coefficients and the observation-level error.

Results

Marsh tits, wood size and coniferization

Marsh tits were detected in 53 (72%) of the 74 woods surveyed, with the mean number of territories in occupied woods being 4.9 (range = 1–35; Broughton et al. 2020). The smallest occupied wood was 3.1 ha, similar to the 3.5 ha that was previously found to be the lower estimate of a typical territory area (Broughton et al. 2012a). All woods smaller than 3.0 ha were unoccupied, as were seven coniferized woods as large as 123.2 ha and seven deciduous woods up to 26.5 ha. Of the 69 woods larger than 3.0 ha, most ancient woodlands were occupied, whether predominantly ASNW (< 30% coniferized: 84% occupied from 45 woods) or significantly PAWS (≥ 30% coniferized: 76% occupied from 14 woods). Only 60% of ten post-1600 woods larger than 3.0 ha were occupied, but these were typically smaller (mean 36.4 ha, SD 49.1 ha) than other woods (45 predominantly ASNW: mean 60.0 ha, SD 109.4 ha; 14 predominantly PAWS: mean 117.3 ha, SD 103.4 ha).

For all woods, the number of marsh tit territories strongly depended on the patch size and the proportion of conifers they contained (Fig. 2), with a significant interaction term between these two predictors being maintained in the top model (ΔAICc < 2; Table 1). The number of marsh tit territories was greater in larger woods (Fig. 2), but this positive association was strongest for wholly or predominantly deciduous woods with a smaller (or no) proportion of coniferization. The positive effect of wood size on the number of marsh tit territories became weaker as the proportion of conifers in a wood increased (Fig. 2–3A). Similarly, the effect of coniferization on the number of marsh tit territories varied with a wood's size, with the coefficient being most strongly negative

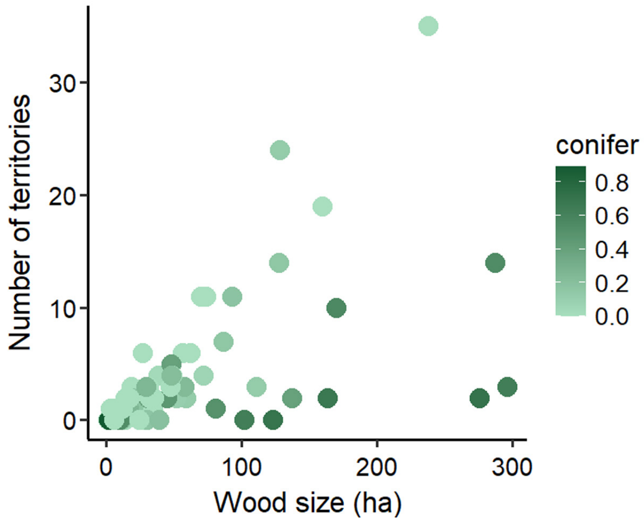

Figure 2. The relationship between the number of marsh tit territories and the area of a wood (ha), and the proportion of conifer plantation (colour gradient) in the wood's tree canopy, n = 74 woods surveyed in England. Where the proportion of conifers was zero, woods were composed of purely deciduous vegetation.

in larger woods over ~ 25 ha (i.e. a log wood size of approximately 3.2: Fig. 3B).

The woodland coverage in the 5 km radius of the study wood was not maintained in the final model (Table 1). As such, for our dataset the wooded landscape context around study woods appeared relatively insignificant for the number of marsh tit territories. Furthermore, the number of marsh tit territories in smaller and/or coniferized woods was not compensated by a greater woodland coverage in the surrounding landscape; the models with two-way interaction terms between the wood size or proportion of conifers and surrounding woodland coverage had ΔAICc > 2, and so were dropped in model selection.

Wood ownership

The size of the study woods and the proportion of conifers they contained differed significantly between the categories of ownership. Public sector woods were much larger (Fig. 4A; GLMM, estimate = 0.86, SE = 0.41, z = 2.1, p = 0.037) and contained a greater proportion of conifers (Fig. 4B; GLMM, estimate = 0.31, SE = 0.11, z = 2.9, p = 0.004) than woods belonging to NGOs. Private woods were generally similar in size to NGO woods (Fig. 4A; GLMM, estimate = –0.65, SE = 0.34, z = –1.9, p = 0.057) and contained similar proportions of conifers (Fig. 4B; GLMM, estimate = 0.13, SE = 0.09, z = 1.4, p = 0.156).

National woodland change

The ancient woodland inventories for England and Wales identified 52 009 contiguous patches of ASNW, of which 21 340 were at least 3.1 ha in size, and so potentially large enough to be occupied by marsh tits according to the minimum occupied wood in our sample. The total combined area of these 21 340 woodland patches was 423 153 ha (mean 19.8 ha per patch, SD 58.2 ha), but 7976 (37.3%) of them contained some PAWS conifer plantation. The total combined area of PAWS plantation in this subset of 7976 woodland patches was 86 337 ha, giving a mean area of 10.8 ha (SD 34.5 ha) of conifers per patch, or a mean conifer coverage of 33.8% per coniferized woodland.

Table 1. Model covariates that best explained the number of marsh tit territories for the top model with ΔAICc < 2. AICc = 270.9, logLik = –130.0, df = 5, weight = 0.763. Random effect of county (intercept): variance = 0.28, SD = 0.53. [a]Natural logarithm of the area (ha); [b]Arcsine transformed.

Variable	Estimate	SE	z	p
Intercept	–3.2	0.44	–7.3	< 0.001
Wood size[a]	1.3	0.10	13.3	< 0.001
Share of conifers[b]	1.8	0.89	2.0	0.046
Wood size : share of conifers	–0.8	0.19	–4.1	< 0.001

The modelled prediction estimated that the median number of recent marsh tit territories in all ancient woodland (including coniferized PAWS) across England and Wales was 29 054 (95% CI 17 255–51 736). This value was remarkably similar to the most recent (2016) national population estimate of 28 500 territories in Britain, by Woodward et al. (2020), which gave confidence to our results; however, not all ancient woodland will contain marsh tits and some territories will occur in other (non-ancient) woodland. When coniferization was set to zero in our prediction, to replicate pre-coniferization or potential future restoration of ASNW, the estimated median of marsh tit territories was 53 664 (95% CI 30 731–97 867). As such, the difference between the two estimates that represented the potential historical loss from coniferization, or future gain from restoration, was a median of 24 610 (95% CI 13 476–46 131) marsh tit territories across England and Wales. This value reflected a potential 23.4% loss from the median estimate by Sharrock (1976) of 105 000 marsh tit territories for the whole of Britain during 1968–1972, when coniferization was still in progress, although some losses would have already occurred by then. Our predicted value of 24 610 marsh tit territories impacted by coniferization also amounted to 86.4% of the most recent estimate of 28 500 territories in Britain in 2016 (Woodward et al. 2020), and so reflected the potential scale of future national gains from complete PAWS restoration back to ASNW.

Discussion

The results provide the first information from Britain for the relationship between the abundance of the marsh tit and its variation with broad woodland type in combination with wood size. As far as we are aware, the study also provides the first estimate for any British species of the potential population losses from an historical forestry policy of coniferization of native broadleaved woodland in the 20th century.

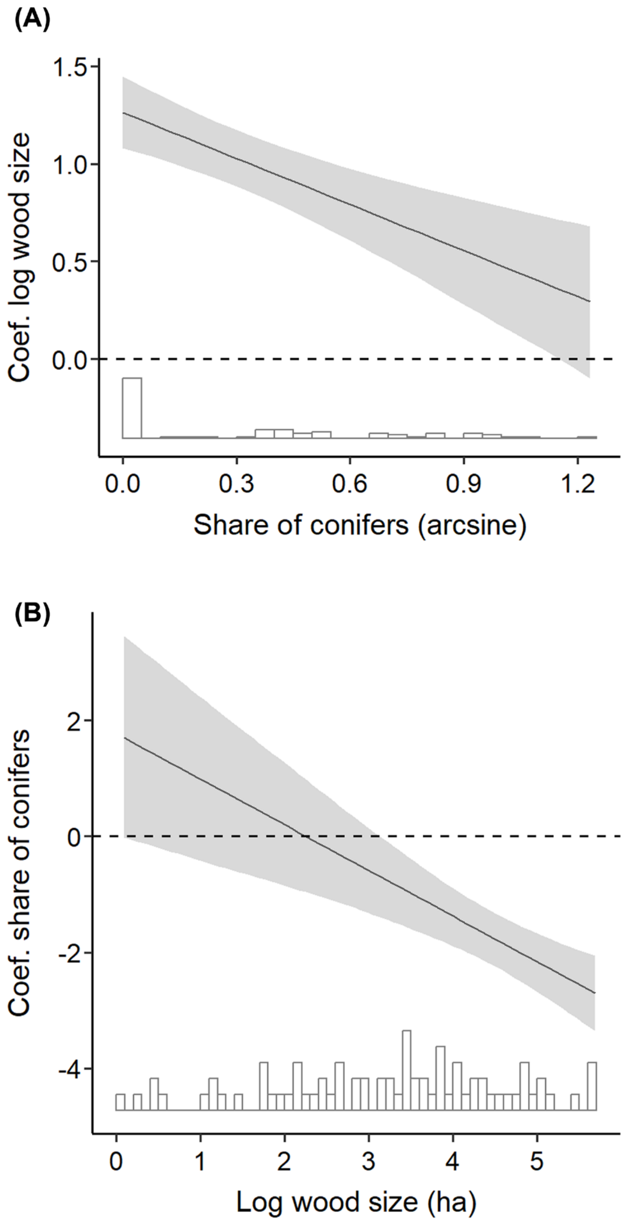

Figure 3. The effect on the number of marsh tit territories of the two-way interaction term that included the wood size (ha, log transformed) and the proportion (share) of conifers (arcsine transformed) in the woods: (A) the decreasing effect on the number of marsh tit territories of the wood size with an increasing proportion of conifers (i.e. the positive effect of wood size declines as the share of conifers increases; (B) the increasingly negative effect of coniferization with increasing wood size, showing the negative effect of conifers was greater in larger woods as the coefficient trend and its confidence intervals fall below zero at a log wood size of around 3.2 (i.e. ~ 25 ha). Both plots are visualised with function *interplot* (Solt and Hu 2021). Shown are trend lines and 95% confidence intervals (shaded area), and also histograms of the conditioning variables for the proportion of conifers (A) or wood size (B). Dashed lines indicate constant moderation effects of the conditioning covariates (null hypothesis).

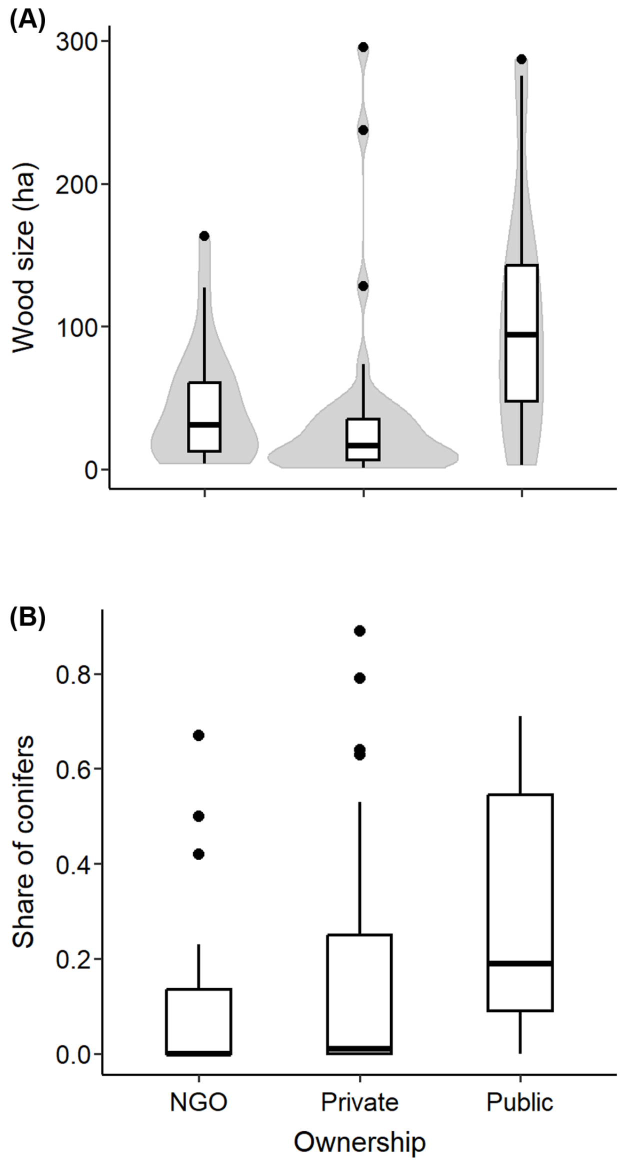

Figure 4. Patterns of ownership of the 74 surveyed woods in relation to (A) the area of the woods (ha), and (B) the proportion (share) of conifer plantation in the woods. Violins show the distribution of data (density curves), boxplots show medians (horizontal lines), 25–75th percentiles (boxes), min–max (± 1.5 * interquartile range: whiskers) and outliers (dots). Woods in public (state) ownership tend to be larger and contain proportionately more conifer plantation compared to those in private ownership or owned by non-governmental organisations (NGOs), such as conservation charities.

Larger woods supported more marsh tit territories, but wholly or predominantly deciduous woods supported many more marsh tits than woods containing significant amounts of non-native conifer plantation. The effect was most pronounced in larger woods, where an increasing proportion of conifer plantation was associated with a progressively lower relative abundance of marsh tits (Fig. 3B), compared to deciduous-dominated woods. This result showed how the negative effects of coniferization were amplified in larger woods which, despite their size, supported low numbers of marsh tits if they were extensively coniferized (Fig. 2), emphasizing the growing disparity in marsh tit abundance as wood size and coniferization both increased.

Ancient woodlands (ASNW or PAWS) were proportionately occupied by marsh tits more frequently than recent woodlands that originated post-1600; this may have reflected the smaller patch sizes of the latter in our sample or a genuinely lower habitat quality for marsh tits in more recently established woodlands. An unexpected result was the insignificant effect on marsh tit abundance of woodland area in the surrounding landscape. Some previous studies showed that greater isolation of a woodland patch in less wooded landscapes is associated with a lower abundance or occupation rate by marsh tits (van Dorp and Opdam 1987, Carpenter et al. 2010, Broughton et al. 2013), although others found no significant effect (Hinsley et al. 1995a). It may be that our sample of study woods were all from landscapes that were sufficiently wooded above the threshold of any negative effect or, perhaps more likely, the effects of coniferization and patch size were far more dominant than local woodland coverage.

Overall, our results reinforced the interpretation of the marsh tit as an indicator species of mature deciduous forest, such as British ancient woodland or ASNW (Broughton 2025). Compared to native deciduous woodland, plantations of non-native conifers have a lower species richness of trees and shrubs, less structural diversity, a higher density of trees and a simplified age structure (Avery and Leslie 1990, Calladine et al. 2018). Marsh tits appear to favour native deciduous woodland with a mature, diverse structure and high species richness (Hinsley et al. 2007, Broughton et al. 2012b). As such, conifer plantations do not represent high-quality habitat for marsh tits, and our results demonstrated that their populations in Britain tend to be lower in such plantations than in deciduous woodland (Broughton 2025). The disparity in marsh tit abundance between deciduous and coniferous woodland is apparent elsewhere in Europe (Nilsson 1979), even in natural forest of both types (Wesołowski et al. 2022).

We estimated that there was 86 337 ha of conifer plantation that had partially or wholly replaced native, deciduous, ancient woodland across England and Wales, mostly during the mid-20th century (Rackham 1990, DataMapWales 2021, Natural England 2024). Conifer plantations were located in 7976 individual patches of ancient woodland that were otherwise large enough to support marsh tits (≥ 3.1 ha). This period of the 20th century coincided with a consistent and severe decline of marsh tit abundance in Britain (BTO 2025), and our results suggest that this occurred alongside the widespread degradation or destruction of more than a third of the high-quality ASNW habitat, via coniferization.

Our predictions estimated that a potential 24 610 marsh tit territories could have been lost due to coniferization of ASNW across England and Wales during the 20th century. However, this estimate requires caution due to its prediction from a model based on a sample of only 74 woods in a limited number of English counties. The prediction also assumed that marsh tits may have occupied essentially all ancient woodlands larger than 3.1 ha in England and Wales, prior to coniferization, which is improbable, although the marsh tit's range in 1968–1972 did include most (79%) of the national 10 km grid squares (Sharrock 1976).

Notwithstanding these important caveats, the predicted number of 24 610 potentially impacted territories reflected 23.4% of the entire population of British marsh tits estimated in 1968–1972 (105 000: Sharrock 1976), part-way through the era of coniferization of ASNW. Although some significant losses due to coniferization had likely already occurred before 1968–1972, these estimates indicate the scale of potential losses of marsh tits during this period, perhaps impacting around one-fifth of the national population at the time. By 1988–1991, shortly after the policy of coniferization of ASNW had ended, the estimated national population of marsh tits had fallen to 60 000 territories (Stone et al. 1997). Consequently, our prediction of 24 610 territories impacted by coniferization could potentially explain more than one-half of the 45 000 territories lost between 1968–1972 and 1988–1991.

The most recent estimate of marsh tit territories in Britain was 28 500 in 2016 (Woodward et al. 2020). Our modelled prediction of 24 610 territories lost to historical coniferization amounts to 86% of this population estimate, indicating the possible future gains if existing PAWS woodland was fully restored to deciduous ASNW habitat and re-occupied by marsh tits. Such restoration could therefore assist with re-establishing a large number of high-quality marsh tit territories, partially reversing or buffering the species from more severe declines in Britain.

Even within the context of other environmental pressures driving or exacerbating the marsh tit's population decline in Britain, such as habitat fragmentation and increasing interspecific competition from blue tits for example (Broughton et al. 2013, Maziarz et al. 2023, Broughton 2025), it seems highly plausible that the scale of widespread conversion of ASNW habitat to coniferized PAWS would have had a serious negative impact. A similar degradation of native woodland by intensive forestry was considered a major factor in widespread declines among forest bird communities in eastern Canada (Betts et al. 2022) and southern Finland (Virkkala 2016).

In Britain, however, our study appears to be the first to quantify the potential effects of habitat degradation on a woodland specialist as a result of the conversion of native ancient woodland to conifer plantation (Fuller 1982). At the community level, Donald et al. (1998) found that hole-nesting birds (like marsh tits) were less abundant in conifer plantations than in deciduous stands. Similar negative associations of non-native forestry plantations were found for marsh tits and other woodland specialists in Italy (Porro et al. 2020). In Sweden, intensive forestry restricted marsh tits to remnants of semi-natural deciduous stands as habitat islands within a matrix of conifer plantation (Enoksson et al. 1995). Also in Sweden, Nilsson (1979) found a significantly lower density of marsh tit territories in managed conifer plantations versus predominantly deciduous, natural forest. Meanwhile, Swedish lesser spotted woodpeckers had greater occurrence and persistence in protected deciduous forests that had not been subject to forestry logging and management (Kost and Olsson 2025). Elsewhere in Fennoscandia, catastrophic declines of the willow tit have been shown to be driven by intensive forestry and homogenization of the woodland habitat (Lehikoinen et al. 2024). These studies strongly support our conclusion of British marsh tits being negatively affected by the historical forestry policy of converting large areas of native woodland to conifer plantations.

The ownership of the surveyed woods in our study reflected national trends, with 16% in the public sector and the remainder in private or NGO ownership (Forest Research 2024). In England and Wales, however, 34% of PAWS woodland is under the public ownership of state forestry agencies (Woodland Trust 2018). Despite our results implying that state forestry policies were originally responsible for significant negative impacts on marsh tit populations, this ownership pattern may now facilitate conservation action to assist native woodland specialists. Because large areas of public sector woodland can be controlled by centralised policies, directed and funded by governments or their agencies, this also includes opportunities for promoting more sympathetic forestry practices or conservation restoration (Thompson et al. 2003, Peterken 2015).

Private woodland is more difficult to influence directly via state policies, as engagement is generally voluntary, but government grant schemes in England have been designed for improving management of woodlands in both public and private ownership to benefit target bird species, with some success (Bellamy et al. 2022). Some NGO conservation charities have also implemented significant PAWS restoration on their own estates, while lobbying for appropriate state funding for wider restoration (Woodland Trust 2018). Nevertheless, large areas of privately owned woodland may not be reached by such policies (Rackham 1990), and their conservation potential may remain unrealised without sufficient incentives.

Our results also underlined the sensitivity of marsh tits to woodland patch size, with larger populations occurring in bigger native woods. This finding suggests a greater resilience of marsh tit populations in larger woods, where they show a lower stochastic turnover and less chance of local extinction (Hinsley et al. 1995b, Broughton et al. 2013). The finding also provides a clear policy recommendation of prioritizing PAWS restoration towards larger woods to gain the greatest benefits for marsh tit populations. In addition to PAWS restoration, the targeted expansion of existing ASNW and creation of future ancient woodlands would also support the resilience and recovery of British marsh tit populations (Broughton 2025). The UK's Climate Change Committee (2025) recommends targets for woodland creation of 37 000 ha per year to achieve 17% national coverage by 2040. Finessing policies to encourage the expansion of woodland adjacent to existing ASNW perhaps offers the greatest benefits for woodland specialists, like marsh tits, by promoting rapid establishment of native woodland, the creation of bigger woodland patches and facilitating colonisation (Broughton et al. 2021, 2022, Hughes et al. 2023).

In summary, this study highlights an additional significant factor that likely contributed to the 81% decline of British marsh tits since the 1960s, via the degradation of formerly high-quality native woodland by its conversion to non-native conifer plantations. The restoration of substantial areas of these coniferized PAWS woodlands is a policy goal in Britain, alongside the wider expansion of native woodland. With suitable and timely application, these policies should benefit many woodland species, including marsh tits and other hole-nesting birds, and also the distinctive biodiversity of native woodlands (Kirby et al. 2017). Our study provides new empirical evidence that can help to underpin the conservation value of such restoration policies.

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Author contributions

Richard K. Broughton: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Paul E. Bellamy**: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Shelley A. Hinsley**: Conceptualization (supporting); Data curation (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Marta Maziarz**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (supporting); Resources (supporting); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Environmental Information Data Centre: https://catalogue.ceh.ac.uk/documents/8d1b93d7-b8cf-4df1-9a5d-352dc16c5195 (Broughton et al. 2020).

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