Forest Ecology and Management 615 (2026) 123833

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Pine mires as key early-season habitat selection sites for Willow Tits in managed boreal forests

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A R T I C L E I N F O

Keywords:
Willow Tit
Acoustic monitoring
Pine mire
Boreal forest
Habitat selection
Forest management

A B S T R A C T

Widespread forestry operations have simplified and fragmented boreal forest structure across Europe, reducing key features such as deadwood and peatlands that support forest specialist species. The Willow Tit (*Poecile montanus*), a declining boreal passerine, is highly sensitive to such changes. While its breeding-season habitat associations are relatively well studied, much less is known about its habitat use during the pre-breeding period, a critical phase of territory establishment that may influence reproductive success. We used passive acoustic monitoring (PAM) at 285 forest sites across a managed boreal landscape in southern Finland to investigate early-season Willow Tit occurrence in relation to forest structure. Species presence was modeled as a function of habitat structure (e.g., modeled deadwood potential, peatland type, foliage biomass, forest age), biotic interactions (presence of Pygmy Owl (*Glaucidium passerinum*) and Crested Tit (*Lophophanes cristatus*)), and proximity to human settlements, at two spatial scales (100 m and 400 m buffers). Willow Tit presence was consistently and positively associated with the area of pine mires, highlighting the ecological value of these pine-dominated peatlands during territory settlement. In contrast, mature forest area and modeled deadwood potential showed no positive effects; the latter exhibited a weak negative association at the landscape scale. This pattern may indicate that modeled deadwood estimates do not fully capture the fine-scale characteristics relevant for Willow Tits during the pre-breeding period, or that decaying wood plays a more limited role in habitat selection at this stage than at later stages of breeding. Detection probability declined with Julian date, likely reflecting seasonal changes in vocal activity. These findings emphasize the ecological and management importance of preserving pine mires and suggest that widely used forest inventory models may overlook key habitat features essential for declining species. We recommend integrating peatland preservation into forestry planning to enhance habitat suitability and resilience under intensive forest management and climate change.

1. Introduction

Boreal forests are among the largest and most ecologically significant terrestrial biomes, providing habitat for many specialist species and supporting key ecosystem functions (Lunde et al., 2025). However, these ecosystems are increasingly threatened by intensive forestry practices and climate change. Common management techniques—such as clear-cutting, ditching, and rotation forestry—have simplified forest structure, fragmented habitat continuity, and reduced old-growth features (Aalto et al., 2023; Girona et al., 2023; Witté et al., 2013), negatively affecting species that depend on structurally complex and moisture-rich habitats (Lunde et al., 2025).

The Willow Tit (*Poecile montanus*), a cavity-nesting passerine of boreal and temperate forests, has undergone marked population declines across much of its European range (Lewis et al., 2009; Fraixedas et al., 2015; Lehikoinen et al., 2024). The species is highly sensitive to structural changes in forests (Kumpula et al., 2023; Lehikoinen et al., 2024; Lewis et al., 2009), relying on soft, decaying wood and moist microhabitats for nesting and foraging (Haartman, 1969; Lehikoinen et al., 2024; Parry and Broughton, 2018). Such conditions are typically found in unmanaged or peatland-dominated forests (Broughton et al., 2021; Kumpula et al., 2023; Lewis et al., 2009). The Willow Tit has declined especially in managed forests dominated by early successional stages where natural decay processes are suppressed (Fraixedas et al., 2015; Kumpula et al., 2023; Lehikoinen et al., 2024; Virkkala et al., 2023). As a weak cavity excavator, it depends on decaying wood typically found in structurally complex forest patches, including peatland-associated woodlands (Broughton et al., 2021; Milner et al.,

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https://doi.org/10.1016/j.foreco.2026.123833
Received 20 January 2026; Received in revised form 22 April 2026; Accepted 24 April 2026
Available online 29 April 2026

2024). For example, population declines in Britain have been linked to the loss of young, damp woodlands (Lewis et al., 2009). This reliance on complex structural features makes the species vulnerable to both direct habitat loss and subtler structural changes caused by modern forest management (Kumpula et al., 2023; Lehikoinen et al., 2024). In northern Europe, common forestry practices such as clear-cutting and thinning have increased distances between suitable nesting patches, reducing overall habitat quality (Kumpula et al., 2023). Consequently, conservation recommendations increasingly emphasize continuous-cover forestry and retaining structural diversity (Kumpula et al., 2023; Virkkala et al., 2023).

While previous studies on habitat-dependency of Willow Tits have focused primarily on breeding-season, and highlighted the importance of mature forest structure (Vatka et al., 2014) and deadwood availability (Kumpula et al., 2023; Parry and Broughton, 2018), habitat selection of Willow Tits during the rest of the year remains poorly understood. However, studies conducted outside the breeding season indicate that habitat and space use in Willow Tits can differ substantially from breeding-period patterns, particularly during winter (Siffczyk et al., 2003). Willow Tits maintain year-round territories and form stable winter flocks, often comprising the same individuals throughout the non-breeding season (Hogstad, 2009, 2015). This territorial stability underscores the importance of understanding habitat selection outside the breeding period. The pre-breeding period, which coincides with territory establishment and pair formation, is important for reproductive success and long-term population viability. Yet, the species' early-season habitat associations—when individuals explore and settle territories—remain understudied. Identifying key habitat features during this period is particularly important in intensively managed landscapes, where forest structure and microclimate can vary markedly at short spatial scales.

To address this gap, we used passive acoustic monitoring (PAM), a non-invasive method that records bird vocalizations without requiring direct observation (Baroni et al., 2023; Fleishman et al., 2023; Swider et al., 2024), to investigate early-season habitat associations of Willow Tits across a managed boreal forest landscape in southern Finland. PAM is particularly effective for detecting vocal passerines during the pre-breeding period, when individuals are highly vocal during territory establishment. The advantages of PAM over traditional monitoring approaches such as point counts and territory mapping is that the latter often lack the spatial or temporal resolution to detect fine-scale habitat use during this brief but ecologically important window (Budka et al., 2021; Newell et al., 2013; Wu and Yang, 2008).

We modeled Willow Tit presence using a range of environmental variables—deadwood potential, peatland type, forest age, foliage biomass, presence of a predator (Pygmy Owl *Glaucidium passerinum*) or potential competitor (Crested Tit *Lophophanes cristatus*), and proximity to human settlements—measured at 100 m and 400 m spatial buffers. These variables were selected based on previous ecological studies and expert knowledge of the species' habitat preferences. Following an initial compilation of candidate predictors, we applied statistical screening to reduce multicollinearity. The final set of variables reflected both ecological relevance and statistical robustness.

We included modeled deadwood potential (DWP) as a proxy for cavity-nesting substrate, given that Willow Tits excavate nests in decaying standing deadwood (Parry and Broughton, 2018; Kumpula et al., 2023). While DWP provides a spatially continuous estimate of deadwood potential across Finland, it is derived from forest inventory attributes and does not capture fine-scale microhabitat characteristics such as snag softness, decay class, or diameter that are likely essential for successful cavity excavation by weak excavators. Thus, although ecologically relevant, DWP must be interpreted with caution when assessing species-specific nesting requirements. Other habitat features were also included for their ecological relevance. Peatlands provide moisture-retaining conditions that may support suitable nesting substrates and high invertebrate availability (Broughton *et al.*, 2020). Forest age is relevant due to the association between mature forest structure and Willow Tit survival and reproduction; the loss of mature forest through clear-cutting and thinning has been linked to population declines (Kumpula et al., 2023; Lehikoinen et al., 2024; Vatka et al., 2014). Foliage biomass influences forest structure, microclimate buffering (Csölleová et al., 2024; Mwamulima et al., 2025), and arthropod availability (Gruner et al., 2005), providing an indirect indicator of habitat quality for a species reliant on invertebrate prey.

We also incorporated biotic and anthropogenic factors. Pygmy Owl presence may influence Willow Tit occurrence through predation risk or avoidance behaviors (Baroni et al., 2023). The presence of Crested Tits reflects overlapping habitat preferences and possible competition, emphasizing the role of interspecific interactions in habitat selection (Atiénzar et al., 2009; Lewis et al., 2009; Suzuki, 2012). Proximity to human settlements may reduce habitat suitability through habitat degradation, fragmentation (Kumpula et al., 2023; Lehikoinen et al., 2024; Rustell, 2015; Siriwardena, 2004), and disturbance that can deter sensitive species from nesting near frequent human activity.

Our objective was to identify structural and compositional habitat features associated with Willow Tit presence during the pre-breeding period. By relating species occurrence to widely used forest inventory metrics and ecologically relevant variables, we aim to support biodiversity-oriented forest management in boreal systems through improved understanding of early-season habitat requirements.

2. Methodology

2.1. Study area and acoustic sampling design

We assessed Willow Tit (Poecile montanus) presence and absence using passive acoustic monitoring (PAM) across 285 forested sites in southwestern Finland, near Turku (60°N, 22°E). Autonomous Recording Units (ARUs; AudioMoth version 1.1; Open Acoustic Devices) were deployed systematically using a 1-km resolution grid, placing one recorder per grid cell. Site coordinates were selected using the Finnish Uniform Coordinate System (YKJ, EPSG:2393), and each ARU was positioned within a 100 m radius of the grid cell center. Grid cells with insufficient forest cover within this buffer—based on national land cover data—were excluded, as they were considered unsuitable for Willow Tits. Final deployment and excluded locations are shown in Fig. 1.

Field surveys were conducted between March 16 and April 25, 2020, a period that aligns with peak territorial behavior in Willow Tits, when individuals engage in active vocalizations, aggressive encounters, and territory formation (Hogstad, 2015). In temperate parts of its range, egg-laying typically begins in April (Parry and Broughton, 2018), although in Finland it may occur later depending on local climate and phenological conditions. Early-season behavior is crucial for reproductive success, but in Willow Tits timing appears to be shaped not only by food availability but also by social interactions and the timing of settlement relative to conspecifics (Parry and Broughton, 2018; Vatka et al., 2011; Pakanen et al., 2016), underscoring the importance of this window for understanding habitat use.

Recorders were initially programmed to monitor Pygmy Owl (*Glaucidium passerinum*) vocal activity and were set to record daily from 00:00–07:00 and 16:00–20:00 UTC. Although not optimized specifically for Willow Tits, these recording periods coincided with their known peaks in early morning and late afternoon vocal activity during territory establishment (Hogstad, 2009, 2015), making them suitable for species detection.

To maximize spatial coverage with limited devices, we used a spatial rotating window design: 90 ARUs were deployed sequentially across the 285 grid cells, with each recorder rotated among 3–4 sites over the survey period. Each site was sampled for 3–5 consecutive days, producing an average of 64 ± 22 h of recordings per location. Devices were mounted at a height of 1.5–2 m above ground on trees selected to reduce acoustic interference from wind and dense vegetation. All sites were

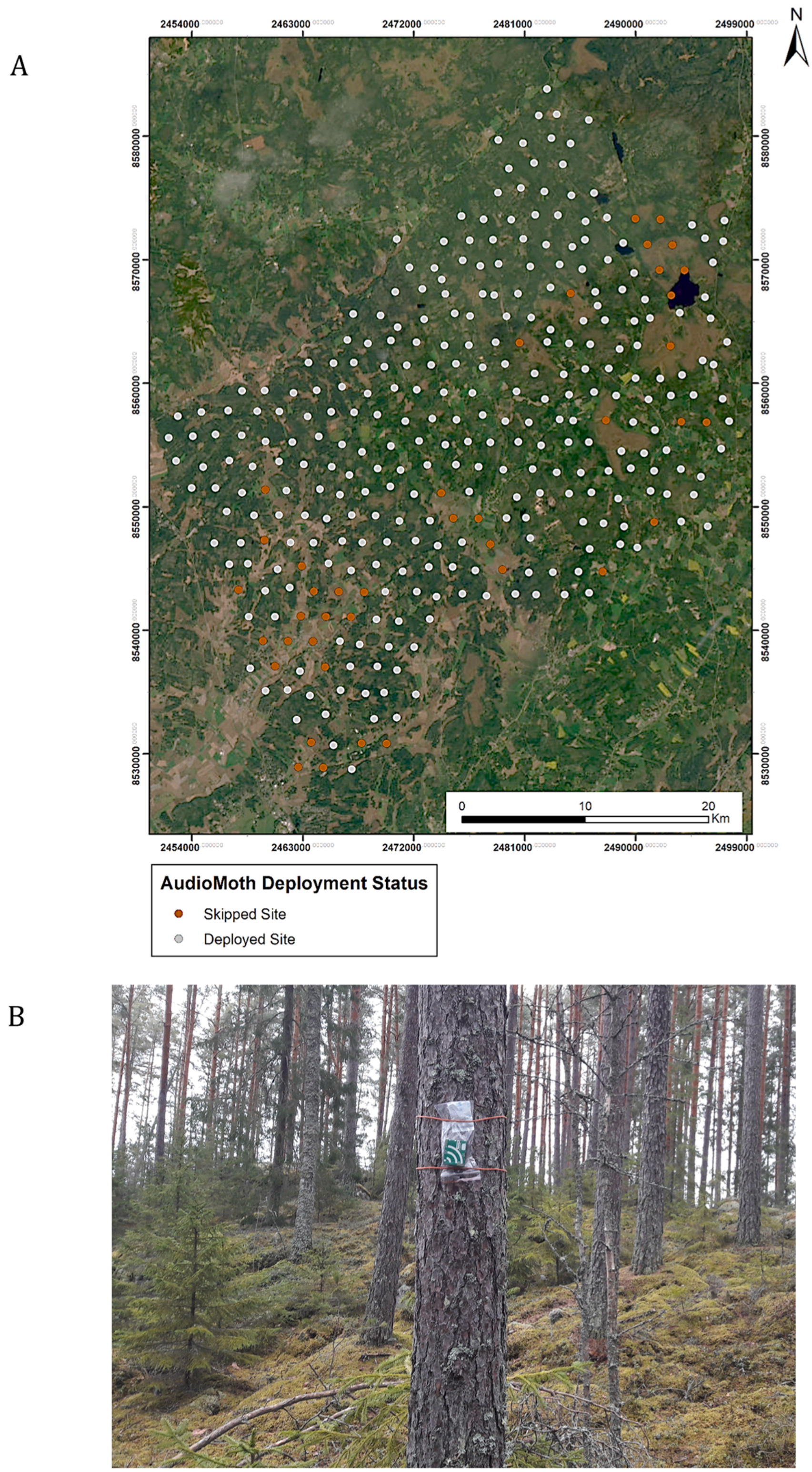

Fig. 1. (A) Example showing the placement of AudioMoth devices within the study area in southwestern Finland. Grey dots represent deployed devices; red dots indicate skipped sites due to insufficient forest cover within the 100 m buffer. (B) Example of an AudioMoth device installed on a tree.

separated by at least 500 m to minimize spatial autocorrelation.

This large-scale, standardized acoustic survey enabled the detection of Willow Tit vocalizations across a managed boreal forest landscape with heterogeneous structural and compositional conditions. To account for declining seasonal detectability as breeding approaches (Yoo et al., 2020), Julian date was included as a covariate in subsequent occupancy modeling.

2.2. Habitat variables

Habitat variables were selected based on known or hypothesized ecological requirements of Willow Tits during the pre-breeding period. Variables were extracted within 100 m and 400 m buffers around each site to capture habitat structure at both local and territory-relevant spatial scales (see Table 1).

Table 1
Habitat variables included in the analysis, with explanations, data sources, and summary ranges (100 m radius).

Variable title	Explanation	Resource	Amount of variable within 100 m radius in applied sites
Julian date	Start date of recording, used to account for seasonal variation in vocal activity	Recording metadata	March 16-April 25
Pygmy owl	Presence/absence of pygmy owl	Passive acoustic monitoring (Baroni et al., 2023)	Present in 63 sites (22%)
Crested Tit	Presence/absence of Crested Tit	Passive acoustic monitoring (Hamedani Raja et al., 2025)	Present in 195 sites (68%)
Distance to house	Minimum distance to the nearest inhabited houses	Cartographic maps	43–3249 m (mean = 715.4)
Sum pine foliage	Sum of pine foliage biomass (kg/ha)	Multi-source National Forest Inventory	30–27900 kg/ha (mean = 15500)
Sum deciduous foliage	Sum of deciduous foliage biomass (kg/ha)	Multi-source National Forest Inventory	84–16500 kg/ha (mean = 4050)
Mean expected dead wood	Modeled deadwood availability	Dead wood potential (DWP) modeling (Mikkonen et al., 2020).	0.08–1 (mean=0.62)
Area of mature forest	Forest area > 80years old	Aerial photographs and satellite imagery	0–3.17 ha (mean= 0.27)
Area of clearcut	Forest < 15 years old	Aerial photographs and satellite imagery	0–3.05 ha (mean = 0.33)
Area of Pine mire	Forested peatland dominated by pine	Multi-source National Forest Inventory	0–2.48 ha (mean= 0.2)
Area of spruce mire	Forested peatland dominated by spruce	Multi-source National Forest Inventory	0–1.02 ha (mean= 0.18)
Area of treeless peatland	Open bogs and fens	Multi-source National Forest Inventory	0–0.74 ha (mean= 0.01)
Initial variables were excluded to avoid redundancy	Mean and standard deviation of Pine foliage biomass, Mean and standard deviation of spruce foliage biomass, Mean and standard deviation of deciduous foliage biomass, mean and standard deviation of canopy cover, minimum distance from main road, ems (Fragmentation index), Forest cover, i.e. forest > 15 years old, Area of agricultural areas, Area of peatbogs, Total area of the raster layers included in the buffers		

Foliage biomasses of spruce, pine, and deciduous species (kg/ha) (each separately) were used as proxies for forest type and potential foraging habitat. This data was obtained from the Multi-Source National Forest Inventory maintained by the Natural Resources Institute Finland (Mäkisara et al., 2016). The same dataset was used to quantify peatland types, including pine mire, spruce mire, and treeless peatland—identified as key forest wetland habitats. Pine mires are particularly sensitive to forestry activities such as ditching and drainage, making them important indicators for evaluating ecological impacts of forest management.

Distance to the nearest house was calculated to assess the potential influence of human disturbance. This metric was derived from housing maps using QGIS tools (QGIS Development Team, 2020).

Forest age structure was classified using aerial and satellite imagery. Historical aerial photographs from 1949 and current Google satellite imagery were analyzed to categorize forests into three age classes: (1) recently clear-cut and young stands (<15 years), (2) mid-aged forests (15–80 years), and (3) mature forests (>80 years). These classes were used as explanatory variables to explore their potential influence on Willow Tit presence or absence. Forest age classes were used as coarse proxies for stand maturity and structural conditions relevant to cavity-nesting forest birds. Evidence from Willow Tit ecology indicates that very young or recently regenerated stands generally lack suitable cavity substrates, whereas habitat suitability tends to increase in mid-aged forests as dead wood begins to accumulate, even in the absence of old-growth conditions (Kumpula et al., 2023). Forest age alone does not capture important management-related factors, such as thinning history, and stands of similar age may therefore differ substantially in structural quality. This limitation is acknowledged in the interpretation of the results.

The presence of Pygmy Owl and Crested Tit were included as biotic variables (categorical: present or not), representing potential predator pressure and ecological overlap, respectively. Pygmy Owls are known predators of small passerines and are associated with mature forest habitat in the study area (Baroni et al., 2023). Crested Tits share similar foraging strategies and habitat preferences with Willow Tits and may indicate suitable forest conditions (Atiénzar et al., 2009; Suzuki, 2012). Presence data for both species were derived from passive acoustic recordings, collected as part of previous studies by Baroni et al. (2023) and Hamedani Raja et al. (2025).

The mean expected amount of decaying wood was calculated using a national raster layer derived from the Dead Wood Potential (DWP) model developed by Mikkonen et al. (2020). This model predicts the spatial distribution of deadwood across Finland based on multi-source forest inventory data, including tree species composition, stand volume and age structure, diameter distributions, and site fertility. The raster has a spatial resolution of 96 × 96 m and provides a standardized estimate of potential deadwood volume per pixel. For each study site, we extracted the mean DWP value within 100 m and 400 m buffers using the best available regional forest data layers. This variable was used as a proxy for the availability of potential cavity-nesting substrates for Willow Tits, although we recognize that it may not fully capture fine-scale features such as wood softness or snag characteristics

Because the recorders were deployed in rotation, not all sites were monitored simultaneously. To account for potential seasonal changes in vocal activity, the Julian date marking the start of recording at each site was included as a covariate in all models.

2.3. Statistical analysis

The software classifiers were trained using verified Willow Tit vocalisations and optimized to minimize false positives. Willow Tit presence/absence was determined using species-specific vocalisations detected with Kaleidoscope version 5.4.2. Automated detections included the characteristic three-note song as well as commonly used call types (including nasal contact/alarm calls) that could be reliably identified, while short or ambiguous call fragments were excluded. Detections were classified as presence (1) or absence (0), and cluster analysis was used to group candidate vocalisations.

The classifiers were trained using verified Willow Tit vocalisations, including both songs and calls, based on publicly available reference recordings and validated recordings from the study region where available. The training dataset included recordings from similar boreal forest environments within Finland, ensuring consistency with the acoustic characteristics of the focal population. All automated detections were subsequently reviewed manually by at least two experienced ornithologists (PR, DB) to ensure accurate species identification and minimize potential classification bias. Collinearity among independent habitat variables was evaluated using a correlation matrix generated with the *usdm* package (Naimi et al., 2014) in R (R Core Team, 2023). Variables with a bivariate correlation ≥ 0.70 were excluded to reduce redundancy. Additionally, Variance Inflation Factor (VIF) analysis was conducted at both spatial scales (100 m and 400 m buffers), with all VIF values below 5, indicating no significant multicollinearity among predictors. The relationships between Willow Tit presence/absence and environmental variables were analysed using generalized linear mixed models (GLMMs) with a binomial error distribution and logit link function. Models were implemented using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2023). Models were fitted using maximum likelihood. To account for spatial dependence among observations, we included an exponentially decaying spatial autocorrelation structure. Julian date was included as a fixed effect to account for seasonal variation in vocal activity and detectability.

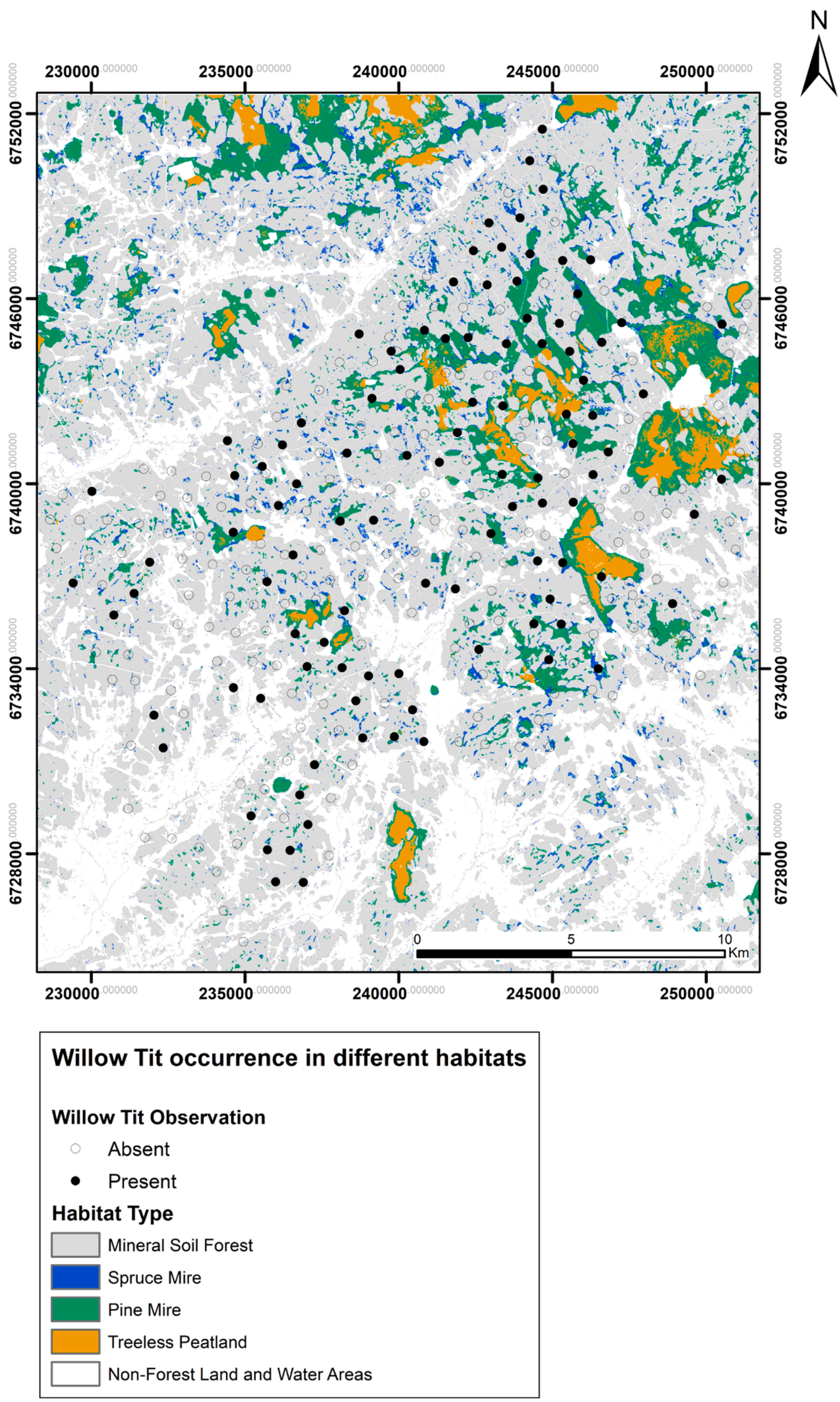

Fig. 2. Willow Tit presence (black dots) and absence (open circles) across the study area, displayed over dominant habitat types. Habitat types include pine mires (dark green), spruce mires (light green), treeless peatlands (orange/brown), and other habitats (white). Areas classified as mineral soil forests (light grey) are shown for spatial context but were not included as separate variables in the habitat analysis.

3. Results

3.1. Willow Tit presence and absence

Willow Tits were detected at 103 out of 285 sites (36%) during the one-week recording sessions. Detections were broadly distributed across the study area, indicating widespread occupancy within suitable forest habitats (Fig. 2). Note that mean values reported in Table 1 represent site-level averages within buffers and are not directly comparable to the visual extent of habitat types shown in Fig. 2.

3.2. Habitat preferences

Pine mire area showed a statistically significant positive association with Willow Tit presence at both the 100 m and 400 m spatial scales (Tables 2 and 3). At the 100 m scale, Willow Tits were more likely to be present in areas with more pine mires and in sites where Pygmy Owls were detected (Fig. 3A–B). At the 400 m scale, in addition to pine mire, there was a marginally positive association with pine foliage biomass ($p = 0.053$), while no clear association was observed with Pygmy Owl presence.

Modeled deadwood potential was significantly negatively associated with Willow Tit presence at the 400 m scale ($p = 0.034$) and showed a near-significant negative trend at 100 m ($p = 0.058$). Detection probability declined with Julian date, with a significant effect at the 400 m scale ($p = 0.018$) and a marginally significant trend at 100 m ($p = 0.059$). There were no other obvious associations between the explanatory variables and Willow Tit presence (Tables 2 and 3).

4. Discussion

This study provides new insights into the habitat preferences of the Willow Tit in boreal forests of Finland during the pre-breeding period, based on passive acoustic monitoring conducted across 285 forest sites. Using spatially explicit habitat data and GLMM analysis at two spatial scales (100 m and 400 m), we identified key environmental variables influencing the species' occurrence during early spring.

A consistent pattern across both spatial scales was the positive association between Willow Tit presence and the area of pine mires—forested peatlands dominated by Scots pine (*Pinus sylvestris*). These moisture-retaining habitats may support soft, decaying wood due to slower decomposition in waterlogged soils, particularly from pine and downy birch (*Betula pubescens*), which could facilitate cavity excavation by weak excavators like the Willow Tit (Broughton et al., 2021; Parry and Broughton, 2018). Previous research has emphasized the conservation importance of wetlands and peatlands for this species (e.g., Broughton et al., 2021; Milner et al., 2024), but few studies have examined specific peatland types. In our study, spruce mires did not show a significant association with Willow Tit presence, while mature

Table 2
Results of the binomial GLMM examining the effects of habitat variables on Willow Tit presence at the 100 m scale (radius around the automatic recording unit). Statistically significant predictors ($p < 0.05$) are shown in bold.

Term	Estimate	SE	Chisq	Df	P
Julian date	-0.032	0.017	3.560	1	0.059
Pygmy owl presence	**0.666**	**0.319**	**4.360**	**1**	**0.037**
Crested Tit presence	0.166	0.297	0.310	1	0.576
Distance to house	0.156	0.128	1.500	1	0.221
Sum Pine foliage	0.244	0.155	2.490	1	0.115
Sum deciduous foliage	0.145	0.145	1.000	1	0.317
Area of mature forest	-0.309	0.247	1.570	1	0.211
Area of clearcut	-0.190	0.143	1.760	1	0.185
Mean expected dead wood	-0.262	0.138	3.590	1	0.058
Area of spruce mire	0.111	0.143	0.610	1	0.436
Area of pine mire	**0.319**	**0.137**	**5.410**	**1**	**0.020**
Area of treeless peatland	0.003	0.148	0.000	1	0.984

Table 3
Results of the binomial GLMM for Willow Tit presence at the 400 m scale (radius around the automatic recording unit). Statistically significant predictors ($p < 0.05$) are in bold.

Term	Estimate	SE	Chisq	Df	P
Julian date	**-0.044**	**0.019**	**5.564**	**1**	**0.018**
Pygmy owl presence	0.627	0.332	3.564	1	0.059
Crested Tit presence	0.121	0.295	0.169	1	0.681
Distance to house	0.007	0.136	0.003	1	0.957
Sum Pine foliage	0.329	0.170	3.732	1	0.053
Sum deciduous foliage	0.049	0.159	0.094	1	0.759
Area of mature forest	-0.287	0.251	1.303	1	0.254
Area of clearcut	-0.194	0.146	1.755	1	0.185
Mean expected dead wood	**-0.300**	**0.141**	**4.504**	**1**	**0.034**
Area of spruce mire	0.132	0.153	0.744	1	0.388
Area of pine mire	**0.417**	**0.163**	**6.586**	**1**	**0.010**
Area of treeless peatland	-0.011	0.146	0.005	1	0.942

forest area—often highlighted as important breeding habitat—also had no detectable effect during the pre-breeding period. This contrast raises the possibility that pine mires may offer distinct early spring benefits not captured by coarse forest classification metrics, such as favorable microclimates or substrate qualities. In addition to structural characteristics, the association with pine mires may also reflect seasonal variation in foraging behavior during pre-breeding period. Willow Tits are known to shift from reliance on cached food during winter to exploiting newly available food resources in spring, including pine seeds released from opening cones. Pine-dominated habitats, including pine mires and plantations, may therefore provide important foraging opportunities during the pre-breeding period, when winter food stores are depleted and energetic demands increase. Previous work has shown that Willow Tits use pine-dominated peatlands outside the breeding season (Siffczyk et al., 2003), supporting the idea that habitat associations observed in pre-breeding period may be driven partly by seasonal resource availability rather than nesting requirements alone. However, as structural and microhabitat differences between mire types are not well documented, further field-based research is needed. The apparent role of pine mires should therefore be interpreted with caution but may reflect important breeding habitat requirements in managed boreal landscapes. It is also important to consider that while foraging areas may extend beyond the immediate nesting location, singing behaviour in territorial passerines is generally associated with territory defence and mate attraction, and therefore typically occurs within the breeding territory and is likely to be spatially associated with the nesting area (e.g. Parry and Broughton, 2018). In the present study, autonomous recordings do not allow direct identification of nest locations, and detections should therefore be interpreted as indicating territorial presence rather than confirmed nesting within a given habitat type. Willow Tit cavities are most commonly excavated in birch, alder, or goat willow, which often occur along forest–mire edges rather than within pine-dominated peatlands. The observed association with pine mires may therefore reflect the combined use of mire-associated foraging habitats and nearby edge habitats that provide appropriate nesting substrates.

Although this study does not directly assess breeding locations, Willow Tits are generally considered sedentary and maintain year-round territories (Hogstad, 2009). Therefore, detections during the pre-breeding period likely reflect individuals associated with the local population, although this cannot be confirmed directly in the present study. Willow Tits maintain relatively stable territories, although home range and territory size vary depending on habitat quality, season, and landscape structure (Broughton et al., 2021); average territory size in the boreal region is 12.6 ha, implying that the average territory area has a radius of about 200 m (Siffczyk et al., 2003). Audio-based detection probabilities of the closely related Marsh Tit (*Poecile palustris*) are 131 m and 181 m for 50% and 5% expected detection probability respectively (Winiarska et al., 2024). As the precise location of the individual relative to the recording unit is not known, our detections should be interpreted

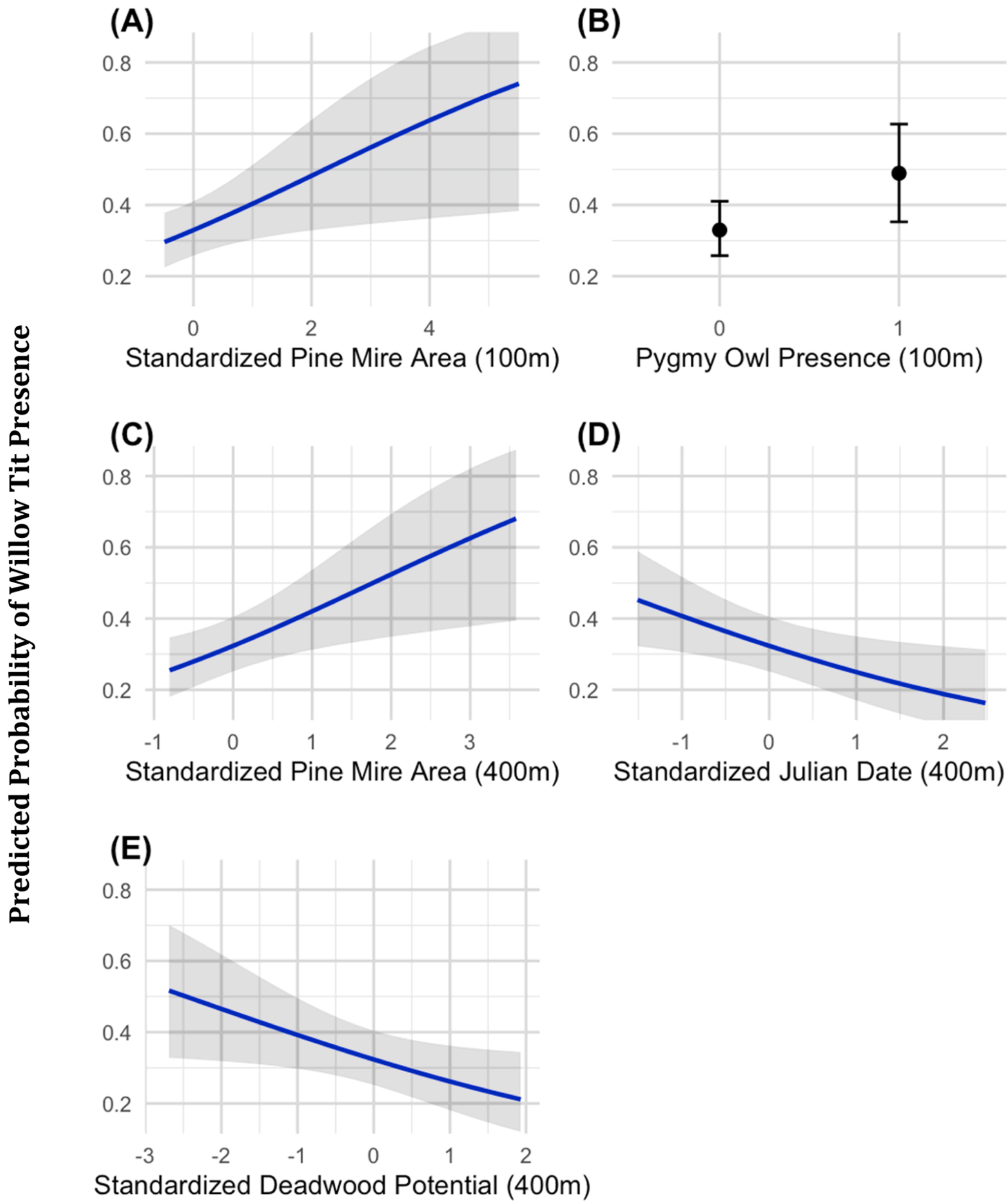

Fig. 3. Predicted probability of Willow Tit presence in relation to key habitat variables at two spatial scales, based on GLMM. Panels A and B show 100 m buffer results: (A) standardized pine mire area and (B) Pygmy Owl presence. Panels C–E show 400 m buffer variables: (C) standardized pine mire area, (D) standardized Julian date, and (E) standardized mean deadwood potential. All predictors were standardized (mean = 0, SD = 1) for effect size comparison. Solid lines represent model predictions with 95% confidence intervals (shaded ribbons or error bars).

as indicating presence of a singing (presumably territorial) individual somewhere in an area covering this distance. Given the territory size and likely detection distances, the radius of 100 m and 400 m around the recording unit, which are the buffers used in our study, presumably capture at least parts of an individual's territory. An additional consideration is that singing behavior may not be evenly distributed within territories. Willow Tits may vocalize more frequently near territory boundaries during interactions with neighboring individuals, which could influence the spatial pattern of acoustic detections. Lastly, the detection range of autonomous recording units in forest environments is variable and depends on factors such as species-specific vocal characteristics, vegetation structure, and weather conditions (Winiarska et al., 2024). Detection distances are therefore not fixed and can vary substantially across habitats and recording conditions, which further constrains the potential for inference about fine-scale habitat use. We here use presence–absence data, which does not capture variation in vocal activity, which may provide additional ecological information relevant to separate different levels of habitat use. While the above considerations highlight the importance of cautious interpretation when linking acoustic detections to habitat use, PAM's power in the study of habitat selection, relative to human-observer based detections, lies in the capacity of PAM to have a large number of audio recordings made simultaneously during a considerable period of time.

The consistent importance of pine mires at both local and landscape scales suggests that these habitats may play a key role in early-season territory settlement for Willow Tits. In contrast, mature forest area—commonly considered a key predictor of Willow Tit occurrence (Lehikoinen et al., 2024; Vatka et al., 2014)—did not emerge as significant in our models. This result may reflect limitations in how forest maturity was defined in our analysis (i.e., >80 years), as this threshold might not adequately capture structural attributes critical to the species, such as deadwood characteristics, understory density, or specific tree species composition. In boreal forest succession, stands over 80 years old may still lack the structural complexity and microhabitat diversity typical of true old-growth forests (typically >120 years), which are often associated with higher biodiversity and the presence of specialist species. The absence of a positive association with mature forest during the pre-breeding period, and the weak negative relationship observed in spring, may reflect seasonal shifts in habitat use across the annual cycle. Willow Tits occupy relatively large winter territories that often include a variety of habitat types, including older forest stands where food caching is common. During winter, such habitats are likely important for survival. In spring, however, cached food resources may become depleted, and birds may increasingly rely on alternative food sources, such as pine seeds that become available in pine-dominated habitats, including pine mires and planted forests. A shift in activity from winter territories rich in old forest toward habitats offering seasonally available food resources could therefore result in a negative association with mature forest during pre-breeding period. Importantly, this pattern does not imply that old forests are unimportant for Willow Tits, but may rather highlight seasonal variation in habitat use and detectability. Acoustic monitoring conducted during the winter period would provide valuable insight into seasonal changes in habitat associations.

Interestingly, Pygmy Owl presence was also positively associated with Willow Tit occurrence at the 100 m scale. As Pygmy Owls are typically linked to mature and structurally rich habitats (Avotins et al., 2022; Baroni et al., 2023), their co-occurrence with Willow Tits may indicate shared use of high-quality forest patches not fully described by available forest age metrics. This finding supports the idea that both species may depend on fine-scale habitat features that are poorly represented in broad-scale forest inventories and thus may require more detailed field-based assessments in future studies (Barbaro et al., 2016; Baroni et al., 2021; Broughton et al., 2021; Kumpula et al., 2023; Nikolov et al., 2022).

We also observed a decline in Willow Tit detections over the course of the study period in spring, with detection probability decreasing significantly at the 400 m scale and marginally at 100 m. This likely reflects reduced vocal activity later in the pre-breeding period as individuals finalize territory establishment. Seasonal variation in detectability has important implications for survey design, particularly for monitoring programs conducted during or after the breeding season, which may underestimate occurrence. However, as monitoring dates were not fully balanced across sites, spatial and seasonal variation were partially confounded. Repeated sampling at fixed locations throughout the early season would help clarify temporal effects on detection.

One unexpected finding was the negative association between Willow Tit presence and modeled deadwood potential (MDW). While deadwood is ecologically important for cavity-nesting birds, including Willow Tits (Haartman, 1969; Lehikoinen et al., 2024; Parry and Broughton, 2018), the MDW index used in this study is derived from regional forest inventory data and reflects potential deadwood volume at the stand level, rather than direct measurements of ecologically relevant features. Specifically, it is based on tree species composition, stand structure, and site fertility (Mikkonen et al., 2020), but does not include field-validated parameters such as snag softness, decay stage, or wood fragmentation, which are essential for cavity excavation by weak excavators. Furthermore, in intensively managed forests, modeled deadwood estimates may not correspond to the actual availability of suitable nesting substrates. Therefore, the lack of a positive relationship in our study may reflect the technical limitations of the modeled proxy, rather than a lack of ecological importance of deadwood itself. This finding underscores the need for improved habitat metrics that capture fine-scale resource availability, particularly when modeling habitat suitability for specialist species like the Willow Tit. In particular, tree diameter (dbh) and ground or shrub vegetation structure are known to influence the availability and suitability of nesting substrates for Willow Tits (e.g. Parry and Broughton, 2018; Kumpula et al., 2023) but were not available in our dataset. Incorporating such field-based variables in future studies would likely improve the characterization of habitat quality.

The negative association with modeled deadwood potential should also be interpreted in the context of seasonal timing and resource use. The species does not necessarily benefit from high quantities of dead wood per se, but rather from the availability of specific nesting substrates, particularly standing snags affected by white rot fungi that produce soft wood suitable for excavation. Such fine-scale qualitative features are not captured by landscape-level deadwood potential indices. Importantly, the lack of a positive association in this study does not imply that old forests or dead wood are unimportant for Willow Tits, but instead highlights the limitations of coarse proxies and the importance of seasonal context when interpreting habitat associations.

At the 400 m scale, we also found a marginally positive association between Willow Tit presence and pine foliage biomass, which may indicate potential foraging resources. The absence of a similar effect at the 100 m scale suggests that foraging decisions may be made at broader spatial scales, while finer-scale selection is influenced more by shelter and nesting features such as those found in pine mires. This scale-dependent pattern consists of hierarchical habitat selection frameworks, where different ecological needs (e.g., foraging versus nesting) operate at different spatial levels (Kristan, 2006; Mayor et al., 2009; McGarigal et al., 2016).

Neither the presence of Crested Tits nor distance to human settlements showed a significant association with Willow Tit occurrence in this study. The lack of a detectable effect of Crested Tit presence may suggest that, during the pre-breeding period, niche overlap or competitive interactions are not strong determinants of habitat use at the spatial scales considered, or that both species respond similarly to underlying habitat features. Alternatively, passive acoustic detections may not fully capture subtle interactions between species, such as fine-scale spatial avoidance.

Similarly, the absence of a clear effect of distance to human settlements may indicate that Willow Tits are not strongly influenced by human disturbance at the landscape scale examined, or that the metric used does not fully capture relevant aspects of disturbance, such as forest management intensity or local habitat alteration. These results should therefore be interpreted cautiously, and further studies incorporating more detailed measures of interspecific interactions and disturbance are warranted.

In addition, nest predation and competition from other cavity-nesting species, such as Great Spotted Woodpecker (*Dendrocopos major*) and Blue Tit (*Cyanistes caeruleus*), may influence habitat selection and breeding success in Willow Tits. However, the very high occurrence of Great Spotted Woodpecker across our study sites suggests limited variation at the spatial scale considered, and such biotic interactions were not explicitly included in the present analysis. Incorporating these factors in future studies would provide a more comprehensive understanding of habitat use across seasons. The blue tit again only infrequently breeds in the forests of the study area (Hanzelka et al., 2023 a,b).

Together, these findings emphasize the need to consider both ecological processes and methodological constraints when interpreting habitat associations.

5. Management implications

Our findings underscore the ecological value of pine mires for Willow Tits during the pre-breeding period. These habitats likely provide essential nesting substrates and adequate food resources that support early territory establishment. The use of passive acoustic monitoring enabled the detection of habitat use across a large spatial extent, demonstrating the method's effectiveness for avian habitat assessment. Importantly, our results show that generalized or modeled habitat metrics—such as forest age and deadwood potential—may fail to capture fine-scale cues critical for habitat suitability. Conservation efforts targeting Willow Tit populations should therefore prioritize the protection and restoration of pine-dominated wet forest patches, even when these occur in small or fragmented areas.

The results further suggest that Willow Tits may benefit from landscapes that maintain a mosaic of relatively old or mature forest stands (Lehikoinen et al., 2024) and mire habitats (our results). Management activities that reduce forest structural complexity, such as intensive logging or thinning, or that alter hydrological conditions through drainage, may reduce habitat suitability for the species.

Although this study focuses on Willow Tits in boreal Finland, the ecological insights gained are relevant for forest planning in other regions facing similar ecological and management challenges. The limitations identified in modeled habitat proxies, together with the importance of structurally complex, moisture-rich habitats, are likely to apply more broadly across boreal and temperate landscapes. From a forest management perspective, long-term shifts in tree species composition—particularly the replacement of natural pine stands with spruce plantations—may further influence habitat suitability for Willow Tits (Lindbladh et al., 2019; Petersson et al., 2019). Management strategies that maintain or restore pine mires, especially in wet or marginal sites, may therefore enhance early-season habitat suitability and contribute to long-term population persistence. Further research into planting trends and peatland loss is needed to inform conservation planning and the development of climate-resilient forestry strategies that integrate biodiversity objectives.

CRediT authorship contribution statement

Jon Egbert Brommer: Writing – review & editing, Supervision, Methodology, Conceptualization. **Pegah Hamedani Raja:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Toni Laaksonen:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Daniele Baroni:** Writing – review & editing, Validation, Methodology, Data curation.

Declaration of Generative AI and AI-assisted technologies in the writing process

AI or AI-assisted technologies were not used in the writing process of this manuscript.

Funding

P.H.R. received a one-year personal research grant from the Emil Aaltonen Foundation, which supported living expenses during the period in which this research was conducted. The funder did not provide direct funding for data collection, study design, or analysis, and had no role in the interpretation of results or the decision to submit the manuscript for publication. Suomen Luonnonsuojelun Säätiö and Vuokon Säätiö supported field work in the study area.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors declare that no additional individuals contributed to this work beyond the listed authors.

Data availability

Data will be made available on request.

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