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Research article

Bird health in forests: exploring relationships between forest structural complexity, body condition, and tick infestation

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ABSTRACT

Forests provide crucial habitats for nature and people, but also harbour organisms, such as ticks, that can act as vectors for pathogens. Understanding how forest management practices influence host-parasite-pathogen interactions is essential for promoting both forest biodiversity conservation and nature's contributions to people. This study investigates the complex relationships between forest structural complexity, body condition, and tick infestation probability in a common forest bird, the great tit (*Parus major*), across 19 forests in the Flemish Ardennes, Belgium. Using Structural Equation Modeling (SEM), we first integrated multiple phenotypic health proxies into a single overall condition index. Subsequently, we assessed how variations in forest structural complexity impact the condition of forest birds and their chances of contracting ticks. Our findings showed that birds in better physiological condition, as indicated by lower levels of cellular stress, were more likely to carry ticks. This may be due to ticks preferring healthier and more nutritious hosts and/or condition-linked differences in bird behaviour (e.g. foraging), resulting in higher contact rates with ticks. While forest structural complexity did not significantly affect the birds' overall body condition, it was responsible for an increased tick infestation probability. Specifically, forests with higher structural complexity were associated with increased densities of questing nymphs, thereby elevating the risk of tick infestation in birds. This study highlights the multifaceted role of forest structural complexity in shaping host-parasite dynamics. These insights are valuable for developing forest policies that balance the enhancement of ecological health with the mitigation of health risks posed by tick-borne diseases.

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1. Introduction

Structurally complex forests with diverse vertical profiles and rich understory provide a wide range of (micro)habitats for a plethora of species, as well as a wide range of ecosystem services that contribute to human well-being [1]. Consequently, such forests are increasingly seen as a desirable management target. However, the complexity of these forests can also provide favourable conditions for pathogens and their vectors, potentially increasing the risk of infection. For example, in North America, Ginsberg et al. [2] found that canopy cover significantly predicted the number of larval and nymphal ticks in flag/drag samples. Increased canopy cover increases the availability of moisture on the forest floor, creating favourable conditions for tick survival and activity. Similarly, several studies have found higher tick densities in forests with denser shrub and herb cover [3–6]. The prevalence of vector-borne pathogens is also influenced by habitat, but such relationships may be particularly complicated. As disease vectors, their hosts and the interactions between them are dependent on habitat and landscape features, high quality habitats can either dilute or amplify the presence of pathogens [7]. Dilution effects have been shown to occur for some vector-borne pathogens, such as *Borrelia burgdorferi*, but not for others (reviewed by Huang et al. [8]). Forest structure and composition may also interact with the characteristics and behaviour of host species. For example, birds with higher body mass and those that forage closer to the ground tend to carry more ticks [9]. While fewer studies have examined intraspecific patterns in tick loads, Heylen et al. [10] found a positive correlation between bracken (*Pteridium*) cover and tick loads within great tit (*Parus major*) populations.

Thus, while structurally complex forests may harbour a wider richness and abundance of parasite vectors and pathogens, they can also improve the health and resilience of the host species, making them less susceptible to disease. Indeed, more complex forests are likely to provide greater and more stable availability of food resources and more sheltered habitats, resulting in birds with better nutritional status [11,12] and lower physiological stress [13]. However, current evidence suggests that individual health and condition may influence parasite burden both positively and negatively [14–17]. A first hypothesis is that parasites are attracted to hosts in optimal condition due to their superior nutritional value, although it is recognized that such hosts may also have stronger anti-parasitic defences [18]. Conversely, an alternative hypothesis suggests that parasites selectively colonize hosts in suboptimal condition, because their reduced defences make them easier targets. In line with the first hypothesis, field and laboratory studies in bat species revealed that ectoparasitic mites show a clear preference for individuals with a higher nutritional status [19]. In support of the second hypothesis, it was found that in breeding house martins (*Delichon urbicum*), blood-sucking ectoparasites fed preferentially on chicks with poorer body condition and a weaker immune response [20].

Despite growing interest in the effects of biodiversity on disease prevalence to inform forest management that maximizes biodiversity while controlling infection risks, direct and indirect relationships between forest structural complexity, animal health and pathogen dynamics remain poorly understood [21,22]. This study addresses that gap by examining how forest structural complexity affects both the body condition of a resident insectivorous bird, the great tit, and its infestation by ticks. In earlier work, we investigated how forest structural complexity influences the nutritional condition of great tits, using feather growth bar widths as a proxy for food intake during moult. This technique, known as ptilochronology [23], revealed that individuals in structurally complex forests exhibited wider and more consistently sized growth bars, indicating better nutritional status likely due to more stable and diverse food availability in such habitats [24]. Here, we build on these findings by broadening the concept of condition to include multiple physiological and developmental dimensions, and by investigating whether and how variation in forest structural complexity affects tick infestation directly (via host condition) and indirectly (via tick habitat).

Birds, as relatively mobile organisms, can transport ticks to different areas within forests, thereby facilitating the spread of ticks and the bacteria they may harbour, such as *Borrelia*, the causative agent of human Lyme disease. While the role of migratory birds in long-distance pathogen dispersal is well documented in the literature [25,26], less attention has been paid to how forest structural complexity as a component of habitat quality influences the contribution of resident birds to tick population dynamics and the potential spread of tick-borne pathogens. The great tit was selected as a study species because it serves as a top predator in insectivorous food webs, playing a critical role in regulating herbivore populations [27,28]. Its foraging behaviour has significant effects on arthropod dynamics, which in turn influence forest ecosystem structure and function [29,30]. As such, the great tit is a valuable indicator species for assessing the broader impacts of forest fragmentation and resource availability on ecosystem functioning and overall biodiversity [31].

The study area covers a range of forest structural complexity, assessed using the Structural Complexity Index (SCI) [24,32,33], which includes several structural forest characteristics such as canopy cover, forest maturity and tree species diversity. To determine the health and condition of great tits, a number of phenotypic proxies were measured and Structural Equation Modeling (SEM) was used to integrate these proxies into five latent aspects of body condition: energy store, nutritional condition, pre-fledging developmental stress, post-fledging developmental stress and cellular (physiological) stress. Such an approach allows for a more comprehensive understanding of how the environment affects individuals than studying a single condition indicator [34]. Subsequently, SEM is used to analyse the direct and indirect relationships between forest structural complexity, bird health and tick prevalence. We hypothesize that birds in structurally more complex forests will have a better body condition and investigate two pathways through which forest structural complexity may affect tick presence on birds: first, by providing favourable conditions for ticks, and second, by influencing tick infestation through its positive effect on host body condition. As previous research has shown that great tits have an ineffective immune response to tick infestation [35,36], we also hypothesize that more ticks will be detected on individuals with high body condition.

2. Material and methods

2.1. Study area

Ticks and birds were trapped in 19 temperate and deciduous forests in the Flemish Ardennes, Belgium, a region characterized by a mean annual temperature of 10.5–11.0 °C and a mean annual precipitation of 800–900 mm (KMI) (for a map see Fig. S1). Three different forest types, beech (*Fagus sylvatica*), oak (*Quercus robur*) and poplar (*Populus* × *canadensis*) were selected along a gradient of forest structural complexity, with the dominant tree species covering more than 60 % of each plot. Variation in forest area (at least 3 ha), land-use history (forested since no later than 1850) and potential natural vegetation (oak-beech forest) was kept to a minimum [37,38]. The structural complexity of each forest was calculated from the characteristics of the forest structure (based on the presence of vertical and horizontal stand structures), woody layer (based on the species composition and diameter of trees and shrubs), herbaceous layer (based on the species composition of the herbaceous layer) and deadwood (based on the extent of standing and lying deadwood) in a 1 ha core plot (detailed in Catfolis et al. [24]). Structural Complexity Index (SCI) values ranged from 0 to 1, with higher values indicating greater structural complexity in the forest (Table S1, Fig. S2).

2.2. Bird trapping and tick load sampling

A total of 260 fully grown great tits (on average 14 ± 6 per plot) were captured between February and April 2021 using 12 m wide four-shelf mist nets with a mesh size of 16 × 16 mm (Ecotone) (Fig. S3). Upon capture, (i) each bird was ringed, sexed (48 % male, 52 % female) and aged (immature: younger than 1 year (58 %); adult: older than 1 year (42 %)) based on plumage characteristics [39]; (ii) body mass was determined to the nearest 0.01 g using an analytical balance and fat content (hereafter 'Fat Score') was determined following [40]; (iii) tarsus and wing length were measured to the nearest 0. 01 mm using a digital calliper; (iv) ca. 50 μL of blood was taken from the brachial vein for telomere length analysis; (v) the second outer right and left rectrices were plucked, placed in labelled envelopes and stored at room temperature prior to growth bar widths (hereafter GBW) and fluctuating asymmetry (hereafter FA) analysis; and (vi) each bird was carefully checked for ticks around its head and abdomen. The feathers were blown apart and the skin inspected. Ticks detected were carefully removed with pointed tweezers and preserved in 70 % ethanol for identification. After measurement and sampling, all individuals were released at their original capture site. Of the 260 great tits captured, 58 individuals were excluded due to missing data, leaving 202 individuals for analysis. Among these, 37 birds were found to carry one or more ticks, totalling 58 ticks. In the lab, ticks were examined using a light microscope (VWR VisiScope TL384P), and images of key morphological features were taken with ProView software (Informer Technologies, 2021) to assist in species determination. Identification was performed using the reference guides by Estrada-Peña et al. [41] and Nosek & Sixl [42]. In total, 22 larvae and 36 nymphs were identified, including the species *Ixodes ricinus* (69 %), *Ixodes frontalis* (16 %), *Ixodes arboricola* (7 %) and *Ixodes* sp. (8 %). In the remainder of this study, 'tick presence' will be used as a binary response variable, indicating whether or not a bird carried at least one tick.

2.3. Questing tick sampling and density estimation

Ticks were collected from the vegetation in the 1 ha core plot during June, July and September 2021. Although the timing of tick collection and bird sampling did not coincide, it can be assumed that tick densities in the different forest plots remain stable enough within the same year to allow for meaningful comparisons across plots. Previous research in the same region (Flanders, Belgium) has shown that although the density of nymphs changes over the months, the relative difference between plots remains consistent [43]. In other study systems, similar patterns have been observed [44–47]. As described in Vanroy et al. [48], tick sampling was carried out by dragging a 1m × 1m cloth over the understory vegetation and litter layer for sampling, avoiding rain and wet conditions. Orientation adjustments were made to minimize dragging over large dead wood and brambles. In each forest plot, ticks were sampled along four 18 m long and 1m wide transects forming a cross shape centred on the plot. To ensure consistency in sampling effort, the dragging was conducted by the same person at a constant pace across all plots, minimizing variability in tick collection. At the end of each transect, ticks were removed from the cloth with tweezers, categorized by life stage (larvae, nymphs, adult males and adult females) and preserved in 70 % ethanol. The density of nymphs (DON) per plot was determined by dividing the total number of nymphs (sum of three months) by the total area sampled (72 m^2). A total of 962 nymphs were collected from the vegetation. Among them, 232 ticks were morphologically identified at the species level using the determination protocol described above, and all were confirmed to be *Ixodes ricinus*. The mean DON per plot was 0.70 ± 0.49. Upon analysing, DON was log-transformed and rescaled.

2.4. Phenotypic measurements

To assess an individual's energy store, two different size-adjusted mass indices were calculated: the ratio of body mass to tarsus length ([49]; hereafter 'Ratio') and the scaled mass index ([50]; hereafter 'SMI'). The SMI standardizes the mass of individuals based on the assumption of an equal body size, and this standardization was achieved by using the linear regression equation derived from log-body mass and log-tarsus length by type-2 regression (standardized major axis). After excluding one outlier (i.e., |standardized residual| > 2), the regression slope was 1.92, while the average tarsus length was 19.57 mm. The scaled mass index was calculated as body mass × $(19.57/\text{tarsus length})^{1.92}$.

To assess an individual's nutritional condition, the average width across a standardized number of growth bars on the second outer right and left rectrices was calculated. Bird feathers have a series of growth bars, visible as a combination of alternating dark and light bands, with each pair corresponding to a 24-h period of feather growth. Experimental and correlational studies of growth bar width (GBW, ptilochronology *sensu* Grubb [23]) in captive and wild birds have shown that this metric allows inferring the relative access and energy costs of individuals to food resources during feather synthesis [51–54]. Following the methodology outlined in Catfolis et al.

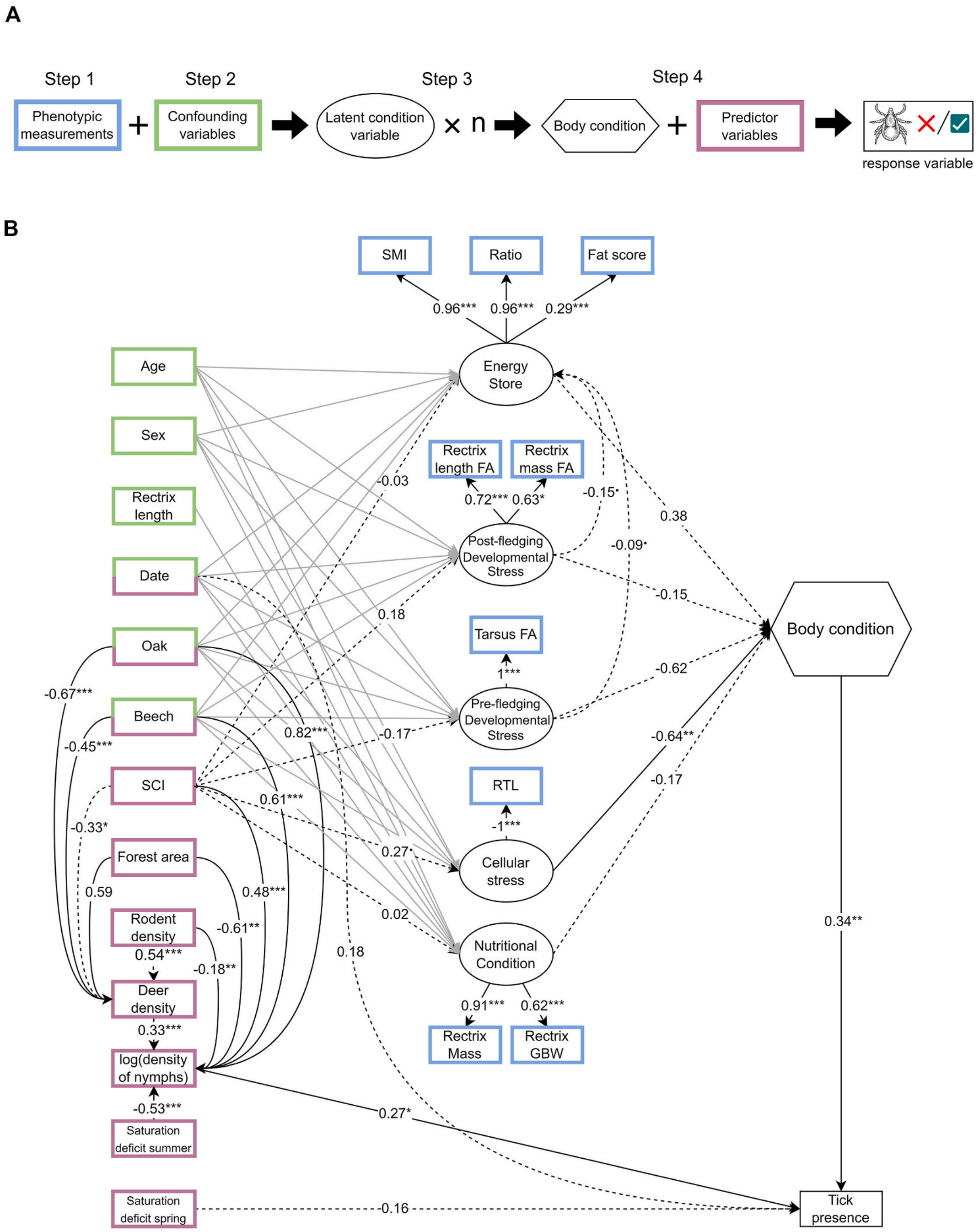

Fig. 1. **A)** Flowchart of the four-step procedure to construct SEM; **B)** Full SEM model including latent (circles), composite (hexagon) and observed (squares) variables. Observed variables are either phenotypic measurements (blue), confounding variables (green) or predictor variables (purple). Values represent standardized path strengths. Solid lines denote significant ($p < 0.05$) positive and negative paths. Significance levels are marked with a point or asterisk(s) next to the standardized strength ($0.05<p < 0.1$. ; $0.01<p < 0.05$ *; $0.001<p < 0.01$ **; $p < 0.001$ ***). Dashed lines indicate non-significant pathways ($p > 0.05$). For simplicity, the path strengths of the confounding variables (except for SCI) are not documented (see Supplementary Material S4). Abbreviations: SCI = Structural Complexity Index; SMI = Scaled Mass Index; FA = Fluctuating Asymmetry; RTL = Relative Telomere Length; GBW = Growth Bar Width.

[24], each cleaned feather was attached to a white paper with a calibration line mounted on a polystyrene board, and its distal and proximal ends were marked with an ultra-fine pin. Visible growth bars in the vane area were marked along the rachis of the feather. The marked paper was then scanned on a light plate (Ricoh IM C300 default settings), showing each mark as a black dot, and an image analysis script in Python was used to automatically measure the distance between each dot, providing measurements for total feather length (for FA analysis) and width of each individual growth bar (for GBW analysis). Mean GBW was calculated as the sum of all GBWs divided by the total number of visible growth bars.

The degree of fluctuating asymmetry (FA) in tarsus length and in tail feather length was calculated as proxies for an individual's ability to cope with developmental stress before (Tarsus FA) and after (Rectrix FA) fledging. FA quantifies the small, random deviations from perfect bilateral symmetry between the left and right sides of an organism's body and is interpreted as an indicator of an individual's ability to undergo stable development under a given set of genetic and environmental conditions [55]. Higher levels of FA are indicative of environmental disturbances that disrupt the normal developmental processes, resulting in greater asymmetry [56]. FA was determined by measuring twice the length of the left and right tarsi and the length and mass of the second outer left and right rectrices. Feather length was measured as described above, while feather mass was determined using an Ohaus Galaxy 110 balance (accuracy equal to 0.001 g). To estimate FA, a mixed regression analysis with restricted maximum likelihood (REML) parameter estimation was performed [57]. This method allows unbiased estimates of individual FA to be obtained by explicitly accounting for heterogeneity in measurement error estimated from repeated measurement of each (left and right) trait (full details in Van Dongen et al. [57]).

Finally, telomere length was calculated to assess an individual's level of physiological stress at cellular level. Telomere length measures the length of the protective end caps of chromosomes, serving as a marker for cellular aging and stress. Telomere lengths are commonly used to assess an individual's health and lifespan potential, with shorter telomeres indicating higher stress or poorer condition. Here, relative telomere length (RTL) was analysed using quantitative PCR (qPCR) by determining the ratio (T/S) of telomere repeat copy number (T) to single control gene copy number (S), relative to a reference sample (DNA mix of all samples). Glyceraldehyde-3-phosphate dehydrogenase (GAPDH) was used as the single control gene [58,59]. Briefly, genomic DNA was extracted from avian blood samples using the DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's protocol. The amount and purity of DNA was measured using a Nanodrop 1000 spectrophotometer. Reactions were performed in 25 μl volumes containing 5 μl DNA (varying concentrations of DNA for serial dilutions of the standard curve and 1/1000 dilutions for unknown samples), 12.5 μl SsoAdvanced Universal SYBR Green Supermix, primers (TelF: 100 nM; TelR: 200 nM; GAPDH F-R: 500 nM) and water to 25 μl. A 1/1000 dilution of a DNA mixture of all samples was included on each plate as a reference sample. The average inter-assay coefficient of variability (CV) of the Ct values was 2.18 % for the telomere assays and 2.28 % for the GAPDH assays. All samples, including the standard curve, were run in duplicate and the average values were used to calculate the relative telomere/GAPDH ratios for each sample relative to the reference sample. Samples with a Cq difference between replicates >1.0 were excluded from the analysis. After correction for interplate variation, the following formula was used to analyse relative telomere length: $2^{-\Delta\Delta Ct}$, where $\Delta\Delta Ct$ = (Ct telomere - Ct GAPDH)sample - (Ct telomere - Ct GAPDH)reference [58,60]. A more detailed description can be found in Supplementary Material S1.

2.5. Structural Equation Modeling

To build a Structural Equation Model (SEM) with predictor and response variables of condition and stress, a four-step procedure was followed (Fig. 1A).

First, the extent and direction of the correlations between phenotypic measurement such as SMI, Rectrix Growth Bar Width or Telomere Length (observables indicated by rectangles in Fig. 1B) and the hypothesized latent variables representing aspects of an individual's overall body condition (indicated by circles in Fig. 1B) were examined. These relationships were expected based on prior theoretical models, as is typical in Confirmatory Factor Analysis (CFA, the first step in SEM), which tests whether the observed data fit a predefined model. Specifically, a set of latent condition variables was created: 'Energy Store' (reflecting the amount of body reserves at the time of capture; expected to be related to 'SMI', 'Ratio' and 'Fat Score' [49]), 'Pre-fledging Developmental Stress' (reflecting environmental or genetic stress before fledging, and described by the birds' tarsus, which is fully-grown by the time birds fledge from the nest; expected to be related to 'Tarsus length FA' [56,61]), 'Post-fledging Developmental Stress' (reflecting environmental or genetic stress during feather growth; expected to be related to 'Rectrix length FA' and 'Rectrix mass FA' [62]), 'Cellular Stress' (reflecting biological aging and physiological stress throughout life; expected to be related to the inverse of 'Telomere Length', as shorter telomers indicate higher cellular stress levels [63,64]) and 'Nutritional Condition' (reflecting the balance of energetic intake versus expenditure during rectrix moult; expected to be related to 'Rectrix GBW' and 'Rectrix Mass' [53]) (see Supplementary Materials Table S2).

Second, the SEM was fitted within a Multiple Indicators Multiple Causes (MIMIC) modeling framework [65,66], which enabled testing the effect of forest structural complexity on the latent condition variables while simultaneously accounting for the potential influence of other observed variables (indicated as confounding variables in Fig. 1B) on the latent variables, apart from their indicators. To this end, individual-level covariates (bird sex, age and rectrix length), forest plot covariates (forest type, i.e. beech, oak or poplar) and a time-related covariate (day of capture) were included.

Third, the latent variables were used to construct a 'composite variable' (indicated by the hexagon in Fig. 1B). This composite variable represents the collective information contained in the five latent variables [67], which underly the overall 'body condition' that is not directly observable in nature. The composite variable 'body condition' was thus defined by the weighted sum of the latent condition variables, where the weights reflect the influence of each latent variable on tick presence. This composite variable was then used as a predictor of tick presence on great tits, incorporating the influences of both internal (i.e. the different condition indices described above) and external (i.e. forest structural complexity and the confounding variables described above) factors. This step thus enabled testing the hypothesis that forest structural complexity influences tick infestation through its effect on host body condition.

Fourth, to test the hypothesis that forest structural complexity affects tick presence on great tits by providing favourable conditions for ticks, direct and indirect relationships were specified between tick prevalence, forest structural complexity, and a number of exogenous predictor variables that have been previously reported to potentially influence tick prevalence, i.e. forest plot covariates (forest area and type, i.e. beech, oak or poplar), weather condition (saturation deficit, i.e. an index integrating temperature and relative humidity to give a measure of the drying power of the atmosphere, with low levels indicating humid air with less drying power, generally beneficial for ticks), and rodent, deer and log-transformed tick nymph densities sampled in the shrub vegetation layer (see Supplementary Materials S2 & S3). These variables were fitted as multiple regressions that either directly or indirectly influenced tick presence.

2.6. Statistical analysis

All statistical analyses were performed in R Studio [68] using the "lavaan" package [69]. Only individuals with complete data for all variables were retained for analysis (n = 202). All numerical data were mean-centred (i.e., each observation was subtracted from the mean) and standardized (i.e., divided by the standard deviation). Model fitting and parameter estimation were performed using the small-sample size WLSMV estimator, which estimates model parameters by minimizing the weighted sum of squared residuals using a diagonal weight matrix based on the variances of the observed variables. Covariation between variables was assessed and accounted for using modification indices, which measure the distance between the fitted and implied covariance matrices, with a modification index value greater than 10 used as a cut-off. Scaled model fit indices were used to assess the adequacy of the model. An acceptable model fit is indicated by a Comparative Fit Index (CFI) and a Tucker-Lewis Index (TLI) both greater than 0.90. In addition, a Root Mean Square Error of Approximation (RMSEA) of 0.07 or less and a Standardized Root Mean Square Residual (SRMR) of 0.08 or less are considered indicative of a good fit [70,71]. The final model fitted the data well (CFI = 0.86, TLI = 0.93, SRMR = 0.055, RMSEA = 0.036) and was identifiable with 135 degrees of freedom and a sample size of 202 great tits.

3. Results

3.1. Forest structural complexity, body condition, and tick presence

Contrary to the expectations, forest structural complexity did not significantly affect great tit composite body condition, although there was a positive association between forest structural complexity and the underlying latent condition variables Cellular Stress ($\beta = 0.27$, $p = 0.056$) and Post-fledging Developmental Stress ($\beta = 0.18$, $p = 0.176$), and a negative association with Pre-fledging Developmental Stress ($\beta = -0.17$, $p = 0.256$). Regression coefficients for Nutritional Condition and Post-fledging Developmental Stress were close to zero. Forest structural complexity was significantly positively correlated to the (log-transformed) density of questing nymphs ($\beta = 0.48$, $p < 0.001$).

In line with the expectations, tick presence on great tits was significantly positively correlated with overall (i.e. composite) avian body condition ($\beta = 0.34$, $p = 0.004$) and with (log-transformed) questing nymph density ($\beta = 0.27$, $p = 0.012$). No significant relationship with the five day average saturation deficit in spring was detected ($\beta = 0.16$, $p = 0.254$).

3.2. Deconstructing body condition into latent condition variables

Composite body condition itself was mainly determined by Cellular Stress (i.e. inverse telomere length, $\beta = -0.64$, $p = 0.004$), but was also positively associated with Energy Store ($\beta = 0.38$) and negatively associated with Pre-fledging Developmental Stress ($\beta = -0.62$), Post-fledging Developmental Stress ($\beta = -0.15$) and Nutritional Condition ($\beta = -0.17$), though none of these associations reached statistical significance (all $p > 0.05$).

Cellular Stress was negatively correlated with Telomere Length ($\beta = -1.00$, $p < 0.001$). Energy Store was positively correlated with the observables SMI ($\beta = 0.96$), Ratio ($\beta = 0.96$), and Fat Score ($\beta = 0.29$) (all $p < 0.001$). Pre-fledging Developmental Stress was positively correlated with Tarsus length FA ($\beta = 1.00$, $p < 0.001$). Post-fledging Developmental Stress was positively correlated with Rectrix length FA ($\beta = 0.72$, $p < 0.001$) and Rectrix mass FA ($\beta = 0.63$, $p = 0.027$). Nutritional Condition was positively correlated with Rectrix Mass ($\beta = 0.91$) and Rectrix GBW ($\beta = 0.62$) (all $p < 0.001$). MIMIC analyses showed that adults have higher scores for Energy Store than immatures ($\beta = 0.19$; $p = 0.048$). Nutritional Condition showed a strong positive correlation with rectrix length ($\beta = 0.81$), and was higher in males ($\beta = 0.20$) (all $p < 0.001$). Forest type and time of capture did not significantly affect any of the latent condition variables (see Supplementary Material S4 for details).

3.3. Correlation and covariance among latent and observed variables

The latent variables Pre-fledging and Post-fledging Developmental Stress were weakly negatively associated with Energy Store, although not significant (Fig. 1B–Supplementary Material S4). Deer density was higher in forests with less structural complexity ($\beta = -0.33$, $p = 0.046$) and poplar dominance (Supplementary Material S4). Deer density was also positively correlated with rodent density ($\beta = 0.54$, $p < 0.001$). Log-transformed questing nymph density was higher in smaller forests ($\beta = -0.61$, $p = 0.002$) and reached its highest levels in oak-dominated stands, while poplar-dominated stands supported the lowest densities (Supplementary Material S4). Log-transformed questing nymph density was also positively correlated with deer density ($\beta = 0.33$, $p < 0.001$) and rodent density ($\beta = -0.18$, $p = 0.004$), and negatively correlated with saturation deficit at the time of sampling (summer) ($\beta = -0.53$, $p < 0.001$). The covariance structure of the model showed a positive correlation between the error terms of Rectrix Mass and Rectrix mass FA ($\beta = 0.35$, $p < 0.001$), and a negative correlation between the error terms of Rectrix GBW, Rectrix length FA and Rectrix mass FA ($\beta = -0.28$, $p = 0.001$ and $\beta = -0.17$, $p = 0.002$, respectively) (Supplementary Material S4).

4. Discussion

Direct and indirect relationships between forest structural complexity, body condition and tick presence were investigated in a common avian insectivore, the great tit (*Parus major*). It was hypothesized that birds in more complex forests would be in better condition and more likely to carry ticks, as these forests typically support higher tick densities. Birds in better condition may also be more susceptible to tick infestation, either because they represent a more nutritious host or because of behaviours that increase exposure risk. The findings confirm that the likelihood of great tits being infested with ticks increases, at least in part, with improved overall body condition. Telomere length emerged as the key factor in this relationship, suggesting that individuals with lower levels of cellular stress, as reflected by longer telomeres, are more likely to carry ticks. While forest structural complexity had no direct effect on body condition, it was positively correlated with the density of questing nymphs, which in turn contributed to the presence of ticks on their avian hosts.

4.1. Avian body condition and tick presence

Body condition here encompasses several dimensions, including those reflecting cellular stress, energy store, developmental stress and nutritional condition, which may collectively influence the dynamics of tick infestation. Among these, the level of cellular stress was the strongest predictor of tick presence through the individual's body condition. Additionally, weak associations were observed between body condition and energy store (positive) as well as pre- and post-fledging developmental stress (negative), further indicating higher likelihood of tick infestation in hosts with better overall condition. This general pattern is consistent with a tendency for ticks to preferentially feed on hosts in better condition. This finding may emerge because host in a better condition provide better nutritional resources and longer feeding opportunities, pointing to possible underlying physiological mechanisms. Alternatively, condition-linked differences in bird behaviour, such as increased foraging activity, could also result in higher contact rates with ticks. The observed association between body condition and tick presence is mainly driven by the cellular stress (telomere length) body condition component, and may arise from an interaction with glucocorticoid levels. Several studies in both captive and wild bird populations have shown that environmental stressors such as food restriction, temperature extremes, social competition, disease or noxious stimuli can increase circulating glucocorticoid hormone levels [63,72,73], which in turn are associated with telomere shortening [74–78]. As a recent *in vitro* experiment by Vanroy et al. [79] showed that ticks prefer blood with low or baseline levels of cortisol and corticosterone, the effect of cellular stress on tick abundance may be mediated by blood stress levels.

However, the majority of ticks detected belonged to the species *Ixodes ricinus*, which does not actively "hunt" for their host but instead waits for a suitable host to pass by and then attaches. Due to factors such as, for example, high desiccations risk and low host contact rates in their environment, these ticks often may not be able to afford to be overly selective about which host they choose [80]. Therefore, an alternative explanation for the higher probability of tick infestation on healthier birds could be that better body condition allows them to be more selective in their foraging. For instance, healthier birds may target different food items or forage in safer habitats with fewer predators, which could result in greater exposure to ticks. Rollins et al. [81], for example, showed that more explorative great tits were more likely to be infested with ticks. They suggest this finding could be due to more explorative birds spending more time foraging near the ground, where tick nymphs and larvae are most abundant. The nutritional component of body condition was not associated with tick presence, which was initially unexpected. However, the lack of such a relationship may be due to temporal discrepancies between nutritional assessments and tick infestation. Both proxies for nutritional condition were measured during feather growth, which in great tits occurs between late summer and early autumn [82], whereas tick load was assessed in late winter and early spring.

4.2. Forest structural complexity, body condition and tick presence

Contrary to expectations, no statistically significant effect of forest structural complexity on any of the latent condition variables, and consequently, on overall body condition was found. However, forest structural complexity did influence tick presence on birds through its positive effect on the density of questing nymphs. This finding aligns with the initial hypothesis and with previous studies showing that structurally more complex forests provide a more favourable microclimate for ticks [3,83–86]. These studies typically examined individual components of complexity, such as habitat type, shrub cover or tree species richness, whereas this study integrated multiple elements into a comprehensive index of structural complexity, allowing for a more holistic understanding of how forest architecture affects nymphal abundance. Importantly, these nymphs, once engorged, will moult into adult ticks, which are capable of transmitting pathogens such as *Borrelia* to humans, highlighting the potential for public health implications of increased nymphal densities in complex forest environments.

4.3. Other (a)biotic factors affecting tick presence on birds

The density of questing nymphs was not only influenced by forest structural complexity, but also by other factors such as tree species. Specifically, tick nymph densities were highest in oak plots, intermediate in beech plots, and lowest in poplar plots. This pattern aligns with previous research demonstrating that oak-dominated forests generally support higher tick densities compared to forests dominated by other tree species [5,6,85,87]. Oak forests are characterized by a dense understory, including grasses, shrubs (e.g., blueberries), and small saplings, which provide ideal microhabitats for ticks to position themselves for questing behaviour in search of suitable hosts. Additionally, European oak and beech forests typically have deep litter layers that maintain high relative humidity, optimal for tick survival [88–90]. These conditions help newly emerged ticks seek refuge from sunlight and desiccation in the leaf litter [80]. For example, *Ixodes ricinus*, the most abundant tick species in this study, thrives in about 80 % humidity [80]. In line with this, nymph foraging activity was found to be negatively affected by saturation deficit at the time of capture (see Refs. [91–95] for similar results).

Smaller forest plots were also associated with higher densities of questing nymphs, a pattern likely driven by the higher proportion of forest edges in these areas. Forest edges are known to support higher tick abundance due to their unique ecological characteristics [96]. These transitional zones receive more sunlight, which promotes the development of a denser and more diverse vegetation layer on the forest floor, providing ideal microhabitats for questing ticks [97]. In addition, cervids and rodents, both key hosts for tick development and reproduction, are often found at forest edges with richer ecotone vegetation [98,99]. Deer density strongly impacts tick abundance [100–103], with even low deer presence in biodiverse areas maintaining high tick levels [104]. The findings of this study support this pattern, revealing higher nymph densities with increasing deer density. A slight negative effect of rodent abundance on nymph density was also observed. However, this should be interpreted cautiously. Rodents are key hosts for tick larvae, and their population dynamics, often shaped by environmental factors such as masting events, can influence nymph densities in subsequent years [105–108]. Therefore, the observed negative correlation may reflect past fluctuations in rodent populations rather than a direct, immediate effect.

4.4. Study limitations

While this study provides valuable insights into the relationships between forest structural complexity, bird body condition, and tick infestation, several limitations should be acknowledged. First, the cross-sectional design limits our ability to infer causality among observed relationships. Longitudinal studies spanning multiple years would provide more robust insights into temporal dynamics. Second, tick densities and bird health indicators were sampled in different seasons, which may reduce temporal comparability. Although previous research suggests that relative differences between plots remain stable over time, this remains a potential source of bias. Third, while Structural Equation Modeling captures complex direct and indirect pathways, unmeasured confounding variables (e.g., microclimatic variability or host behaviour) may still influence the observed patterns. Fourth, immune function was not assessed as part of the composite body condition index. Future studies could strengthen physiological interpretations by including immune-related biomarkers, such as heterophil-to-lymphocyte ratios or total white blood cell counts [109,110]. Finally, the study was geographically limited to temperate deciduous forests in Flanders. While this enhances internal consistency, it may restrict the generalizability of our findings to other forest types or regions. Moreover, the structural complexity gradient across our sites may have been too narrow to detect significant differences in body condition, as all sites were relatively mature, broadleaf forests of similar size and age. Future research could benefit from including more diverse forest types, such as monocultures, coniferous stands, or mixed forests, to capture a broader range of structural complexity and ecological variation.

4.5. Conclusion

The results of this study suggest that structurally more complex forests may lead to higher tick infestation rates in birds, particularly those in better physiological condition, as indicated by lower levels of cellular stress. This, in turn, may increase the risk of pathogen transmission. These findings highlight how forest policies that promote structural complexity may have unintended consequences for host-parasite interactions. Possible strategies to mitigate these effects could include directing recreational activities toward less structurally complex forest stands to minimize human exposure to areas with high tick densities. In addition, maintaining well-defined trails with minimal vegetation encroachment could reduce tick-friendly microhabitats and limit human-tick contact [43]. To fully understand these dynamics, future research should further explore the mechanisms driving host-vector interactions, with a particular focus on behavioural factors. Integrating ecological, physiological, and behavioural perspectives is needed to allow for better predicting and managing the complex interplay between forest structural complexity, wildlife health, and disease dynamics.

CRediT authorship contribution statement

Bram Catfolis: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Magali Frauendorf:** Writing – review & editing, Validation, Methodology, Conceptualization. **Kris Verheyen:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Lander Baeten:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Tosca Vanroy:** Writing – review & editing, Validation, Methodology. **An Martel:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Frank Pasmans:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Elin Verbrugghe:** Writing –

review & editing, Validation, Resources, Methodology. **Luc Lens:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Diederik Strubbe:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Ethics statement

Bird ringing and mammal trapping on private land was authorized by the respective landowners. Permits for BC and RA ringing were issued by the Belgian ringing program and the Flemish authorities (Agentschap voor Natuur en Bos; ANB/BL-FF/V21-00035). Rodent trapping was also approved by the Flemish authorities (Agentschap voor Natuur en Bos; ANB/BL-FF/V21-00034). All sampling protocols used were approved by the Ethical Committee of the VIB Ghent site (EC2020-095, January 6, 2021).

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2025.e44058.

Data availability

Phenotypic and physiological data, tick data and environmental data have been deposited on Figshare: https://doi.org/10.6084/m9.figshare.27037849.v1.

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