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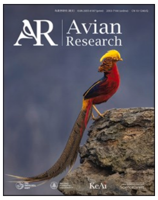

Host ecology shapes chigger mite parasitism on wild, captive, and domestic birds across Malaysia and Thailand

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ABSTRACT

Southeast Asia is one of the global biodiversity hotspots, renowned for its rich bird fauna and diverse arthropod communities among other taxa. This comprehensive multisite study investigated trombiculid mite (chigger) infestation patterns among birds in Thailand and Malaysia, focusing on the interactions between host taxonomy, host ecological traits, and environmental factors. Previous surveys have frequently recorded *Leptotrombidium* spp., the main vectors of scrub typhus in humans, parasitising birds. We examined 2006 birds representing 191 species across 51 families and 13 orders, revealing a parasitism rate of 17.74% (356 infested birds). Twenty-one chigger species were identified across diverse host habitat types, including captivity, urban and rural settlements, agricultural lands, aquatic environments, and diverse forest ecosystems. The most prevalent species were *Toritrombicula densipiliata* (4.3% of individual birds infested), followed by *Odontacarus audyi* (3.9%) and *Eutrombicula wichmanni* (3.6%, only recorded from Thailand), whereas *Leptotrombidium* spp. were rare (0.3% in aggregate). Host ecology, including habitat breadth, geographical scale, and degree of forest dependency, significantly impacted infestation patterns. Notably, bird species with no forest dependency (e.g., synanthropic species in urban environments) exhibited the lowest infestation rates and chigger species richness. Analysis by season was restricted to Malaysia, where birds captured during the drier period showed higher chigger diversity compared to the wet season. There was no host phylogenetic signal associated with chigger infestation or species richness. However, in a meta-analysis restricted to five heavily-sampled bird species, the significant effects of host ecology were confirmed. This study provides critical insights into bird-parasite associations, offering valuable information for the ecological monitoring of ectoparasite infestation and potential disease vectors. The results have important implications for understanding public health risks, wildlife conservation, and the complex disease ecology of understudied ectoparasitic relationships in tropical ecosystems.

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1. Introduction

Chiggers are the larvae of trombiculid mites (Acari: Trombiculidae) and constitute a major group of ectoparasites that feed on the skin and tissue of various vertebrate hosts, including mammals, reptiles, and birds. Only this six-legged larval stage is parasitic, while the subsequent eight-legged stages (nymphs and adults) are free-living predators in the environment that consume small arthropods or their eggs in the soil. Chiggers are known as the sole vectors of scrub typhus, a bacterial cause of febrile illness and potentially severe complications in many parts of the world, particularly the Asia-Pacific region (Xu et al., 2017; Masakhwe et al., 2018; Elliott et al., 2019; Weitzel et al., 2022). In addition to scrub typhus caused by *Orientia* spp., several other microbial pathogens of either public health or veterinary importance have been detected in chiggers, including hantaviruses, *Anaplasma* spp., *Bartonella* spp., *Borrelia* spp., and *Rickettsia* spp. (Chaisiri et al., 2023). Moreover, chigger bites can cause localised pruritus, irritation, and dermatitis (known as trombiculiasis) in many species of hosts, including humans (Ornelas-Almeida et al., 2007; Molín et al., 2020; Santibáñez et al., 2020; Alexander et al., 2024).

Chiggers exhibit complex patterns of parasitism across diverse vertebrate hosts and more than 3013 species have been discovered (Nielsen et al., 2021). They are cosmopolitan and are highly diversified across various habitat types on earth, including forest, woodland, grassland, shrubland, agricultural land, swamps, and seacoasts; with some species existing in extreme environments such as at high altitudes, in desert biomes, or in tundra (Traub et al., 1967; Traub and Wisseman, 1968; Loomis, 1973; Takahashi et al., 2012a; 2012b). Thus, the ecology of chiggers is impacted by both host factors (density, behaviour, seasonal availability) and environmental variables (temperature, precipitation, humidity, land use).

Studying and monitoring chigger infestation on wildlife, particularly birds, are important as birds represent the most abundant group of terrestrial vertebrate hosts on the planet (Brusatte et al., 2015). Birds may serve as bioindicators for environmental monitoring, with chigger infestations potentially reflecting the consequences of ecological change or environmental stressors. The taxonomic diversity of potential bird host species extends from ground-dwelling galliforms and perching passerines to wading charadriiforms and includes long-distance migrants, thereby creating a multifaceted ecological nexus of potential host-parasite associations, with the possibility of transport of chigger species across the globe. Recently, a rising number of studies reporting chigger-bird associations have been published, particularly in Europe and the Americas (Literak et al., 2008; Fuentes-Castillo et al., 2016; Makol and Korniluk, 2017; Kaluz et al., 2018; Servat et al., 2018; Molín et al., 2020; Bassini-Silva et al., 2021a; 2021b; Stekolnikov et al., 2022; Trnka et al., 2023), but to a much lesser extent, from Asia and particularly the Southeast Asian region (Kaluz et al., 2016; Koosakulnirand et al., 2023; Rajasegaran et al., 2024). From the approximately 260 chigger genera identified globally, *Hypogastia*, *Neoschoengastia*, *Ornithogastia*, *Toritrombicula*, and *Whartonacarus* are recognised for their consistent or exclusive relationships with avian hosts (Makol and Korniluk, 2017). Following the checklist of chigger mites of Southeast Asia (Stekolnikov, 2021), 87 chigger species (from a total of around 450) were associated with birds residing in or migrating to the region. Among these bird-associated chigger species, about 34 and 44 species were recorded on birds from Malaysia and Thailand, respectively, with at least 19 species appearing to be bird specialists in Southeast Asia (Stekolnikov, 2021).

Recent research has predominantly focused on faunistic findings, taxonomic descriptions, and some implications of chigger parasitism on birds, such as the pathological effects of chigger infestation on the hosts and their potential role as disease vectors or reservoirs of microbial pathogens (Ornelas-Almeida et al., 2007; Literak et al., 2008; Kaluz et al., 2016; Molín et al., 2020; Stekolnikov et al., 2022; Bassini-Silva et al., 2023; Koosakulnirand et al., 2023), while overlooking critical ecological dimensions such as host-parasite relationships, seasonal patterns, ecological specialisation, and geographical distributions. Although previous studies (e.g., Varma, 1964; Dietsch, 2005; Trnka et al., 2023) provided some limited ecological information in relation to chigger parasitism on birds, the impact of habitat heterogeneity, bird characteristics, and migratory strategies have not been adequately addressed to explain infestation rates, diversity, and community structure. These represent significant knowledge gaps for understanding the ecological and evolutionary drivers of bird-parasite interactions for these widespread and abundant mites, particularly in the Southeast Asian region, where the prior focus has been on chigger infestations on small mammals (Chaisiri et al., 2019; Wulandhari et al., 2021; Alkathiry et al., 2022).

Accordingly, this study comprised a geographically extensive, multisite survey across Thailand and Malaysia that aimed to investigate chigger infestation patterns between diverse wild, captive, and domestic bird taxa and varied habitats over both countries. Specific objectives of the study included: (1) to estimate rates of infestation and diversity of chiggers on birds across different categorical variables (e.g., avian taxa, avian ecological group, habitat types, and season); (2) to identify potential factors explaining chigger infestation on birds from the two countries; and (3) to explore patterns of chigger dissemination and the community structure of bird-chigger associations through host-parasite network analyses. We show that habitat, forest dependency, and migratory status all impact chigger infestations on birds, with important implications for wildlife health, conservation, and zoonotic disease risk—as well as for broadening our understanding of the complex ecology of these understudied ectoparasitic relationships.

2. Materials and methods

2.1. Study sites for bird trappings and habitat categorisation

Field sampling of birds in Malaysia was carried out between August 2020 to November 2023. A total of 23 study sites were selected for bird collection covering Peninsular Malaysia (21 sites) and Malaysian Borneo (two sites in Sarawak) (Fig. 1). Multiple trapping strategies were applied to capture different groups of birds according to their habitat preferences and behaviour, with expert assistance from the Department of Wildlife and National Parks (DWNP). For passerines, mist nets were deployed in different habitat types during the daytime from 07:00 h – 18:30 h for six consecutive days. Waterbirds were captured for three consecutive nights using mist nets from 22:00 h – 07:00 h, following the timings of the tide. The nets were checked regularly every 20 min, and individual trapped birds were removed and relaxed in cloth bags prior to standard morphological measurements, species identification, and ectoparasite examination. All passerines and waterbirds were ringed on their left legs to provide a record of recapture status and released immediately at the same spot where they were caught. In rural villages, free-range chickens were obtained from villagers and examined for chigger infestation in the morning. King Quail (*Synoicus chinensis*), Barred Buttonquail (*Turnix suscitator*), and Red Junglefowl (*Gallus gallus*) were trapped with the help of the villagers using custom-designed traps set up near the village boundaries and plantations. Captive pheasants were sampled from sanctuaries under the protection of DWNP. All these ground-nesting birds were released or returned to their owners, or back into captivity, on the same day. Urban invasive birds comprised House Crows (*Corvus splendens*) and Barn Swallows (*Hirundo rustica*). Crows were obtained with the assistance of the local municipal councils during authorised shooting sessions for population control. The dead crows were collected immediately and examined for the presence of chiggers. Swallows were captured between 00:00 h and 04:00 h, a period when they are less active and perched on electric wires or buildings. After chigger inspections, the birds were released at their point of capture before dawn (around 06:30 h).

In Thailand, the bird field sampling was performed between

December 2020 to April 2023 across 10 study sites covering 8 provinces (Fig. 1). To investigate the occurrences of chiggers on wild birds, our parasitology team participated in the preexisting bird ringing and monitoring projects from different institutions that conducted bird surveys annually; i.e., the Department of National Parks, Wildlife and Plant Conservation (DNP), the Department of Marine and Coastal Resources (DMCR), and Mahidol University Kanchanaburi Campus (MUKA). Mist nets were deployed for 2–4 consecutive days between 06.00 h and 12.00 h to trap wild birds in different habitat types. Shorebirds were trapped using the cannon-netting method, which was conducted by experienced and certified ornithologists and the wildlife research team from DNP. This was performed for 2–4 consecutive days between 05.30 h and 12.00 h following the local tide times. Captured birds were carefully extracted from the mist nets or the cannon nets and placed in individual cloth bags prior to banding, biometric data collection, species identification, and ectoparasite examination. In the case of backyard Chickens (*Gallus gallus domesticus*), the animals were obtained through collaboration with the FutureHealthSEA project (a One Health observatory activity in Nan Province) and local communities. Villagers brought their backyard chickens to assembly points, and the field parasitologists performed chigger investigation and specimen collection. No culling was involved, and all the chickens were returned to the owner immediately.

In terms of habitat types, the 33 study sites across the two countries were classified into 9 categories as shown in Fig. 1. Each study site was visited between one to two times, depending on accessibility and ongoing research activities. Sites with lower bird diversity or chigger prevalence were resampled to ensure adequate representation, such as shorebird sites (e.g., Kapar Energy Ventures) and forest passerine sites (e.g., Pusat Penyelidikan Luar, Universiti Malaya, Ulu Gombak). Bird trapping periods in both countries can be divided approximately into dry and wet seasons. In Malaysia, the climate remains consistently hot and humid throughout the year, with limited variation between seasons (Muhammad et al., 2020), although a higher amount of rainfall is seen around November to January (peaking in December). In this study, the seasons are divided into dry (March to October) and wet (November to February) (Alkathiry et al., 2022). In Thailand, the seasons are characterised by rather distinct wet and dry periods. The wet season typically ranges from May to October, while the dry season occurs from November to April. Note that bird trapping and chigger investigation sessions in Thailand were conducted only in the dry season according to the predetermined schedule of each responsible institution and project,

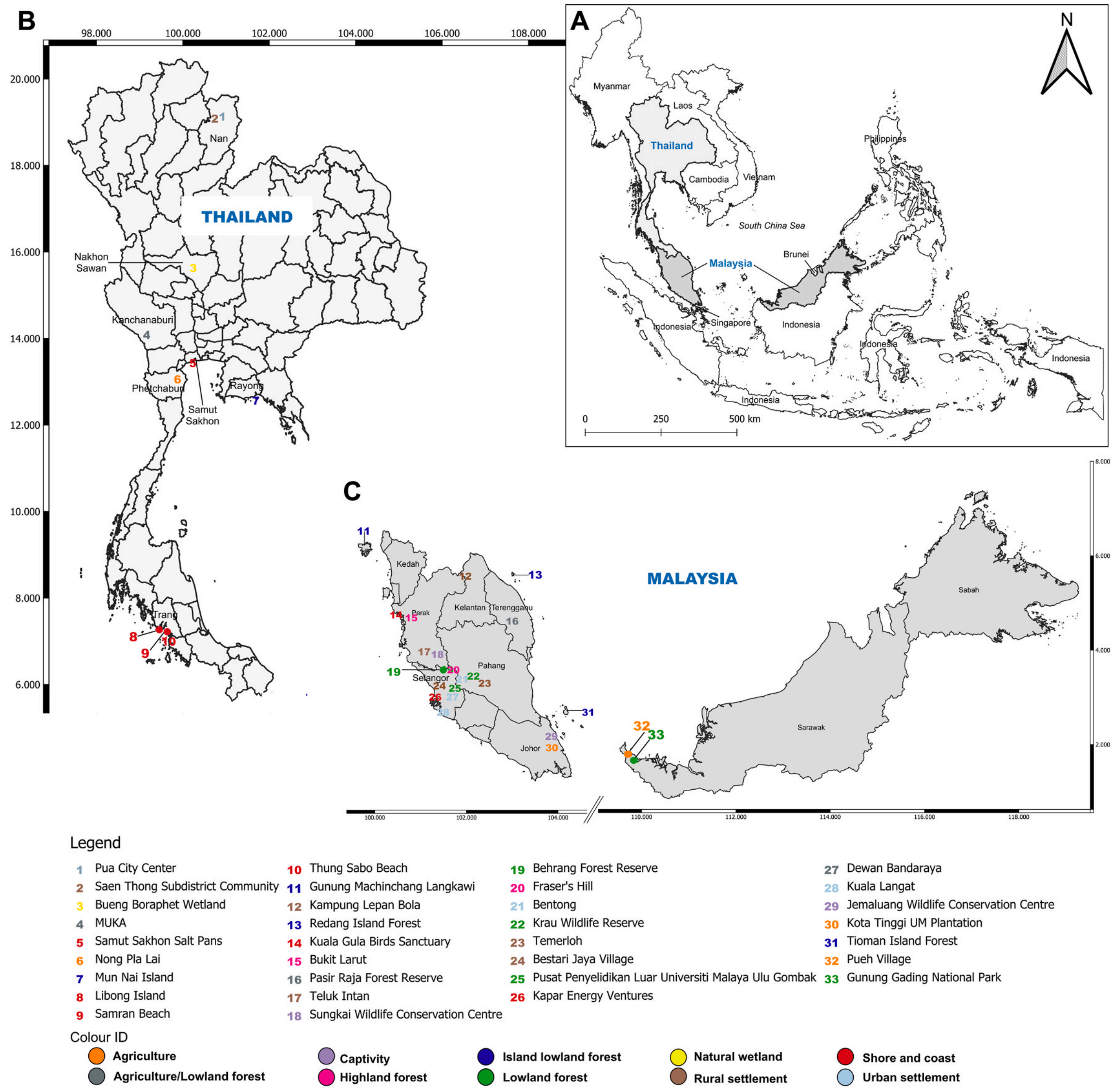

Fig. 1. Map showing the geographical distribution of the 33 study sites in Malaysia (23 sites) and Thailand (10 sites) where bird trapping for chigger collection was conducted. Site labels (1–33) are colour-coded according to habitat types, as indicated by the colour legend. The inset map (**A**) shows the location of Thailand (**B**) and Malaysia (**C**) within the Southeast Asian region.

resulting in seasonal sampling bias. All study sites are listed in Appendix Table S1, with relevant GPS coordinates.

2.2. Extraction of bird species-associated data

Bird species were identified following the bird guides from the two countries (Lekagul and Round, 1991; Robson, 2018; Treesucon and Limparungpatthanakij, 2018). Bird taxonomy and classification followed the IOC World Bird List (Gill et al., 2024). Additional attributes from each bird species; e.g., migratory status ("Full migrant", "Altitudinal migrant" and "Non-migrant"), forest dependency ("high", "medium", "low", or "no forest dependency"), geographical occurrence, and habitat occurrence following the level-1 classification, were extracted from the Data Zone of BirdLife International (BirdLife International, 2024a). More details of the extracted data for each bird species are provided in Appendix Table S2.

2.3. Chigger collection, specimen preparation and identification

Birds were handled gently and thoroughly examined for the occurrence of chiggers (see Fig. 2). The attached chiggers were counted and removed from the birds' skins using fine forceps and stored in 70–95% ethanol. For each infested bird, a subsample of 10–20% of ethanol-preserved chiggers was selected (with attention to differences in size and gross appearance) for permanent slide preparation. For birds with a low abundance of chigger infestation (a few or no more than five chiggers), all available specimens were prepared on glass slides. Chiggers were cleared and permanently mounted in Berlese fluid (TCS Bioscience Ltd., UK) individually, and then subjected to morphological observation, morphometry, and imaging using a Zeiss Axio Imager M2 microscope equipped with ZEN 2011 imaging software (Carl Zeiss, Germany), combining brightfield and autofluorescence imaging to aid visualisation (Kumlert et al., 2018). Initial taxonomic identification of chigger specimens was performed locally by parasitologists in Thailand and Malaysia. Consequently, representatives of putative chigger species

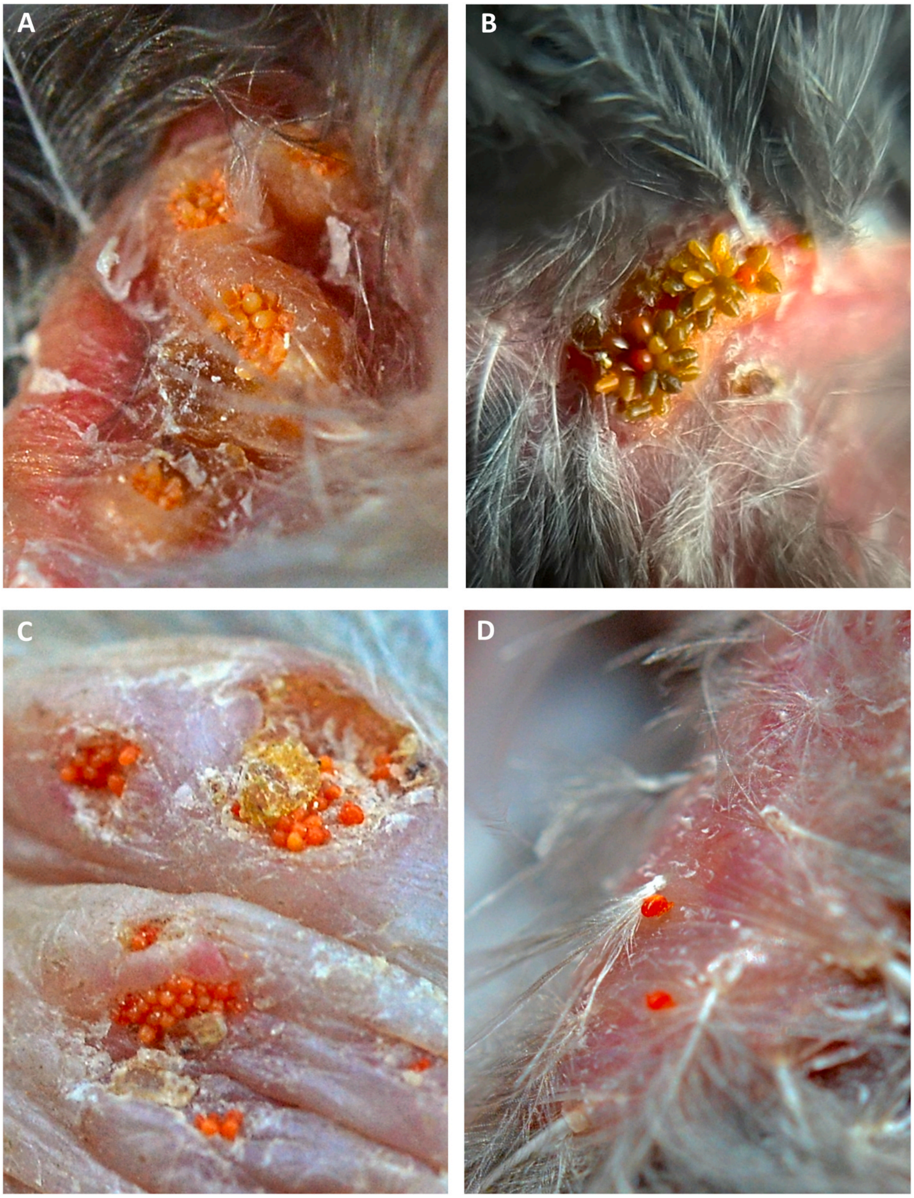

Fig. 2. Clusters of chigger infestation on the skin of avian hosts illustrating variation in appearance, particularly in mite colouration, from brown to yellow, orange, and bright red. Examples include landbirds (**A**,**B**), a backyard chicken (**C**), and a shorebird (**D**). Note the prominent nodular skin lesions and large numbers of chiggers attached to the landbirds and chicken (**A**–**C**) in contrast with the shorebird (**D**).

were selected and sent to an expert acarologist at the Zoological Institute of the Russian Academy of Sciences (Dr Alexandr Stekolnikov, ZIN, Saint Petersburg, Russia) for final identification. Chigger identification to species was performed with guidance from the published taxonomic descriptions (Vercammen-Grandjean, 1960; Nadchatram, 1967a, 1967b; Nadchatram and Traub, 1971; Nadchatram and Dohany, 1974; Vercammen-Grandjean and Langston, 1976; Tanskul and Linthicum, 1999; Shaw, 2010; Stekolnikov, 2013). Detailed information on morphological identification of chiggers, descriptions of new species, and new records associated with this study are available in our previously published work (Koosakulnirand et al., 2023).

2.4. Exploratory analyses on chigger infestation rate and estimated diversity

Individual birds and chigger infestation data were compiled into a raw dataset for exploratory ecological analyses. Chigger infestation rates and mean chigger abundance across different categorical parameters (i.e., bird taxa, migratory status, forest dependency, habitat, season, and country) were computed using R freeware (R Core Team, 2024). For chigger diversity estimation, observed species richness of chigger infestation, species richness estimators (1st Jackknife, Chao and Bootstrap), and diversity index (Shannon index) were calculated using the "vegan" and "BiodiversityR" packages (Kindt and Coe, 2005; Oksanen et al., 2024) implemented in the R freeware. Species accumulation curves were also created to visualise the cumulative number of chigger species against the total number of bird samples examined, and the plots also helped to assess the adequacy of sampling effort by using the same R package mentioned above. Seasonal analyses were conducted for Malaysia only.

2.5. Multivariate analyses of independent variables explaining chigger infestation on birds

To elucidate the ecological drivers of chigger infestation status, we employed a multi-faceted analytical approach that integrated host phylogenetic effects using comparative methods and a meta-analysis (Seifertová et al., 2008; Desdevises et al., 2015). First, we assessed the potential phylogenetic signal in chigger infestation patterns by examining the influence of bird phylogenetic relationships on biological traits and infestation status. Subsequently, we utilised a phylogenetic linear regression model to explore the complex interplay between bird traits and habitat characteristics in shaping chigger infestation and chigger species richness, accounting for the non-independence of species data arising from shared evolutionary relationships. To further contextualise our findings, we conducted a meta-analysis focused on quantifying the consistency and magnitude of habitat effects on chigger diversity (species richness) across different bird host taxa. This approach was designed to illuminate patterns among habitat generalist species, providing a robust synthesis of environmental influences on chigger ecology.

2.6. Test of bird phylogenetic effect against different biological traits and chigger infestation status

In order to avoid phylogenetic autocorrelation and potentially false conclusions in the regression model, the phylogenetic effect of the bird species was investigated against eight variables: (1) number of hosts examined (nhost), (2) migratory status (migrant), (3) level of forest dependency (forestdependcy), (4) geographical area size of occurrence (occurrence), (5) number of habitats occupied (nhabitat), (6) habitat type (habitat), (7) chigger infestation (infestation), and (8) chigger species richness (chigger richness). First, a phylogenetic tree of bird species involved in this study (192 species) was created with the Open Tree of Life (OTL) using the "rotl" package (Michonneau et al., 2016) implemented in R freeware. Phylogenetic comparative analysis as well as tree manipulation and visualisation were performed using the "phytools" package in R (Revell, 2024). We standardised the tree branch length to "1" in all branches of the tree for the comparative analysis method. Phylogenetic signals were explored across the biological traits and chigger infestation status using the "phylosignal" package in R (Keck et al., 2016). Calculated indices for general estimations of phylogenetic signal included measurements of autocorrelation; i.e., Moran's I index or "I" (Gittleman and Kot, 1990) and Abouheif's index or "Cmean" (Abouheif, 1999), as well as indices based on evolutionary models such as Blomberg's K or "K-star" (Blomberg et al., 2003) and Pagel's λ or "Lambda" (Pagel, 1999).

2.7. Phylogenetic generalized linear regression model (PGLS)

To control for the phylogenetic effect among the bird species, we applied phylogenetic generalized least squares regression models (PGLS) to analyse relationships among the selected bird traits and chigger infestation status (chigger infestation and chigger species richness). Habitat (both number of habitats occupied and habitat type) together with area size of occurrence, migratory status, and forest dependency level of each bird species were selected as predictive variables. Models were fitted with Pagel's Lambda Correlation Structure methods using the "ape" (Paradis et al., 2004), "nlme" (Pinheiro et al., 2017) and "geiger" (Pennell et al., 2014) packages in R. Multicollinearity of the predictive variables in the fitted models was assessed using pairwise scatterplots and correlation coefficients. In general, if the correlation coefficient is above 0.7–0.8, this indicates potential collinearity between the variables (Shrestha, 2020).

2.8. Meta-analysis of habitat influencing chigger species richness

To examine the influence of habitat characteristics on chigger infestation patterns across different bird host species, we conducted a meta-analysis using data from our previously compiled dataset. This permitted the quantification of the consistency and magnitude of habitat effects on chigger species richness across multiple bird host taxa. We implemented two filtering inclusion criteria for dataset preparation: (1) bird species with a minimum sample size of 20 individuals were selected to ensure adequate statistical power; and (2) only bird species that occupied at least three different habitat types (i.e., habitat generalists) were included in order to enable meaningful comparison of habitat effects. For each bird species retained from the inclusion criteria, we calculated the standardised effect size to quantify the relationship between habitat type and chigger species richness.

The meta-analysis was conducted using the "metafor" package in R (Viechtbauer, 2010). The random-effect model was fitted using the Restricted Maximum Likelihood estimation method, accounting for between-study heterogeneity while providing robust parameter estimates. Each bird species was treated as a separate "study" in the meta-analytic framework, with effect sizes weighted by the inverse of their variance. The overall effect size was calculated along with 95% confidence interval using the "effsize" package (Torchiano, 2020). In addition, we assessed heterogeneity among bird species using the Q-statistic, I^2, and H^2 indices (Huedo-Medina et al., 2006) to quantify the proportion of observed variance that reflects true differences in effect sizes rather than sampling error.

To evaluate potential biases in the dataset, a funnel plot was generated to visually inspect the relationship between effect sizes and their precision. Asymmetry in the funnel plot would suggest potential biases in the data. This assessment is of particular importance for meta-analyses to ensure the robustness of the findings. Also, forest plots were created to represent the effect sizes and their confidence intervals for each bird species, as well as the overall pooled effect. This visualisation provides an intuitive representation of the consistency and strength of habitat effects on chigger species richness across different bird host species.

2.9. Network analyses of bird-chigger associations

Bird-chigger associations were explored through bipartite and unipartite network analyses. Bipartite network analyses were conducted using quantitative matrices between chigger species and categorical variables; i.e., bird taxa, migratory status, forest dependency, habitat, season (Malaysia), and country. The matrices were visualised for bipartite network graphs and module web plots using "plotModuleWeb" and "plotweb" functions in the "bipartite" (Dormann et al., 2009) package in R freeware. In order to control sampling effort bias in the analyses, only chigger species that infested >5 individual birds were included in the matrices.

To illustrate the relative interaction patterns among bird host taxa regarding the co-occurrence of chigger species shared within the community, the bipartite network was transformed into a unipartite network using the "tnet" package (Opsahl, 2009). Network centrality scores (Eigen centrality) of the bird taxa (nodes) were calculated using the "evcent" function from the "igraph" package (Csárdi and Nepusz, 2006) to estimate the role of each bird taxon as a connector linking with the other hosts in sharing chigger species. A higher value of centrality of a

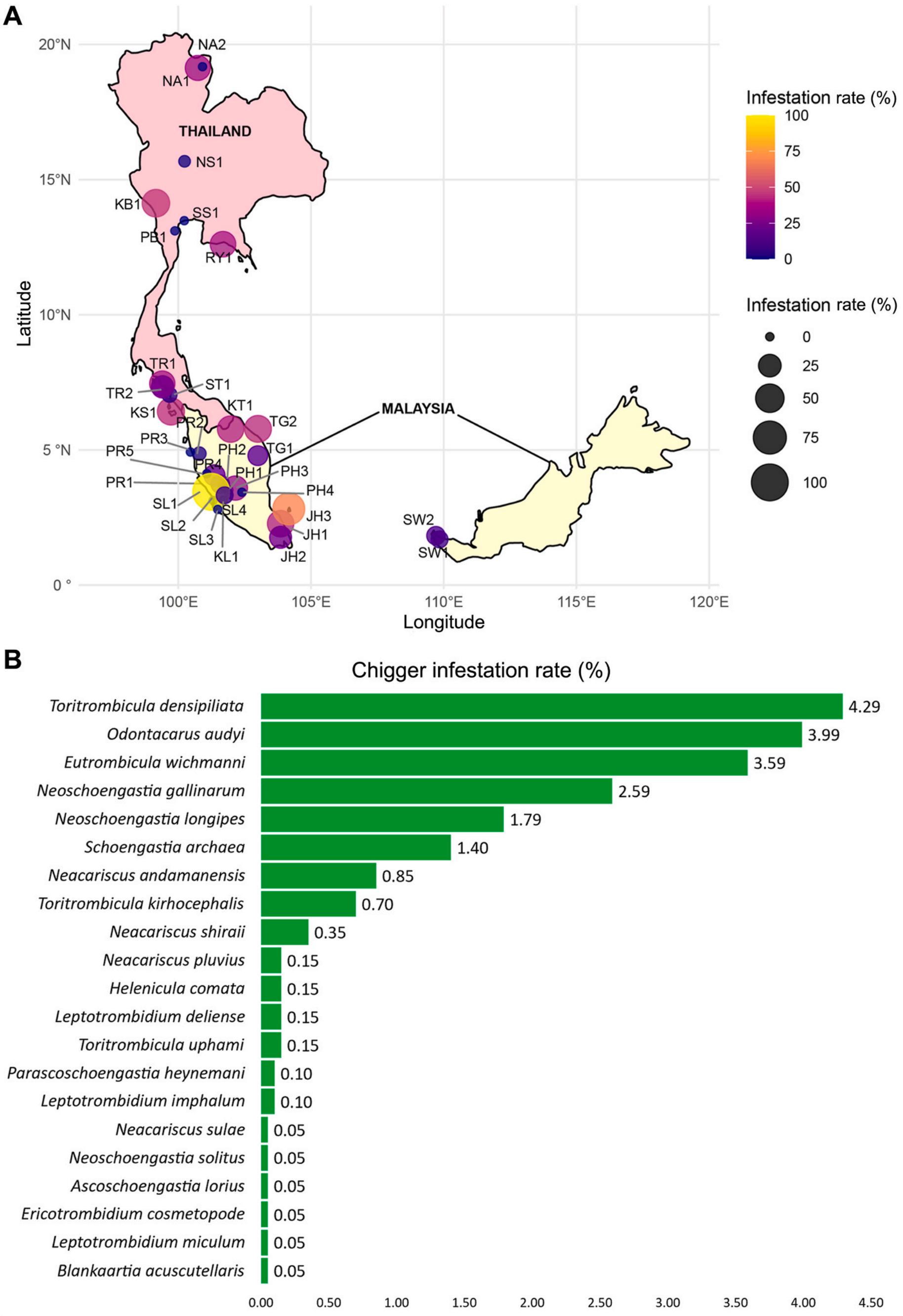

Fig. 3. **A**, Distribution of chigger infestation rates on birds across the 33 study sites in Malaysia (23 sites) and Thailand (10 sites). Colours and sizes of the circles indicate the level of infestation at the study sites. Site abbreviation – Malaysia: Johor1 (JH1), Johor2 (JH2), Johor3 (JH3), Kedah1 (KS1), Kelantan1 (KT1), Kuala Lumpur1 (KL1), Pahang1 (PH1), Pahang2 (PH2), Pahang3 (PH3), Pahang4 (PH4), Perak1 (PR1), Perak2 (PR2), Perak3 (PR3), Perak4 (PR4), Perak5 (PR5), Sarawak1 (SW1), Sarawak2 (SW2), Selangor1 (SL1), Selangor2 (SL2), Selangor3 (SL3), Selangor4 (SL4), Terengganu1 (TG1) and Terengganu2 (TG2); Thailand: Kanchanaburi1 (KB1), Nakhon Sawan1 (NS1), Nan1 (NA1), Nan2 (NA2), Petchaburi1 (PB1), Rayong1 (RY1), Samut Sakhon1 (SS1), Satun1 (ST1), Trang1 (TR1) and Trang2 (TR2). **B**, Infestation rates of 21 chigger species parasitising birds captured in Malaysia and Thailand.

node (host) is associated with a higher connection to the other nodes (other hosts), suggesting a high number of parasite species shared with the other hosts in the community.

2.10. Canonical correspondence analysis of bird-chigger associations

To explore bird-chigger association at a broader scale, individual bird infestation data was aggregated at the species level to perform canonical correspondence analysis (CCA) with data on global occurrence and habitat occurrence of each bird species derived from the Data Zone of BirdLife International (BirdLife International, 2024a). The chigger species included in this analysis were selected from those species which occurred on >5 individual birds to control sampling bias effort. The CCA was performed using the "FactoMineR" and "ade4" packages (Lê et al., 2008; Thioulouse et al., 2018) in R.

3. Results

3.1. General information on chigger infestation rates and mean abundance on birds

In total, there were 2006 individual birds belonging to 191 species (51 families from 13 orders) as the subjects for chigger investigation in this study (Appendix Table S2). Chiggers were found on 356 birds, yielding a total infestation rate of 17.7%. Between the two countries, the chigger infestation rate was higher for the birds captured in Thailand (23.9%; $n = 860$) compared to those birds captured in Malaysia (13.1%; $n = 1146$). This remained statistically significant even if only dry season data were considered from each country (revised Malaysian infestation rate, 14.5%; $n = 774$; $\chi^2 = 23.37$, df = 1, $p < 0.0001$) to account for a lack of wet season data from Thailand. Chigger infestation rates across all the study sites in Thailand and Malaysia are illustrated in Fig. 3A. Rufous-winged Philentoma (*Philentoma pyrhoptera*; $n = 17$), Tickell's Blue Flycatcher (*Cyornis tickelliae*; $n = 15$), and White-rumped Shama (*Copsychus malabaricus*; $n = 53$) appeared as the most infested bird species with chigger infestation rates of 88.2%, 86.6%, and 77.3%, respectively. However, in the case of the following bird species, only one bird individual per species was examined and infestation rates could not be calculated: White-breasted Waterhen (*Amaurornis phoenicurus*), Verditer Flycatcher (*Eumyias thalassinus*), Slaty-breasted Rail (*Lewinia striata*), Bold-striped Tit-babbler (*Mixornis bornensis*), Oriental Scops Owl (*Otus sunia*), Japanese Paradise Flycatcher (*Terpsiphone atrocaudata*), and Large Wren-babbler (*Turdinus macrodactylus*). Chigger infestation rates were not significantly ($\chi^2 = 3.21$, df = 1, $p = 0.073$) different between non-migrant (18.9%; $n = 1353$) and full-migrant species (15.6%; $n = 634$). Bird species with no forest dependency were infested with chiggers at a much lower rate (5.6%; $n = 568$), compared to those bird species with low- (23.4%; $n = 592$), medium- (22.0%; $n = 627$), and high-forest dependencies (21.4%; $n = 219$).

In terms of habitat, high chigger infestation rates were recorded from birds captured from island lowland forests (45.9%; $n = 98$). Notably, birds examined from urban settlements—House Swift (*Apus nipalensis*), House Crow (*Corvus splendens*), Barn Swallow (*Hirundo rustica*), House Sparrow (*Passer domesticus*), Bank Swallow (*Riparia riparia*), and Scaly Breasted Munia (*Lonchura punctulata*) ($n = 213$)—were all negative for chigger infestation. Birds captured during the Malaysian dry season presented a higher chigger infestation rate (14.5%; $n = 774$) than those from the wet season (10.2%; $n = 372$), although this difference was not statistically significant ($\chi^2 = 2.79$, $p = 0.095$). More details of chigger infestation rates across different categorical parameters are shown in Table 1 and Appendix Table S3.

Focusing on chigger species, infestation rates at the level of different species of birds appeared to be quite low (ranging from 0.05% to 4.3%) compared to total chigger infestation, although this may be explained in part by uneven sampling effort (see results of PGLS analysis below). *Toritrombicula densipiliata* was the dominant chigger species (4.3%; 86 birds infested) found on birds in this study, followed by *Odontacarus audyi* (3.9%; 80 birds infested) (Fig. 3B). Although three *Leptotrombidium* spp. were recorded, they were very rare (0.3% in aggregate; Fig. 3B).

In terms of chigger abundance on hosts, the highest counts were recorded during the dry season in Malaysia from Buff-necked Woodpecker (*Meiglyptes tukki*; 239 chiggers) captured in lowland forest at Krau Wildlife Reserve, Pahang, and *Gallus gallus* (Red Junglefowl; 237 chiggers) captured in an agricultural habitat (oil palm plantation), Johor. Focusing on the host family level, the highest mean chigger abundance (>50 chiggers found on a bird) was recorded in Rallidae (56.5 chiggers; $n = 2$) and the lowest in Nectariniidae (0.01 chiggers; $n = 88$). Next, non-migrant bird species tended to have a higher mean chigger abundance (4.6 chiggers; $n = 1353$) compared to altitudinal migrants (1.4 chiggers; $n = 19$) and full-migrant species (1.3 chiggers; $n = 634$). Bird species with no forest dependency were infested with significantly lower mean chigger abundance (0.2 chiggers; $n = 568$), compared to those bird species with forest dependencies. Birds in captivity harboured the highest mean chigger abundance (15.8 chiggers; $n = 60$), substantially higher than that observed in the other eight habitat types examined. Mean chigger abundance was not significantly different between the birds captured in the dry (3.2 chiggers; $n = 774$) and wet season (2.8 chiggers; $n = 372$) in Malaysia. Overall, birds captured from Thailand (4.2 chiggers; $n = 860$) and Malaysia (3.1 chiggers; $n = 1146$) displayed no significant difference in the mean chigger abundance (Table 1, Appendix Table S4).

3.2. Diversity of chigger infestation on birds

Species richness of chiggers on birds was recorded through observed chigger species richness (ObCSR) and estimated with the 1st Jackknife (Jack1), Chao, and Bootstrap (Boot) species richness estimators. In total, 21 chigger species were identified from the bird hosts. Birds from the order Passeriformes (ObCSR = 9, Jack1 = 11.9, Chao = 11.9, Boot = 10.2) and the family Pellorneidae (ObCSR = 6, Jack1 = 8.9, Chao = 10.4, Boot = 7.2) exhibited the highest chigger species richness among all taxa examined. Non-migrant bird species harboured a slightly higher chigger species richness (ObCSR = 15, Jack1 = 19.9, Chao = 21.2, Boot = 17.2) than full-migrant species (ObCSR = 12, Jack1 = 15.9, Chao = 17.9, Boot = 13.5). However, estimation of Shannon diversity index revealed a contrasting result, with higher chigger diversity in the full migrants (Shannon = 2.02) compared to non-migrant species (Shannon = 1.86). In terms of forest dependency, bird species with low (ObCSR = 14, Jack1 = 17.9, Chao = 17.9, Boot = 15.8) and medium forest dependency (ObCSR = 9, Jack1 = 11.9, Chao = 13.5, Boot = 10.3) harboured higher chigger species richness compared to high or non-forest-dependent species.

Among the nine habitat types, birds captured in the island lowland forest had the highest chigger species richness (ObCSR = 8, Jack1 = 11.9, Chao = 13.9, Boot = 9.4), followed by the birds from agriculture (ObCSR = 7, Jack1 = 8.9, Chao = 8.9, Boot = 7.9). Regarding chigger species richness of Malaysian birds, the dry season showed higher observed richness (ObCSR = 10) and higher richness estimators (Jack1 = 14.9, Chao = 16.2, Boot = 12.1) compared to the wet season (ObCSR = 6, Jack1 = 7.9, Chao = 7.9, Boot = 6.8) (Table 1). Birds examined from study sites in Thailand harboured a slightly higher chigger species richness (ObCSR = 14, Jack1 = 16.9, Chao = 18.5, Boot = 15.3) than did Malaysian birds (ObCSR = 11, Jack1 = 14.9, Chao = 13.6, Boot = 12.9) (Table 1, Fig. 4, Appendix Table S5).

3.3. Phylogenetic signals on the bird traits and chigger infestation status

Phylogenetic signal analyses revealed clear phylogenetic conservation in several basic ecological traits of birds, whereas chigger-related parameters displayed no phylogenetic signal (Appendix Table S6, Fig. 5). Forest dependency exhibited strong phylogenetic effects, with all

Table 1
Infestation rate, mean abundance, species richness, and diversity index of chigger infestation on birds captured in Malaysia and Thailand.

Group	No. of birds	Infestation rate (%) [95% CI]	Mean abundance [95% CI]	Observed species richness	Species richness estimator		Shannon index
					Jack1	Chao	
Bird taxonomic order							
Bucerotiformes	1	0	0	0	0	0	0
Caprimulgiformes	33	3.03 [0.16–17.51]	0.03 [0–0.09]	1	1.97	1	0
Charadriiformes	420	11.90 [9.04–15.48]	0.50 [0.26–0.74]	5	5.99	5	1.1971
Columbiformes	12	0	0	0	0	0	0
Coraciiformes	28	17.86 [6.76–37.58]	5.50 [0–11.72]	4	5.93	4.96	1.3296
Cuculiformes	8	25.00 [4.45–64.42]	0.50 [0–1.27]	2	3.75	2.88	0.6931
Galliformes	385	29.35 [24.90–34.22]	9.65 [7.01–12.30]	4	4.99	4.00	0.8154
Gruiformes	2	100.00 [19.78–100]	56.50 [0–748.99]	2	2.5	2.25	0.6365
Passeriformes	1093	16.47 [14.34–18.83]	2.47 [1.92–3.02]	9	11.99	11.99	1.3891
Pelecaniformes	3	0	0	0	0	0	0
Piciformes	8	12.50 [0.65–53.32]	29.87 [0–100.52]	1	1.88	1.00	0
Strigiformes	4	50.00 [15.01–84.99]	7.75 [0–28.39]	2	3.50	2.75	0.6931
Trogoniformes	9	0	0	0	0	0	0
Migratory status							
Full migrant	634	15.62 [12.92–18.73]	1.34 [0.89–1.79]	12	15.99	17.99	2.0242
Altitudinal migrant	19	5.26 [0.27–28.11]	1.42 [0–4.41]	1	1.95	1.00	0
Non migrant	1353	18.92 [16.89–21.13]	4.65 [3.70–5.60]	15	19.99	21.25	1.8617
Forest Dependency							
None	568	5.63 [3.94–7.94]	0.22 [0.08–0.35]	5	5.99	5.49	1.1779
Low	592	23.48 [20.16–27.15]	5.21 [3.72–6.70]	14	17.99	17.99	1.7064
Medium	627	22.01 [18.87–25.51]	3.60 [2.74–4.46]	9	11.99	13.49	1.4093
High	219	21.46 [16.34–27.61]	7.78 [4.07–11.48]	5	5.99	5.49	1.1516
Habitat							
Captivity	60	26.67 [16.45–39.89]	15.82 [5.98–25.66]	1	1	1	0
Urban settlement	213	0	0	0	0	0	0
Rural settlement	307	33.88 [28.66–39.51]	8.61 [6.33–10.89]	5	5	5	1.0801
Agriculture	126	15.08 [9.55–22.80]	3.53 [0–7.65]	7	8.98	8.98	1.7923
Natural wetland	73	1.37 [0.07–8.42]	0.02 [0–0.08]	1	1.98	1	0
Lowland forest	548	21.53 [18.21–25.26]	3.54 [2.36–4.72]	7	7.99	7.17	1.2586
Island lowland forest	98	45.92 [35.91–56.25]	9.92 [5.96–13.88]	8	11.96	13.94	1.3753
Highland forest	148	2.03 [0.52–6.27]	0.06 [0–0.16]	4	6.98	8.47	1.3321
Shore and coast	433	11.55 [8.76–15.03]	0.48 [0.25–0.72]	5	5.99	5.00	1.1971
Season (Malaysia)							
Dry	774	14.47 [12.2–17.0]	3.16 [3.03–3.29]	10	14.99	16.24	1.1194
Wet	372	10.22 [7.42–13.86]	2.89 [1.23–4.55]	6	7.99	7.99	1.3569
Country							
Malaysia	1146	13.09 [11.22–15.21]	3.07 [2.14–4.01]	11	14.99	13.66	1.3261
Thailand	860	23.95 [21.16–26.98]	4.24 [3.32–5.16]	14	16.99	18.49	2.0209
Total	**2006**	**17.75 [16.57–18.93]**	**3.57 [2.91–4.23]**	**21**	**26.99**	**29.99**	**2.1997**

phylogenetic signal indices showing significant values ($p < 0.01$), indicating that related bird taxa tended to exhibit a similar level of forest dependency. In terms of migratory status, a moderate phylogenetic signal was reported with a K-star value of 0.232 ($p = 0.030$), and a relatively high Lambda value (0.444), which was close to statistical significance ($p = 0.071$). Additionally, habitat type also revealed a strong phylogenetic effect with a significant Lambda value (0.346, $p = 0.007$). Thus, migratory behaviour and habitat preference appear to be somewhat conserved phylogenetically.

In addition, phylogenetic signal was found to be significantly associated with the number of hosts examined ($C_{\text{mean}} = 0.111$, $p = 0.026$; and $I = 0.003$, $p = 0.045$). This could reflect research bias (certain bird lineages being studied more intensively) rather than a biological pattern (Appendix Fig. S1).

3.4. PGLS explaining chigger infestation and chigger species richness on birds

Since significant phylogenetic signals were observed on some of the bird traits, generalized linear regression models were fitted using a correlation structure based on Pagel's lambda to account for phylogenetic relationships. The negative lambda values (Pagel's lambda), which were near zero in both models (Table 2), indicate virtually no phylogenetic signal in the distribution of either chigger infestation or chigger species richness across bird host, confirming previous phylogenetic effect analysis (Appendix Table S6). This suggests that closely related bird taxa do not share similar chigger parasitism patterns beyond what would be expected by chance. The models show that both chigger infection and species richness were strongly predicted by number of habitat types occupied (n_{habitat}) and significantly influenced by bird sampling effort (n_{host}) (Fig. 6). The area of geographical range occupied by bird species significantly affected chigger infestation, but not chigger species richness, possibly due to exposure to a greater number of chigger populations across their distribution range. Habitat type showed a marginally significant relationship with chigger species richness, suggesting specific habitat types might promote bird hosts to be exposed to a greater diversity of chigger species. Forest dependency level appeared to be an important influencing variable for both chigger infestation rate (strong effect) and chigger species richness (marginal significance). Thus, forest-specialised birds may have traits that render them more suitable hosts. In contrast, bird migratory status showed no influence on either variable.

Pairwise correlation analysis between the five predictive variables was also performed to assess potential collinearity. Evidently, all correlation coefficients in the analyses were below 0.5, which is considered acceptable, and did not raise serious concerns about collinearity affecting the PGLS models.

3.5. Meta-analysis confirms habitat influence on chigger species richness

The five bird species included in the meta-analysis (Appendix Table S7) revealed variation in sample sizes and effect magnitudes for

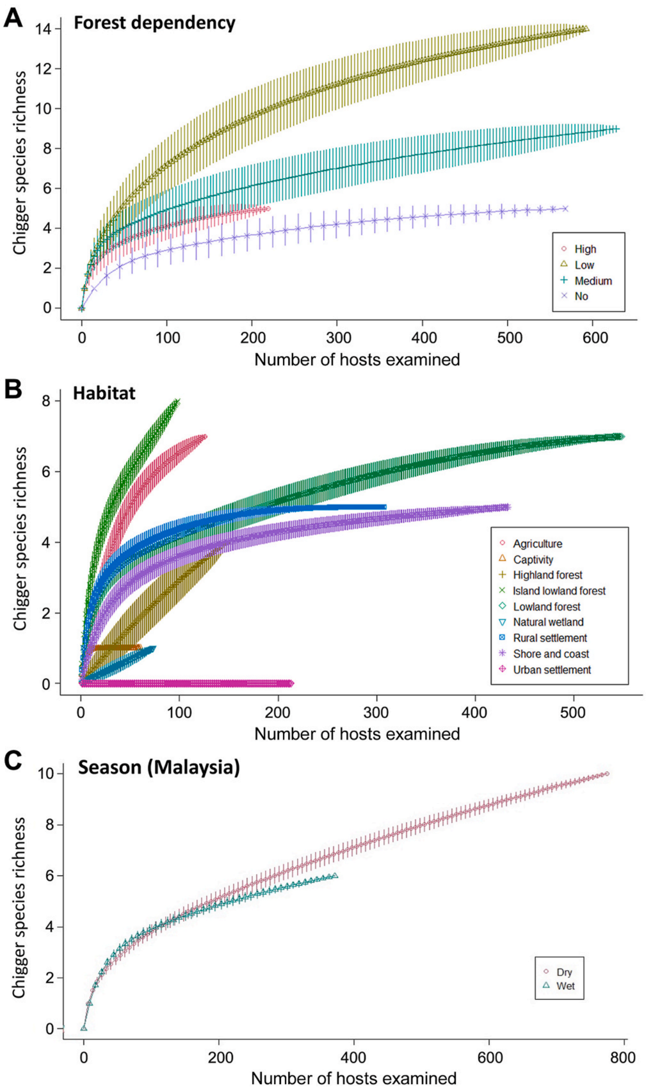

Fig. 4. Species accumulation curves showing the effect of birds' categorical parameters, including forest dependency (**A**), habitat (**B**) and season (Malaysia) (**C**), on chigger species richness.

habitat. The White-rumped Shama (*C. malabaricus*, $n = 53$, Cohen's $d = 0.27$) and the Siberian Blue Robin (*L. cyane*, $n = 38$, Cohen's $d = 0.26$) both showed the strongest positive association between habitat and chigger species richness. In contrast, the Streak-eared Bulbul (*P. conradi*) demonstrated a minimal effect (Cohen's $d = 0.02$) despite a moderate sample size ($n = 35$), suggesting habitat had little influence on chigger species richness in this bird species. The Red Junglefowl (*G. gallus*) also showed a weak association (Cohen's $d = 0.05$) with a sample size of 27 individuals. Finally, the Malayan Pied Fantail (*R. javanica*) had the smallest sample size ($n = 23$) with a modest effect size (Cohen's $d = 0.08$). The forest plot (Appendix Fig. S2A) illustrates these species-specific effects and the overall random-effect model estimates, while the funnel plot (Appendix Fig. S2B) indicated symmetrical data distribution, suggesting minimal bias.

Subsequently, species-specific effects were synthesised in the random-effect model. The analysis included 11 study comparisons ($k = 11$), which is more than five bird species because there were multiple habitat comparisons for some bird species. The overall effect size was 0.1564 (95% CI = 0.0552–0.2576; $z = 3.0282$; $p = 0.0025$), indicating a statistically significant positive association between habitat and chigger species richness across these five bird species. Tests for heterogeneity yielded a non-significant result ($Q = 4.4753$, df = 10, $p = 0.923$) with an I^2 value of 0%, indicating minimal variation in effect sizes across the studied bird species. In addition, an H^2 value of 1.00 confirms the absence of heterogeneity ($H^2 = 1$ means total variability equals sampling variability). This suggests a consistent ecological pattern in how habitat influences chigger species richness across these bird species.

3.6. Bird-chigger network analysis

Bipartite network analysis between host taxonomic rank and chigger species revealed a complex but structured pattern of bird-chigger relationships. Passeriformes showed broad connections to multiple chigger species, whereas Charadriiformes exhibited infestations restricted mainly to *Neacariscus andamanensis, N. shiraii,* and *S. archaea*. Galliformes displayed strong interactions with specific chigger species, particularly *N. gallinarum* and *E. wichmanni.* In contrast, some chigger species, e.g., *O. audyi*, *T. densipiliata*, and *N. longipes*, showed broad host ranges (Appendix Fig. S3).

Chigger–habitat associations showed that parasitism patterns varied across habitats, with some species acting as generalists and others as specialists. Birds captured from rural settlements, lowland forests, island lowland forests, and agricultural habitats exhibited highly diverse chigger associations, whereas captive birds and shore or coastal birds showed rather specialised associations. *Neoschoengastia gallinarum* showed a preference for human-modified habitats, whereas *T. densipiliata* had strong connections with forested habitats, particularly mainland and island lowland forests. *Neacariscus* spp. and *S. archaea* showed exclusive associations with birds from shore and coastal habitats, whereas *O. audyi* appeared to be a habitat generalist. However, most chigger species tended to associate strongly with birds from lowland forests compared to the other types of habitats (Fig. 7A). In summary, three main modules (clusters) were visible from the analysis comprising: (1) captivity and rural settlement (e.g., *N. gallinarum* and *E. wichmanni*); (2) coastal habitats (e.g., *Neacariscus* spp. and *S. archaea*); and (3) forests and agricultural habitats; e.g., *O. audyi*, *N. longipes*, and *Toritrombicula* spp. (Fig. 7B).

Bipartite network analyses of chigger species in association with forest dependency of the bird host species, and season when the bird hosts were captured, revealed some clear patterns (Appendix Fig. S4). Bird species with low-, medium- and high-forest dependency supported a high diversity of chigger species, whereas non-forest dependency showed rather selective associations. The most prevalent chigger species, *T. densipiliata* and *O. audyi*, displayed broad connections across multiple forest dependency levels, while *Neacariscus* spp. and *S. archaea* were more restricted. Moreover, chigger diversity was slightly higher in birds captured in Malaysia during the dry season than during the wet season (Appendix Fig. S4B).

Next, the unipartite network analysis illustrated that Passeriformes appeared to support high connectivity of the shared chigger species in the community (Fig. 7C), suggesting that the bird families in this order share more chigger species than the other bird taxa. Among these, Muscicapidae (flycatchers) constituted the most central node (highest centrality score of 1.00), followed by Pycnonotidae (bulbuls) with a centrality score of 0.93. Lower connectivity was observed in Phylloscopidae, Pachycephalidae, as well as in the shorebirds (Charadriidae and Scolopacidae), reflecting more specialised chigger associations. The latter two were completely isolated in the network with low centrality scores, depicting distinct chigger communities from the main cluster.

3.7. Canonical correspondence analysis (CCA) from aggregated data for bird species at a global scale

The CCA indicated that chigger species may have distinct habitat preferences regarding land use by the bird host species, with a clear separation between aquatic, terrestrial and modified environments. The plot revealed some specific patterns of interspecific clustering among chiggers. Birds from terrestrial land categories were associated with

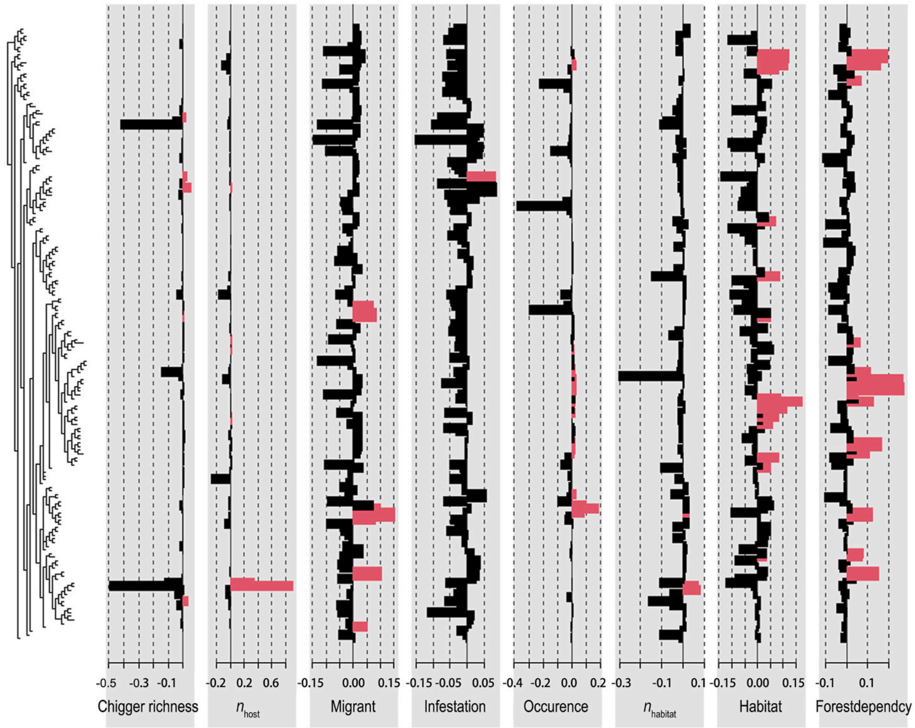

Fig. 5. Phylogenetic signal analysis of ecological variables in bird-chigger associations. The figure displays phylogenetic signal across the eight variables under a Brownian motion model (100 simulation replicates). The leftmost panel shows the bird host phylogeny. The eight columns represent different ecological variables: chigger richness, number of hosts examined (n_{host}), migratory status (migrant), chigger infestation (infestation), geographical area of occurrence (occurrence), number of habitats occupied (n_{habitat}), habitat type (habitat) and level of forest dependency (forestdependcy). Black bars indicate values for each trait across bird species, arranged according to the phylogeny. Red bars highlight traits with statistically significant phylogenetic signals as determined by Moran's I index.

Table 2

Phylogenetic generalized linear regression (PGLS) analysis of factors affecting chigger infestation and chigger species richness in birds.

Dependent variables	Predictive variables	Estimate	Std error	*t*-value	*p*-value	Model fitting details
Chigger infestation	(Intercept)	−0.2141	0.2143	−0.9989	0.3193	AIC = 273.462
	n_{host}	0.0061	0.0021	2.9506	0.0037**	BIC = 310.082
	n_{habitat}	0.1720	0.0427	4.0222	0.0001***	Log-likelihood = −127.731
	Migratory status	−0.1034	0.0819	−1.2619	0.2088	Phylogenetic signal (Pagel's lambda) = −0.026
	Area occurrence	0.0000	0.0000	4.3783	<0.0001***	
	Habitat	−0.1292	0.0177	−0.7293	0.4669	
	Forestdependcy	0.1809	0.0398	4.5458	<0.0001***	
Chigger species richness	(Intercept)	−6.2109	2.2512	−2.7588	0.0065**	AIC = 1022.057
	n_{host}	0.0950	0.0216	4.3952	<0.0001***	BIC = 1049.677
	n_{habitat}	3.4297	0.4522	7.5841	<0.0001***	Log-likelihood = −502.028
	Migratory status	−1.0873	0.8686	−1.2518	0.2125	Phylogenetic signal (Pagel's lambda) = −0.025
	Area occurrence	0.0000	0.0000	0.4356	0.6637	
	Habitat	0.3312	0.1895	1.7476	$0.0825^{\#}$	
	Forestdependcy	0.7276	0.4237	1.7172	$0.0879^{\#}$	

Models were fitted using a correlation structure based on Pagel's lambda to account for phylogenetic relationships. The analysis examined the influence of a number of predictive factors on two dependent variables: chigger infestation prevalence (binomial data) and chigger species richness (continuous data).

Note: Significance is coded as * $p < 0.05$, **$p < 0.01$, ***$p < 0.001$, and # indicates a trend close to statistical significance. Significant predictive variables are highlighted in bold.

E. wichmanni, *N. gallinarum*, *N. longipes*, *O. audyi*, *T. densipiliata*, and *T. kirhocephalis*. In contrast, bird species frequenting aquatic environments were associated with *N. andamanensis*, *N. shiraii*, and *S. archaea* (Fig. 8A).

In terms of global occurrences of the bird species, CCA revealed that two distinct chigger community patterns were apparent: one associated with bird species recorded only in the Indomalayan-Palearctic regions, and another with species that occur in additional realms (for instance, long-distance migrants ranging into the Afrotropical, Antarctic, Nearctic or Oceanian regions). Thus, *E. wichmanni* appeared to be more strongly associated with bird species restricted to the Indomalayan region, whereas *O. audyi*, *T. densipiliata*, and *T. kirhocephalis* were associated with bird species in both the Indomalayan and Palearctic regions. Furthermore, wide-ranging migratory bird species extending into the Afrotropical, Antarctic, Nearctic, and Oceanian realms were instead associated with distinct chigger species assemblages (i.e., *N. andamanensis*, *N. shiraii*, and *S. archaea*) (Fig. 8B).

4. Discussion

Southeast Asia hosts a notable variety of chigger species, with Malaysia and Thailand standing out as key global centres for chigger taxonomy research. Malaysia has documented 202 species, while Thailand has recorded 156 species (Stekolnikov, 2021). However, the

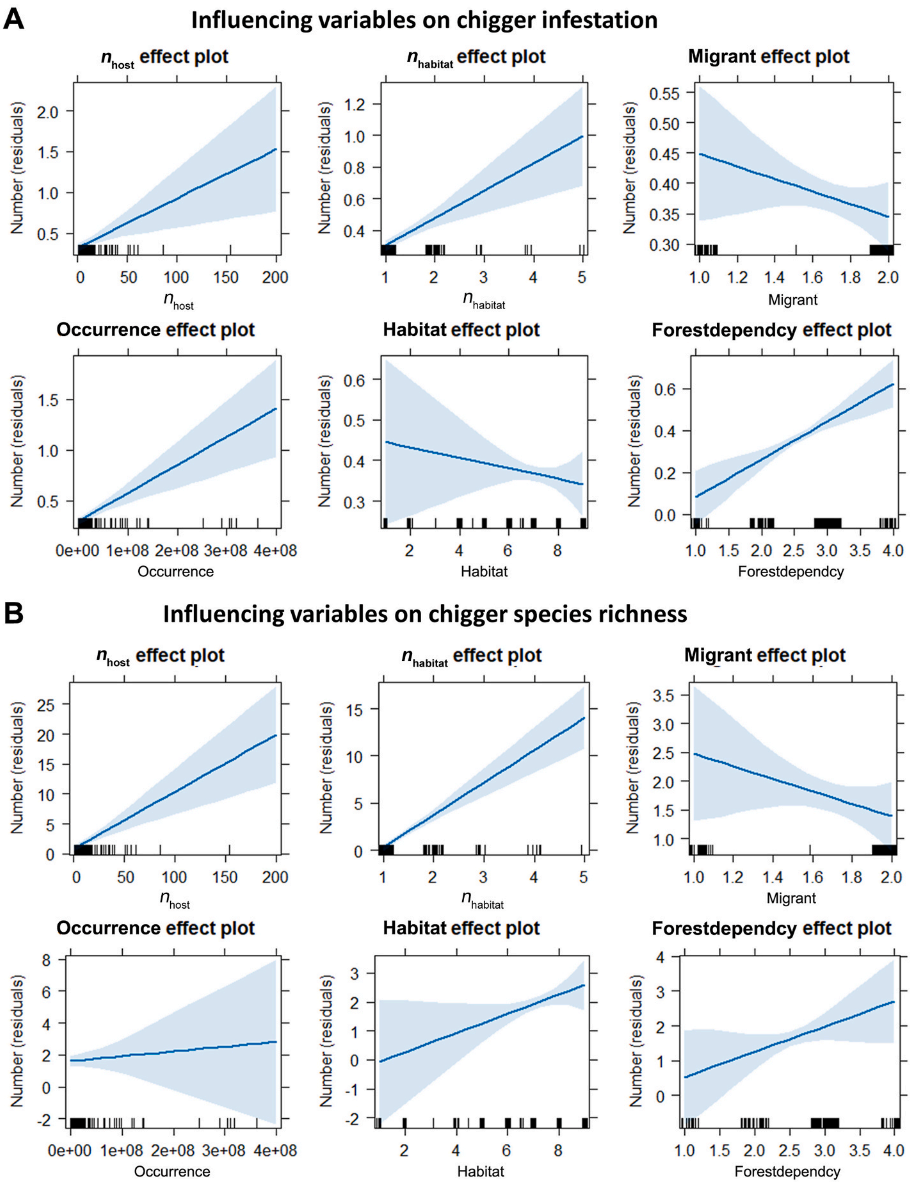

Fig. 6. Effect plots from a phylogenetic generalized linear regression (PGLS) model examining the influence of host-related variables on (**A**) chigger infestation, after accounting for phylogenetic relatedness among bird species and (**B**) chigger species richness, while accounting for phylogenetic relatedness. The predictive variables included: (i) number of host individuals examined (n_{host}), (ii) number of habitat types occupied ($n_{habitat}$), (iii) migratory status (migrant), (iv) geographic occurrence range (occurrence), (v) habitat type (habitat), and (vi) forest dependency level (forestdependcy). Solid blue lines represent the estimated effect of each predictor, with shaded areas indicating 95% confidence intervals. Tick marks along the *x*-axis represent data distribution for each predictive variable.

majority of studies have focused on collecting chiggers from small mammal hosts, while research on chiggers associated with birds has been relatively uncommon, being restricted to faunistic surveys and taxonomic descriptions, mostly from the mid-20th century (for example see Nadchatram and Upham, 1966; Nadchatram, 1967a, 1967b; Nadchatram and Traub, 1971). Such studies have generally neglected important ecological aspects, such as host-parasite interactions and the effects of season, habitat variability, and host geographical distributions on chigger communities. Apart from Thailand and Malaysia, Vietnam is the only other country in Southeast Asia where a survey on bird-associated chiggers has been conducted relatively recently (Kaluz et al., 2016).

An overall chigger infestation rate of 17.7% was observed from birds captured in the two countries, with infestation rates of 23.9% and 13.1% in Thailand and Malaysia, respectively. Although the number of bird samples (860 samples versus 1146 samples), the number of bird species examined (79 species vs 139 species), and the number of local study sites (10 sites vs 23 sites) in Thailand were much lower than in Malaysia, the chigger infestation rate was significantly higher in birds from Thailand. In addition, a higher chigger diversity was observed on birds captured from study sites in Thailand compared to Malaysia. This may be due to differences in sampling between zoogeographical subregions of the Oriental realm, as most of the study sites in Thailand were located at northern latitudes in the Indochina subregions (except Trang and Satun Provinces), whereas all the study sites in Malaysia were within the Sundaic region (Woodruff, 2010). The latitudinal distribution of chigger diversity observed on small mammalian hosts in China and Thailand exhibited a positive correlation up to approximately 25–26° North (Peng et al., 2016; Chaisiri et al., 2019; Chen et al., 2022), suggesting ecological adaptation and enhanced diversity of these ectoparasites within temperate and sub-temperate biogeographic zones, which was apparently corroborated by the bird infestation patterns in Thailand and Malaysia identified in the current investigation.

Odontacarus audyi and *T. densipiliata* were the most frequently

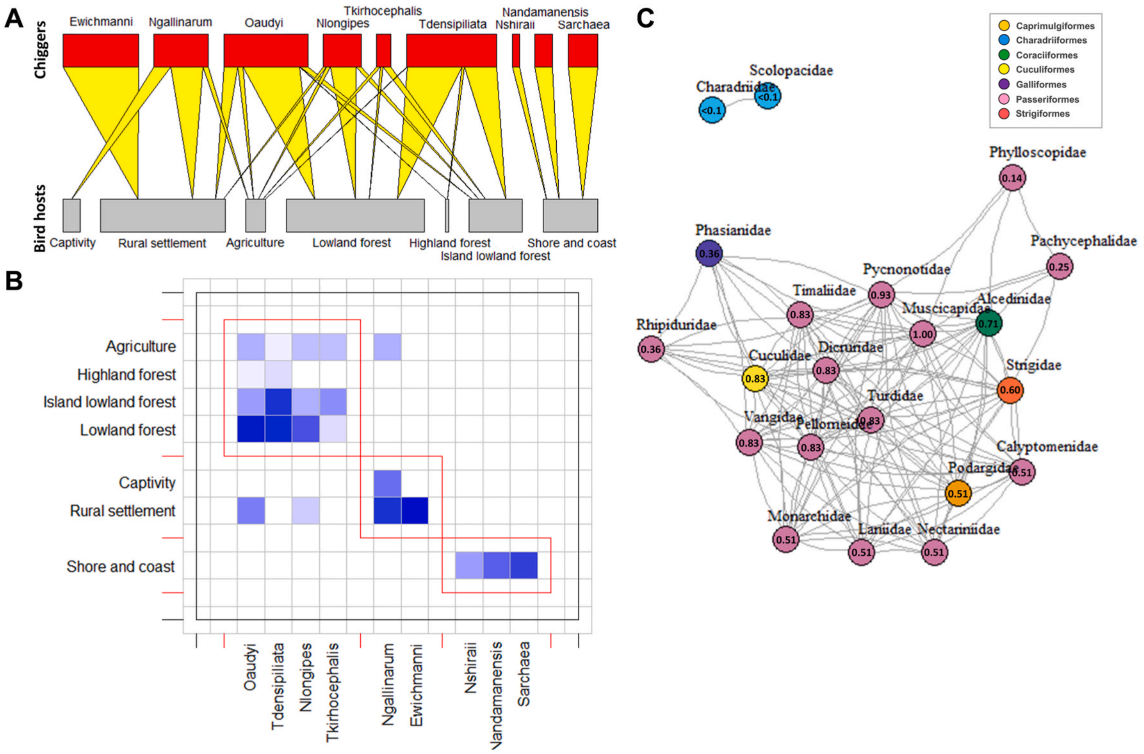

Fig. 7. Bipartite network graph (**A**) and module web plot (**B**) of bird-chigger associations showing patterns of chigger species infestation among different habitats where the birds were captured. Unipartite network analysis (**C**) of bird families (nodes) connected by shared chigger species (edges). Node colours represent different bird orders as shown in the legend. Values within nodes represent network centrality score (Eigen centrality), ranging from 0 to 1.

recorded chigger species on the birds from Thailand and Malaysia, and across different habitats. These chigger species exhibited pronounced generalist characteristics, with extensive distributions across diverse habitat typologies, encompassing both pristine forested environments (lowland, island lowland, and highland forests) and anthropogenically modified landscapes (agricultural and rural settlements), but apparently lacked colonisation potential in coastal ecosystems. *Odontacarus audyi* has a geographical distribution spanning India, Malaysia, Thailand, and Vietnam; whereas *T. densipiliata* exhibits a more expansive continental and insular range, including Indonesia, Malaysia, Papua New Guinea, the Philippines, Taiwan, and Thailand (Stekolnikov, 2021). The CCA indicated that the biogeography of these chigger species overlaps with host stopover sites along the East Asian-Australian and Central Asian migratory flyways for birds that breed in the Palearctic, although it is noteworthy that neither has become established north of the Tropic of Cancer.

In the current investigation, *O. audyi* was documented parasitising 23 avian species representing the Cuculiformes, Galliformes, and Passeriformes orders across multiple provinces in Thailand (Kanchanaburi, Nan, and Rayong) and Malaysian states (Kedah, Pahang, Selangor, and Terengganu). Conversely, *T. densipiliata* demonstrated a broader host range, parasitising 34 bird species spanning the Caprimulgiformes, Coraciiformes, Cuculiformes, Passeriformes, and Strigiformes, and had a wider distribution across Malaysian states (Johor, Kedah, Pahang, Perak, Sarawak, Selangor, and Terengganu). However, in Thailand, we observed this species only on two thrush species—Orange-headed Thrush (*Geokichla citrina*) and Siberian Thrush (*Geokichla sibirica*), which were encountered on Koh Mun Nai Island (a small island in the Gulf of Siam), Rayong Province. It seems likely that *T. densipiliata* parasitised these thrush species during their migratory trajectory. Both host species traverse maritime routes across the Gulf of Siam when returning from Sundaic wintering grounds, then head towards their breeding territories in the eastern Himalayan region (for *G. citrina*) or East Asia and Russia (for *G. sibirica*) via the Asian–Australian Migratory Flyway (Yong et al., 2015; BirdLife International, 2024b, 2024c).

Among the 21 chigger species found on birds in this study, *L. deliense*, *L. imphalum*, and *B. acuscutellaris* are well-known as vectors for *Orientia tsutsugamushi*—the intracellular rickettsial pathogen responsible for scrub typhus in the Asia-Pacific region (Frances et al., 2001; Elliott et al., 2019; Chaisiri et al., 2023). In addition, *Leptotrombidium* and *Blankaartia* have been implicated as potential vectors of *Bartonella tamiae*, one of several *Bartonella* spp. that cause illness in Asian populations (Kosoy et al., 2008; Kabeya et al., 2010). *Leptotrombidium deliense*, the primary vector of scrub typhus in Southeast Asia, exhibits low host specificity, parasitising a wide range of terrestrial vertebrates in the Rodentia, Scandentia, Eulipotyphla, Chiroptera, Carnivora, Artiodactyla, and Primates as well as multiple avian hosts (Lv et al., 2018; Stekolnikov, 2021). *Leptotrombidium imphalum* is primarily associated with ground-dwelling small mammals, with more limited interactions with bird hosts compared to *L. deliense* (Tanskul and Linthicum, 1999; Stekolnikov, 2021). *Blankaartia acuscutellaris* is less likely to act as a vector of scrub typhus compared to *Leptotrombidium* spp. but may play a key role in maintaining *O. tsutsugamushi* infection in wild vertebrates. This chigger species is also recognised as having a wide host range, parasitising birds and rodents as primary hosts, and occasionally bats, carnivores, and reptiles (Ripka and Stekolnikov, 2006; Makol and Korniluk, 2017; Stekolnikov, 2021). All these vector species were rarely observed in our study and the diversity of *Leptotrombidium* spp. was much lower than recorded on birds in Vietnam (Kaluz et al., 2016).

Both *L. deliense* and *L. imphalum* are associated with hosts inhabiting either natural or human-altered habitats, such as forest, shrubland, grassland, agricultural land, and public parks, particularly on plains and valleys at lower altitudes (Tanskul and Linthicum, 1999; Peng et al., 2016; Lv et al., 2018; Chaisiri et al., 2019; Wulandhari et al., 2021). In contrast, *B. acuscutellaris* has been recorded consistently from aquatic environments and prefers hosts dwelling in floodplains and wetlands (Ripka and Stekolnikov, 2006; Makol and Korniluk, 2017; Chaisiri et al., 2019; Trnka et al., 2023). In the present study, *L. deliense* was found on

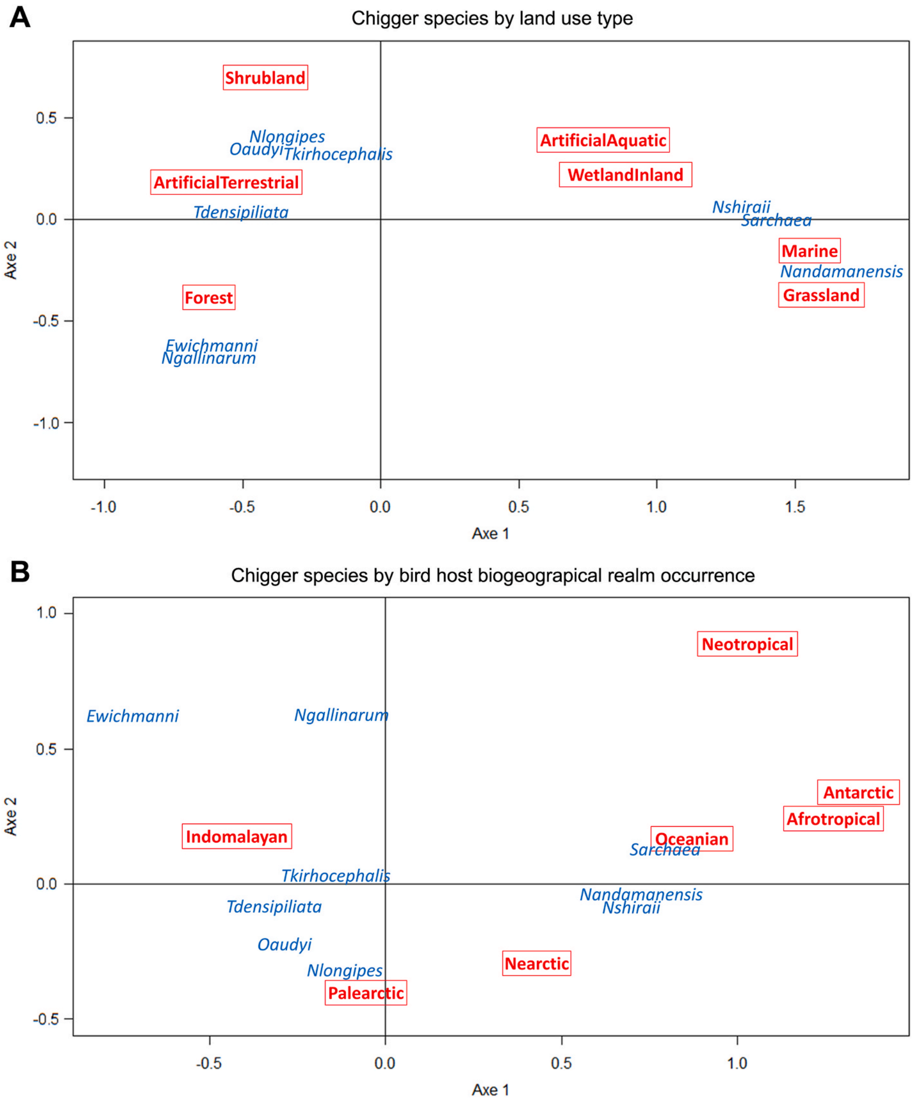

Fig. 8. Canonical correspondence analysis showing the associations between the nine chigger species within (**A**) the land use types, with the first and second dimensions explaining 94.46% of total variance; and (**B**) within the biogeographical realms where the bird host species were recorded, with the first and second dimensions explaining 88.39% of total variance.

Siberian Rubythroat (*Calliope calliope*) from a natural wetland habitat in Thailand and on Puff-throated Babbler (*Pellorneum ruficeps*) from a highland forest and an island lowland forest in Malaysia. *Leptotrombidium imphalum* occurred on the two ground-dwelling waterbird species, White-breasted Waterhen (*Amaurornis phoenicurus*) and Slaty-breasted Rail (*Lewinia striata*), from agricultural lands in Sarawak, Malaysian Borneo. Interestingly, *B. acuscutellaris* was found co-infesting the same individual Slaty-breasted Rail. To the best of our knowledge, this study represents the first time specific avian species have been identified as hosts of *L. imphalum* (although there is a generic report of *L. imphalum* recorded on "Aves") (Stekolnikov, 2021). It is apparent that both small mammals and birds serve as critical reservoir hosts for chiggers of public health significance. Sympatric birds and small mammal species occupying similar habitats and comparable ecological niches may facilitate interspecific transmission of chiggers and associated pathogens, which bear significant implications for understanding epidemiological patterns and disease ecology dynamics.

We found that passerine hosts often showed higher infestation rates than birds from other orders, attaining 52–88% in the families Vangidae (e.g., *P. pyrhoptera*), Muscicapidae (e.g., *L. cyane*, *C. malabaricus*, *Cyornis brunneatus*, and *C. tickelliae*) and Pachycephalidae (*Pachycephala cinerea*). Moreover, chigger species richness reached a maximum in the Pellorneidae (e.g., *P. ruficeps*, *P. nigrocapitatum*) and Muscicapidae. The most widely-parasitised species hosted a chigger fauna composed predominantly of *L. deliense*, *O. audyi*, *T. densipiliata*, and *T. uphami*, which mediated the consistent infestation patterns within the Pellorneidae and Muscicapidae in particular. While sampling bias in terms of phylogenetic breadth of birds was a recognised limitation of our study, our meta-analysis of the effect of habitat on chigger species richness (restricted to heavily-sampled host species) confirmed the importance of ecological factors. Hence, it is noteworthy that the species we sampled from these passerine families tend to exhibit congruent adaptations, characterised by life in predominantly lowland habitats with a medium level of forest dependency and nest construction either in holes or on tree branches (e.g., bamboo clumps), utilising organic substrates strategically concealed within dense vegetation (Palko et al., 2011; Wee, 2016; Mansor and Ramli, 2017). Furthermore, these bird taxa demonstrate similar foraging strategies, manifesting as ground-level, insectivorous feeding behaviours with deliberate, low-velocity movements through dense vegetation. Breeding behaviour is another potentially important risk factor, as there is the potential for prolonged exposure to ectoparasites within the nest environment due to an enclosed, continuous reproductive cycle, including free-living stages (Heeb et al., 2000; Moreno et al., 2009). Accordingly, while few woodpeckers (Picidae) were sampled in this study, it is noteworthy that the single bird individual with the highest level of chigger infestation was a Buff-necked Woodpecker (*M. tukki*) parasitised by *Ascoschoengastia lorius*. This same chigger species was recovered alongside post-larval stages in the tree-hole nests of psittaciform birds in Queensland, Australia (Shaw, 2010). As woodpeckers also nest in tree holes, this is strong evidence for a nidicolous lifecycle in this chigger species, and sampling of nests in Southeast Asia could shed light on the prevalence of *A. lorius* and potentially other chigger species with heretofore undescribed nidicolous habits.

Overwhelmingly, it was the Passeriformes, exemplified by the Muscicapidae, Pellorneidae, and Pycnonotidae, which also emerged as the core component of bird-chigger associative networks. In contrast, peripheral communities, represented by aquatic ground-dwelling bird taxa such as Charadriidae and Scolopacidae (Charadriiformes), exhibited entirely separate interconnections. Nevertheless, the Charadriiformes demonstrated high chigger species richness, with their trombiculid community presenting a markedly distinct species composition compared to passerines and other bird orders. Remarkably, no chiggers were found from Malaysian shorebirds in our study, while four previously described chigger species (*N. shiraii*, *Neacariscus sulae*, *Neacariscus pluvius*, and *S. archaea*) and a new species (*N. andamanensis*) were reported from shorebirds in Thailand. *Neacariscus* spp. and *S. archaea* have been documented in association with aquatic and shorebird hosts across disparate regions other than Southeast Asia, including the Oceanian and Afrotropical ecological zones (Vercammen-Grandjean and Langston, 1976; Mertins et al., 2009; Koosakulnirand et al., 2023). This demonstrates a high degree of ecological specificity for seacoast environments, particularly in tropical ecosystems, and indicates potential carriage not only along the East Asian–Australian and Central Asian flyways, but on the East Asian–East African and/or East Atlantic routes too.

Our findings revealed a pronounced habitat selectivity among chigger species, with forested habitats including island lowland and lowland forests—and anthropogenically modified landscapes such as agricultural and rural settlement areas—exhibiting the highest bird chigger infestation rates and diversity. In contrast, urban bird populations, including resident species such as House Crows and migratory species such as Barn Swallows, showed no signs of chigger infestation. Meanwhile, captive, endangered galliform birds from the sanctuary were colonised by a single chigger species, *N. gallinarum* (Rajasegaran et al., 2024), which highlights that even in managed environments, birds may still be susceptible to infestation under conditions that support parasite persistence and transmission. While comparative studies on bird-chigger interactions in relation to habitat remain limited, our observations align with previous research on small mammalian hosts across different ecological contexts. Investigations in Malaysia and Thailand consistently revealed heightened chigger species richness and abundance in hosts inhabiting forest border regions and agricultural plantations (Chaisiri et al., 2019; Alkathiry et al., 2022). Similarly, research in Yunnan documented high chigger species diversity in marginal, human-disturbed mountainous uncultivated habitats, with elevated infestation rates but lower diversity observed in cultivated, flatland environments (Peng et al., 2018). Matthee et al. (2020) reported significantly higher chigger species richness in agricultural and natural landscapes, contrasting sharply with depauperate urban habitats. Accordingly, Wulandhari et al. (2021) identified only two chigger species in small mammal populations within a highly urbanized area (Bangkok's public parks), despite high infestation rates. The ecological mechanism underlying these observations potentially resides in the complex dynamics of ecotone landscapes, especially transitional zones between natural forests and agricultural lands. These heterogeneous environments provide critical resources and shelters for generalist host species, including small mammals, birds or other vertebrates to adapt while navigating diverse habitat configurations. Moreover, such ecologically complex interfaces may sustain microhabitat conditions that support off-host trombiculid mite development, facilitating their predatory interactions within invertebrate ecological networks.

While short-term sampling methodologies present inherent limitations in characterising the temporal dynamics of chigger communities, our observations revealed significant seasonal differences in chigger species assemblages in Malaysia. Specifically, bird hosts captured during the dry season exhibited markedly higher chigger species richness compared to those sampled during the wet season. This finding emphasises complex seasonal variations in chigger parasitism within tropical ecosystems and underscores the critical role of environmental parameters such as rainfall and humidity in mediating bird-chigger-environment interactions. Multiple ecological mechanisms potentially explain these observed patterns. During the dry season, habitat conditions (e.g., reduced flooding) may create more conducive circumstances for trombiculid survival and reproductive success (Peng et al., 2018). Alterations in host movement and habitat utilisation across seasonal gradients can substantially influence parasite transmission dynamics. For instance, hosts might expand their home and foraging ranges during resource-scarce drier periods, consequently increasing their probability of encountering and becoming parasitised by ectoparasites (Hamidi et al., 2015; Shilereyo et al., 2022). Previous ecological investigations in Southeast Asian small mammal populations have documented similar seasonal trends of increased chigger occurrence and species richness during drier periods (Chaisiri et al., 2019; Alkathiry et al., 2022). However, comparable empirical evidence for avian hosts remains scarce, highlighting the need for additional research to unravel the underlying dynamics shaping parasitism by chiggers.

Certain methodological constraints warrant critical examination in the present study. The sample size of individual birds was insufficiently representative in some host species, potentially limiting the generalisability of the findings. Notably, while Audy and Harrison (1951) reported an exceptionally high infestation rate—18,500 *L. akamushi* larvae from nine quails in Kuala Lumpur, Malaysia—the present study found no evidence of chigger infestation in King Quail (*S. chinensis*, $n = 13$) and Barred Buttonquail (*T. suscitator*, $n = 4$), two species from different families but with similar ecologies. Thus, additional studies on hosts from the Phasianidae and Turnicidae in wild habitats are warranted to clarify their role in chigger ecology. Importantly, this study did not explore the potential influence of host-specific characteristics (e.g., host sex, maturity, and moulting status) on chigger infestation rates, abundance, and diversity. Underlining these limitations, previous research has demonstrated the profound impact of host-specific attributes on ectoparasite infestation. For instance, Hamstra and Badyaev (2009) conducted an intensive study on *Carpodacus mexicanus* (House Finches), revealing that ectoparasite communities (feather mites, gamasid mites, and lice) were influenced by host breeding season, moulting cycles, sex, and age-related factors. Similarly, Sáez-Ventura et al. (2022) undertook a comprehensive longitudinal investigation on *Athene cunicularia* (Burrowing Owl), analysing multiple ectoparasite taxa in relation to diverse host attributes and environmental parameters. Future research on chigger infestations on birds should adopt a more holistic approach, systematically incorporating host-related variables such as demographic characteristics, population abundance, nesting typology, and spatial movement patterns between study sites. Such a multifaceted investigative strategy would provide more nuanced insights into the complex ecological mechanisms underlying bird-parasite dynamics.

CRediT authorship contribution statement

Praveena Rajasegaran: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sirikamon Koosakulnirand:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Krairat Eiamampai:** Supervision, Methodology, Investigation, Data curation. **Jirut Khamaye:** Methodology, Investigation, Data curation. **Ahmad Khusaini Mohd Kharip Shah:**

Methodology, Investigation, Data curation. **Nuramirah Diyanah Mohd-Johan:** Methodology, Investigation, Data curation. **Siti Nurul Izzah Mohd-Azami:** Methodology, Investigation, Data curation. **Muhammad Al Amin Mohd-Redzuan:** Methodology, Investigation, Data curation. **Mohamad Fizl Sidq Ramji:** Supervision, Methodology, Investigation. **Mohammad Saiful Mansor:** Supervision, Methodology, Investigation. **Philip Round:** Supervision, Methodology, Investigation, Data curation. **Sazaly Abubakar:** Supervision, Project administration, Funding acquisition. **Zubaidah Ya'cob:** Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Serge Morand:** Visualization, Validation, Supervision, Methodology, Formal analysis. **Benjamin L. Makepeace:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Kittipong Chaisiri:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Ethics statement

In Thailand, research protocol involving animals was approved by the Faculty of Tropical Medicine, Mahidol University, Animal Care and Use Committee (FTM-ACUC, Certification No. 011/2020E) and the Department of National Park Wildlife and Plant Conservation (DNP), Ministry of Natural Resources and Environment with the permission letter no. 0907.4/21997.

In Peninsula Malaysia, animal handling work was approved by the Universiti Malaya Institutional Animal Care and Use Committee (permission no: G8/07052020/09012020-01/R) and biosafety protocols of the Universiti Malaya Institutional Biosafety and Biosecurity (IBBC No.: UMIBBC/PA/R/TNCPNI/TIDREC-004/2020). In Peninsular Malaysia, a wildlife research permit was obtained from the Department of Wildlife and National Parks (DWNP) with the permission no. W-00064-15-21. In Sarawak, permit documents were obtained from the Sarawak Forest Department, National Parks and Nature Reserves, East Malaysia: permission no. SFC.810-4/6/1 – 033 for collecting biological resources and permission no. WL 13/2022 for entering the parks for research purposes.

The study was also approved by the Animal Welfare and Ethical Review Body of the University of Liverpool with the reference no. AWC0179 for study in the Thailand and no. AWC0219 for Malaysia.

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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

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