

Thermal Refugia within Temperate Habitats: Modelling Microclimate Landscapes to Predict Bird Distribution Responses

Vidya PADMAKUMAR ^{©*1}, Murugan SHANTHAKUMAR ^{©2}

¹ EcoDiversity Research Centre, Hazelton, BC, Canada

² EcoDiversity Research Centre, Bengaluru, India Corresponding author: vidyapkumar3@gmail.com

Abstract

Temperate ecosystems are undergoing accelerated warming and increasingly frequent thermal extremes, yet the vulnerability of avian species within these landscapes is not determined solely by broad-scale climate metrics. Rather, the microclimate the fine-scale thermal environment experienced by individual birds in their habitat plays a critical role in mediating exposure, behaviour, and ultimately distributional responses. This paper presents a framework for modelling microclimate landscapes in temperate habitats and applying these models to predict bird distribution responses under climate change. We synthesise empirical evidence linking microclimate heterogeneity and avian population trends, describe methodological approaches for deriving fine-scale thermal layers, and implement a conceptual modelling workflow that integrates microclimate availability, thermal safety margins and habitat connectivity. We illustrate how this framework could be applied in temperate forest and shrub-grassland systems, and discuss how structural habitat features (e.g., canopy complexity, northerly aspects, dense shrubs) may act as thermal refugia. Our review of long-term breeding bird data shows that sites with cooler sub-canopy conditions in structurally complex forests exhibit less negative population trends, supporting the microclimate-buffering hypothesis. We conclude that incorporating high-resolution micro-climate layers into species distribution modelling significantly refines predictions of vulnerability for temperate birds and highlight key management implications: preserving structural complexity, enhancing connectivity of cooler patches, and targeting micro-climate refugia in conservation planning.

Research Article

Article History

Received : 04.11.2025 Accepted : 16.12.2025

Keywords

Temperate Birds, Microclimate Modelling, Thermal Refugia, Species Distribution, Canopy Structure, Climate Change

1. Introduction

Temperate ecosystems are facing increasing challenges attributed to global climate change, marked by notable warming trends of approximately 0.2–0.3°C per decade, as reported by the Intergovernmental Panel on Climate Change (IPCC) (Dobrowski, 2011). This trend brings about a rise in the frequency and intensity of extreme heat events, leading to considerable physiological stress on avian species that depend on behavioral and microhabitat adaptations for temperature regulation (Kim et al., 2022). Traditional species distribution models (SDMs), which primarily rely on macroclimatic data such as annual mean temperature and monthly precipitation, often inadequately capture the microenvironmental conditions experienced by individual birds within heterogeneous landscapes (Chardon et al., 2023). Microclimates defined as localized climatic conditions that differ from the broader region play a critical role in mediating how species respond to shifting macroclimatic patterns (Norris et al., 2011). Factors such as habitat structure, topography, and vegetation density profoundly influence microclimatic conditions. In temperate forests, attributes such as canopy height and density can significantly mitigate maximum temperatures, providing crucial thermal refugia during periods of extreme heat (Arx et al., 2013). For example, birds residing in structurally complex habitats in temperate forests may exhibit less adverse population trends than those in simplified or open-canopy environments, reflecting the adaptive advantages afforded by microclimatic buffering (Pradhan et al., 2023). The "microclimate buffering hypothesis" posits that avian species inhabiting micro climatically diverse habitats will likely experience reduced exposure to extreme temperatures. Consequently, these birds may face slower population declines compared to those in uniform habitats (Sunday et al., 2019). This hypothesis is supported by empirical data indicating that birds in varied habitats, characterized by complex vegetation and topographical features, show improved resilience to climatic extremes (Kim et al., 2022). Researchers emphasize the need to incorporate high-resolution microclimate modeling into broader ecological frameworks to accurately assess avian vulnerability and potential distribution responses amid climate change (Chardon et al., 2023). Despite the recognition of microclimate's essential role, relatively few studies have integrated these fine-scale climatic variables into conventional assessments of species distribution or vulnerability (Frenne et al., 2013). Future research should prioritize the integration of microclimatic data with habitat structural metrics and species-specific thermal tolerances, facilitating a comprehensive modeling framework that identifies potential thermal refugia and evaluates population-level responses to environmental changes (Liu et al., 2025). This synthesis not only underscores the importance of localized climate dynamics but also highlights the necessity for adaptive management strategies aimed at preserving biodiversity in temperate ecosystems under the mounting pressures of climate change. The present study focuses on temperate habitats and develops a framework for modelling microclimate landscapes to predict bird distribution responses under climate change scenarios. By focusing on temperate ecosystems and microclimatic variation, this work aims to bridge the gap between macroclimate predictions and the actual thermal landscapes experienced by birds. The approach provides a mechanistic basis for improving forecasts of species vulnerability, identifying priority habitats for conservation, and guiding adaptive management strategies in the face of ongoing climate change.

2. Material and Method

To construct a microclimate-based modelling framework suitable for temperate bird habitats, a comprehensive synthesis of the existing literature and methodological approaches was undertaken. Studies were selected that met the following criteria:

(1) focused on temperate forest, shrubland, or grassland habitats,

- (2) incorporated fine-scale microclimate measurements or modelling,
- (3) linked microclimate data to bird distribution, abundance, or demographic parameters, and
 - (4) provided methodological transparency suitable for replication or adaptation.

Data Sources and Study Selection:

Peer-reviewed literature from 2000 to 2025 was surveyed across Web of Science, Scopus, PubMed, and Google Scholar. Priority was given to studies providing high-resolution microclimate datasets, habitat structural metrics, and empirical or modelled relationships with bird occupancy or population trends.

The resulting studies span multiple temperate regions, including North America, Europe, and East Asia, and encompass various habitat types:

- Forests: Old-growth and secondary deciduous forests, mixed coniferous—broadleaf stands.
- Shrublands and Grasslands: Temperate steppe, heathlands, and mosaic landscapes with patches of dense vegetation.
- Riparian and wetland edges: Areas providing structural heterogeneity and potential cooling microhabitats.

3. Results and Discussion

3.1. Empirical evidence of microclimate effects on temperate birds

Microclimate heterogeneity in temperate habitats has gained recognition for its significant impact on avian distribution, behavioral strategies, and population dynamics. Empirical research across varied environments, including forests, shrublands, and grasslands, has demonstrated that fine-scale variations in temperature and humidity serve as buffers against macroclimatic extremes, thereby reinforcing the microclimate buffering hypothesis (Kim et al., 2022). This hypothesis posits that microclimatic diversity allows avian species to adapt behaviorally to changing environmental conditions, offering refuge during periods of extreme heat or cold.

In forest ecosystems, the presence of complex structural features such as varying canopy heights and densities can create localized microclimatic conditions that mitigate temperature fluctuations and humidity levels. Studies indicate that species occupying these heterogeneous environments may show stable or increasing populations compared to those in more homogenized settings (Frey et al., 2016). Microclimates play an essential role in temperate forests by providing localized environmental conditions that differ from the broader regional climate. Structural features of the forest, such as canopy cover, understory vegetation, and topographic variation, create these microclimatic refugia. These refugia help buffer plant and animal populations from extreme temperature and moisture fluctuations associated with climate change. This buffering capacity is crucial for sustaining species diversity and ecological stability in forest ecosystems increasingly affected by global climate shifts.

In shrubland and grassland ecosystems, similar patterns emerge. Research has shown that areas characterized by dense vegetative cover can maintain cooler microclimates, which provide relief to birds during heat extremes. This allows them to optimize their foraging behavior and nesting success (Bernath-Plaisted et al., 2023). This microclimate resilience is crucial for species that rely on specific habitat conditions for breeding and foraging. Studies indicate that birds often shift their nesting and foraging behaviors in response to varying

microclimatic conditions, enabling them to track these subtle changes in their environment (Champlin et al., 2009; Bernath-Plaisted et al., 2025).

Moreover, advancements in microclimate modeling have shown that many avian species, particularly those dependent on forest understoreys, operate within buffered microclimates that differ significantly from macroclimatic conditions. These models underscore the need for conservation strategies that account for microclimatic complexities present in different habitats, as they can provide insights into potential refugia for species facing climate-induced habitat changes (Padmakumar and Joseph, 2022; Stark and Fridley, 2022). As our understanding of forest ecology and climate interactions advances, it is increasingly important to incorporate microclimate dynamics into habitat management and conservation planning. Considering fine-scale climatic variation can enhance the capacity of management strategies to support species persistence under changing environmental conditions. In particular, integrating microclimate data into habitat models and restoration efforts can improve the resilience of avian populations facing future climate scenarios (LeBrun et al., 2016; Coulson et al., 2025).

Despite these insights, there remains a pressing need for further rigorous research that systematically incorporates microclimate data into broad-scale species distribution projections and vulnerability assessments. Doing so is vital for identifying critical habitats that provide microclimatic refuge and for developing adaptive management framework that enhance avian biodiversity conservation in the face of a changing climate (Schwartz et al., 2020).

3.2. Forested habitats

In temperate forest ecosystems, structural components such as canopy height, density, and understory complexity play a crucial role in creating substantial microclimatic variation. Sub-canopy temperature measurements in deciduous and mixed-coniferous forests reveal differences of up to 5–7 °C between exposed forest edges and cooler interior understories during peak summer conditions (Padmakumar and Shanthakumar, 2023). This temperature fluctuation can create unique microhabitats that influence the distribution and population dynamics of avian species. For instance, birds inhabiting structurally complex forests, characterized by denser canopies and stratified understory layers, tend to exhibit higher occupancy rates and more stable population trends compared to species in simpler or homogeneous stands (Davis et al., 2018).

Long-term monitoring efforts of forest passerines have shown an inverse relationship between sub-canopy temperatures and population decline; sites that maintain cooler microclimates are associated with significantly less negative population trends (Padmakumar et al., 2020). This phenomenon highlights the importance of structural complexity in mitigating thermal stress, which can adversely affect avian populations in increasingly warmer climates. Species such as the wood thrush (Hylocichla mustelina) have been observed to preferentially select nest sites within cooler, shaded microhabitats, where canopy cover and leaf litter depth substantially influence nest-site temperatures and subsequent reproductive success (Frenne et al., 2013; Lombaerde et al., 2022).

Similar patterns are documented in European temperate forests, where species such as the European robin (Erithacus rubecula) and wood warbler (Phylloscopus sibilatrix) are known to occupy cooler, densely vegetated microhabitats, particularly during summer months when macroclimatic extremes become pronounced (Zellweger et al., 2019). The canopy structure and composition directly regulate these microclimatic conditions, providing birds with thermal refugia and enhancing local humidity levels, which fosters a conducive environment for nesting and foraging.

As global temperatures rise and climatic extremes become more frequent, understanding and preserving microclimatic heterogeneity within forest ecosystems will be crucial for the conservation of temperate forest avifauna. Maintaining structural complexity in forests can enhance the resilience of avian communities against challenges posed by climate change (Spicer et al., 2020; Ulyshen et al., 2024). Integrating knowledge of microclimatic dynamics into forest management and conservation practices will be essential for ensuring the longevity and stability of avian populations within these vital ecosystems (Barry and Schnitzer, 2021; Giberti et al., 2023).

3.3. Shrubland and grassland habitats

Temperate grasslands and shrublands are characterized by significant microclimatic variation, which is influenced by several factors, including vegetation density, slope aspect, and proximity to water bodies. Research has demonstrated that dense shrub patches or north-facing slopes serve as small-scale refugia, effectively reducing operative temperatures and providing essential thermoregulatory opportunities for avian species (Eastman et al., 2013; Roonjho et al., 2020). For example, in steppe ecosystems, obligate ground-nesting birds, particularly the little bustard (Tetrax tetrax), select cooler microsites for nesting. Their nest survival rates are positively correlated with microhabitat shading and overall vegetation cover, highlighting the ecological importance of these microhabitats (Fa and Funk, 2007; Moradi et al., 2024).

Microclimatic studies have shown that these microhabitats can effectively reduce maximum daytime temperatures by 2–4 °C compared to surrounding open areas. This reduction is critical for mitigating heat-induced stress and mortality among avian populations (Fa and Funk, 2007; Pierce et al., 2016). The occupancy rates and reproductive success of birds are positively impacted when nesting sites are sheltered from extreme temperatures, allowing them to maintain more stable physiological conditions during the critical summer months (Murphy et al., 2013).

Specifically, investigations into the sagebrush songbird complex have revealed that nest-site selection is profoundly influenced by microclimatic conditions. Nests positioned under dense shrubs or within natural depressions experience diminished temperature fluctuations and lower peak temperatures compared to those in more exposed locations. This buffering effect is vital for reducing thermoregulatory stress for both adult birds and their nestlings (Criado et al., 2020; Mancuso et al., 2022).

Moreover, the notion of microclimatic refugia underscores the adaptive significance of microhabitat selection in the context of climate change. Such microhabitats provide critical resources that enable birds to thrive despite fluctuations in macroclimatic conditions. The increasing awareness of these dynamics reinforces the need to incorporate microclimatic considerations into land-use planning and conservation strategies aimed at preserving avian biodiversity in temperate grasslands and shrublands (Zhu et al., 2025; Li et al., 2025).

The role of microclimatic variation in temperate grasslands and shrublands cannot be overstated. It significantly influences avian habitat selection, reproductive success, and overall biodiversity resilience. As climate change continues to exert pressure on these ecosystems, understanding and conserving microclimatic features will be essential for safeguarding avian populations and, more broadly, the ecological integrity of these habitats.

3.4. Topographic influences

Topography plays a critical role in modulating microclimatic conditions within temperate habitats, especially influencing temperature and moisture availability through various elements such as slope inclination, aspect, and elevation. In the northern hemisphere,

north-facing slopes typically exhibit lower maximum temperatures and increased moisture retention relative to south-facing slopes. This difference in insolation creates essential microhabitats for species that are sensitive to thermal extremes (Pandita et al., 2019). For instance, north-facing slopes often maintain cooler, more humid conditions, which favor moisture-loving plant species and can significantly impact local herbaceous and shrub communities (Lin, 2006).

In addition to slope orientation, valley bottoms play an important role in microclimatic regulation. These areas often retain cooler, moister conditions compared to ridge tops, largely due to the accumulation of cold air during nocturnal inversion events and reduced exposure to solar radiation (Kang et al., 2004). This can influence the distribution and occupancy of various avian and terrestrial species, as cooler valley microhabitats provide refuge against high temperatures that may prevail on adjacent ridges (Sørensen et al., 2006; Egli et al., 2007).

A case in point is observed in upland temperate regions where meadow pipits (Anthus pratensis) demonstrate preferential occupancy of north-facing slopes and moist depressions. Their habitat selection reflects a significant reliance on microtopography to maintain thermal refugia, which is vital during warmer seasons when heat stress can impact physiological well-being and reproductive success (Gilliam et al., 2014; Pan et al., 2022). Studies have indicated that the availability of cooler microhabitats within these environments is positively correlated with the stability of local bird populations, highlighting the adaptive significance of microclimatic influences on species distribution and habitat utilization (Berryman et al., 2015).

Topographically controlled differences in microclimate, including variations in soil moisture and temperatures, significantly shape ecosystem dynamics and species interactions within these habitats. For example, moisture availability is closely tied to topographic features, influencing vegetation patterns, seedling establishment, and overall biodiversity in these specialized environments (Regüés et al., 2006; Gutiérrez-Jurado et al., 2013). As climate changes and elevational ranges shift, understanding the nuances of topographically influenced microclimatic variations will be essential for effective conservation and management strategies aimed at preserving avian communities and the ecological integrity of temperate habitats.

3.5. Structural drivers and modelling microclimates

Microclimate heterogeneity is primarily governed by structural habitat features and terrain, both of which can be quantified and integrated into predictive models.

3.6. Canopy and vegetation structure

In forested landscapes, LiDAR-derived data have significantly enhanced our understanding of canopy structure and its impact on microclimatic dynamics, particularly concerning bird habitats. High-resolution measurements of canopy height, leaf area index, and understory density provide crucial insights into how these structural variables correlate with the moderation of sub-canopy temperatures (Kim et al., 2022). Denser canopies, characterized by a complex arrangement of foliage, significantly reduce solar radiation penetration, which in turn limits maximum temperature extremes while enhancing humidity retention within the forest understory (Frey et al., 2016).

The concept of structural complexity is increasingly recognized as vital for thermally sensitive avian species. In simplified or homogeneous forests, birds experience increased physiological stress, lower occupancy rates, and reduced reproductive success due to a lack of available thermal refugia (Betts et al., 2017; Jemal et al., 2020). For instance, avian diversity

studies have demonstrated that structural heterogeneity can predict bird density and species richness, aligning with the "habitat heterogeneity hypothesis" (Mulwa et al., 2012; Smith et al., 2021). Species thriving in rich, multi-layered environments with varied microclimatic niches tend to exhibit better survival and reproductive outcomes compared to those inhabiting monoculture or minimally structured habitats (Akresh et al., 2023).

The implications of structural complexity extend beyond spatial arrangement; they play a critical role in facilitating ecological interactions and resource availability necessary for successful nesting and foraging (Schall et al., 2020; Bitani et al., 2023). Birds that depend on specific structural features frequently adapt their behaviors based on available resources linked to microclimatic conditions. For example, species utilizing dense understory foliage for nesting or foraging benefit from the cooler and more stable microclimates created by robust tree canopies (González-Gómez et al., 2006).

Moreover, the relationship between forest management practices and structural complexity is essential. Thinning or selective logging can modify forest stand structures, enhancing microclimatic variability and resilience to climate disturbances (Menge et al., 2023). Conversely, reduced structural complexity can lead to declines in avian biodiversity as habitat homogenization increases, emphasizing the conservation value of maintaining diverse and structurally complex habitats (Tews et al., 2003; Betts et al., 2017; Smith et al., 2021).

As climate change poses increasing challenges, the need for conservation strategies that prioritize structural heterogeneity in forest management becomes imperative. Such strategies not only support avian populations but also contribute to broader ecological resilience (Jemal et al., 2020; Kim et al., 2022). Efforts to incorporate LiDAR data into conservation planning can inform effective habitat management practices, ensuring that avian species continue to thrive within their ecological niches as environmental conditions evolve (Zellweger et al., 2019; Frenne et al., 2021).

3.7. Shrub density and patch heterogeneity

In open shrubland and grassland habitats, vegetation density plays a crucial role in creating microhabitat variation that effectively moderates thermal extremes. Spatially heterogeneous patches containing taller shrubs, grasses, or dense ground cover provide shaded areas essential for avian species, significantly reducing operative temperatures during hot periods. These shaded microhabitats serve as critical refugia for birds, enhancing their ability to survive under extreme climatic conditions (He et al., 2010).

The connectivity and spatial distribution of these vegetation patches greatly influence bird movement, access to resources, and overall habitat suitability. Birds benefit from the availability of shaded microhabitats, which can mitigate the adverse effects of high temperatures associated with climate warming (Sankey et al., 2013). Greater patch density and spatial configuration can contribute positively to the ecological health of bird populations, allowing for easier access to food and shelter (He et al., 2015). In addition, LiDAR technology has proven valuable in modeling vegetation density and complexity, providing detailed insights into how structural attributes interact with microclimatic gradients (Acebes et al., 2021).

Effective modeling that incorporates variables such as patch density, spatial arrangement, and vegetation height allows for better predictions of avian responses to habitat modifications and climate change scenarios. Such models have been shown to capture microclimatic gradients, enabling researchers and land managers to assess potential impacts on bird populations and to develop conservation strategies that prioritize the maintenance of heterogeneous vegetative structures (Alonso et al., 2019).

The configuration of shrub patches can significantly affect soil moisture retention and surface temperatures, enhancing habitat suitability for avian species. This is particularly important in regions subject to drought or extreme heat, where access to cooler microhabitats can lead to improved survival rates and reproductive success (Rotenberg and Yakir, 2010). The integration of high-resolution data collection methods, such as LiDAR, into ecological research and management plans will further support efforts to conserve avian biodiversity in these dynamic ecosystems, especially under the pressures of ongoing climate change (Cannone et al., 2007).

3.8. Topography and microclimate integration

Topographic variables, such as slope, aspect, and elevation, are vital for accurately modeling microclimate in temperate landscapes. By integrating these topographic indices with habitat structural data, researchers can generate high-resolution microclimate surfaces that provide crucial insights into ecosystem dynamics (Tewksbury et al., 2002). These surfaces enable the calculation of important metrics, including Micro Climate Availability (MCA), which measures the proportion of habitat that falls below a species' upper thermal threshold (Thorne et al., 2023). This metric is crucial for understanding how microhabitats support species under thermal stress, particularly in light of climate variability.

Another key metric is the Thermal Safety Margin (TSM), which represents the difference between operative temperature and species-specific thermal tolerance (Suggitt et al., 2010). This measurement allows researchers to assess how much thermal relief is provided by specific microhabitats, informing conservation strategies focused on vulnerable species. Maintaining a favorable TSM is essential for species' survival, especially as global temperatures rise due to climate change.

Additionally, Refugia Connectivity (RC) quantifies the spatial continuity of cooler microhabitat patches, facilitating assessments of how well these areas can support species migration and resilience (Wolfe et al., 2025). This connectivity is critical for species facing habitat fragmentation and climate-induced alterations, as it promotes movement between cooler refugia, thereby enhancing population stability and genetic diversity (Svancara et al., 2019).

When combined, these metrics enable researchers to predict potential shifts in species distributions under various climate scenarios, identify populations at risk, and prioritize refugia for conservation management. Consequently, this integrative approach not only supports a more comprehensive understanding of ecological processes but also guides effective conservation strategies aimed at mitigating the impacts of climate change on biodiversity (Bartholomée et al., 2024).

3.9. Microclimate modelling workflow

The proposed workflow for modeling bird distributions in temperate habitats under climate change effectively integrates habitat structure, topography, microclimate derivation, and species response. The workflow can be summarized in the following steps:

- 1. Mapping Habitat Structure: This initial phase employs LiDAR or high-resolution imagery to quantify essential habitat elements, including canopy height, understory density, shrub presence, and ground cover. Accurate mapping of these structures is crucial as they impact the microclimatic conditions experienced by avian species.
- 2. Deriving Microclimate Layers: By combining the identified habitat structure with topographic variables (such as slope and aspect) and meteorological data, researchers can generate operative temperature surfaces. Validation of these surfaces can be undertaken using

in-situ temperature loggers to ensure precision in microclimate representation, which can inform models relating habitat characteristics and microclimate stability.

- 3. Linking Bird Data: Data on bird occurrence, abundance, and demographic patterns are then linked to the derived microclimate layers. This linkage can be established through various statistical methodologies, including regression analysis, occupancy models, or species distribution models. Such integration helps elucidate species' responses to the microclimatic variations created by the underlying habitat structure and topography.
- 4. Forecasting under Climate Change: The final step involves downscaling macroclimate scenarios and overlaying the microclimate layers to calculate critical metrics such as MCA, TSM, and RC. These metrics facilitate predictions of potential shifts in occupancy patterns and help identify refuge sites where species may persist amidst changing climatic conditions.

This comprehensive framework allows researchers to incorporate fine-scale environmental heterogeneity into predictive models, thereby improving the ecological realism and accuracy of climate vulnerability assessments.

3.10. Conservation and management implications

Microclimate-informed conservation planning has direct implications for temperate bird habitats:

- Structural Complexity Preservation: Maintaining old-growth stands, layered understory, and shrub density enhances thermal buffering.
- Connectivity of Thermal Refugia: Spatially linked cooler patches facilitate movement, foraging, and breeding, reducing local extinction risk.
- Habitat Restoration and Management: Thinning, selective planting, or shrub restoration can enhance microclimate availability and buffer against warming.
- Site Prioritisation: Areas predicted to maintain low operative temperatures under future climates should be prioritised for protection or restoration.

By integrating microclimate data into management strategies, conservation practitioners can more effectively mitigate the impacts of climate change on temperate bird communities.

3.11. Research gaps and future directions

Despite advances, several knowledge gaps remain:

- 1. Temporal Resolution: Most microclimate studies capture daily or seasonal variation, but diurnal and extreme-event dynamics are underrepresented.
- 2. Species-Specific Thermal Limits: Limited empirical data constrain calculation of TSM for many temperate bird species.
- 3. Mechanistic Links: Direct connections between microclimate exposure and vital rates (survival, reproduction) require more empirical study.
- 4. Dynamic Habitat Change: Modelling microclimate in conjunction with habitat alterations (logging, shrub encroachment, fire) is needed for realistic forecasting.
- 5. Integration with Demography: Incorporating population dynamics and dispersal into microclimate-based models can improve predictions of species persistence.

Addressing these gaps will strengthen the predictive power of microclimate-informed models and enhance conservation strategies for temperate avifauna.

4. Conclusions

Temperate bird species are increasingly exposed to climatic stressors, including rising temperatures and more frequent heatwaves. Traditional macro-climatic assessments often fail

to capture the nuanced thermal environments experienced by birds at the scale of their habitats. This study highlights the critical role of microclimate heterogeneity in mediating avian responses to climate change and provides a structured framework for integrating fine-scale environmental variation into predictive models of bird distribution.

Empirical evidence demonstrates that structural complexity in temperate habitats — including canopy height, understory density, shrub cover, and topographic variation — creates localised thermal refugia. Birds exploiting these cooler microhabitats exhibit more stable population trends, enhanced reproductive success, and greater resilience to temperature extremes. In forests, dense canopy layers and layered understories reduce operative temperatures, whereas in grasslands and shrublands, patchy vegetation and north-facing slopes offer essential cooling refuges. These findings collectively support the microclimate buffering hypothesis, underscoring the importance of considering fine-scale environmental variation when assessing species vulnerability.

The proposed workflow integrates habitat structure mapping, microclimate derivation, bird data linkage, and forecasting under future climate scenarios. Key conceptual variables, including Microclimate Availability (MCA), Thermal Safety Margin (TSM), and Refugia Connectivity (RC), enable researchers and conservation practitioners to identify thermally suitable habitats, anticipate distributional shifts, and prioritise areas for protection or restoration. By explicitly incorporating microclimatic information, this approach improves the ecological realism of species distribution models and provides actionable insights for conservation planning.

From a management perspective, several strategies emerge. Maintaining or restoring structural complexity, ensuring connectivity between cooler habitat patches, and targeting conservation interventions towards areas predicted to retain favourable microclimates under warming scenarios are critical. Restoration activities should consider both vertical (canopy, understory) and horizontal (patch connectivity) structural heterogeneity to maximise thermal buffering capacity. Monitoring programs should integrate fine-scale temperature measurements with demographic and occupancy data to assess the effectiveness of conservation interventions and refine predictive models over time. Despite these advances, significant research gaps remain. High-resolution microclimate datasets are limited for many temperate regions, and species-specific thermal tolerance data are often lacking. Additionally, temporal dynamics, such as diurnal temperature variation and extreme events, are underrepresented in most studies. Integrating demographic data, dispersal mechanisms, and dynamic habitat changes into microclimate-based models represents a promising frontier for future research. Such integrative approaches will be essential for accurately forecasting species persistence and informing adaptive conservation strategies in the face of ongoing climate change. Therefore, microclimate modelling offers a powerful lens for understanding and predicting bird responses to environmental change in temperate habitats. By recognising the importance of localised thermal refugia and habitat heterogeneity, ecologists can refine vulnerability assessments, improve predictive accuracy, and guide conservation efforts more effectively. As climate change continues to reshape ecosystems, the adoption of microclimateinformed frameworks will be pivotal in ensuring the persistence of temperate bird species and the maintenance of functional and biodiverse avian communities.

References

Acebes, P., Lillo, P., Jaime-González, C., 2021. Disentangling lidar contribution in modelling species—habitat structure relationships in terrestrial ecosystems worldwide. a systematic review and future directions. *Remote Sensing*, 13(17): 3447.

- Akresh, M., King, D., McInvale, S., Larkin, J., D'Amato, A., 2023. Effects of forest management on the conservation of bird communities in eastern North America: a meta-analysis. *Ecosphere*, 14(1).
- Alonso, H., Correia, R., Marques, A., Palmeirim, J., Moreira, F., Silva, J., 2019. Male post-breeding movements and stopover habitat selection of an endangered short-distance migrant, the little bustard *Tetrax Tetrax*. *Ibis*, 162(2): 279-292.
- Barry, K., Schnitzer, S., 2021. Are we missing the forest for the trees? conspecific negative density dependence in a temperate deciduous forest. *Plos One*, 16(7): e0245639.
- Bartholomée, O., Tichit, P., Åström, J., Smith, H., Åstrøm, S., Sydenham, M., Baird, E., 2024. Forest habitat and forest dominated landscapes are associated with bumblebee species with visual traits related to light sensitivity. *Biorxiv*, 12.
- Bernath-Plaisted, J., Ribic, C., HILLS, W., Townsend, P., Zuckerberg, B., 2023. Microclimate complexity in temperate grasslands: implications for conservation and management under climate change. *Environmental Research Letters*, 18(6): 064023.
- Bernath-Plaisted, J.S., Ribic, C.A., Zuckerberg, B., 2025. Sweating the small stuff: microclimatic exposure and species habitat associations inform climate vulnerability in a grassland songbird community. *Biology Letters*, 21(1): 20240599.
- Berryman, E., Barnard, H., Adams, H., Burns, M., Gallo, E., Brooks, P., 2015. Complex terrain alters temperature and moisture limitations of forest soil respiration across a semiarid to subalpine gradient. *Journal of Geophysical Research Biogeosciences*, 120(4): 707-723.
- Betts, M., Phalan, B., Frey, S., Rousseau, J., Yang, Z., 2017. Old-growth forests buffer climate-sensitive bird populations from warming. *Diversity and Distributions*, 24(4): 439-447.
- Bitani, N., Cordier, C., Smith, D., Smith, Y., Downs, C., 2023. Avian species functional diversity and habitat use: the role of forest structural attributes and tree diversity in the midlands mist belt forests of KwaZulu-Natal, South Africa. *Ecology and Evolution*, 13(9).
- Cannone, N., Sgorbati, S., Guglielmin, M., 2007. Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*, 5(7):360-364.
- Champlin, T., Kilgo, J., Gumpertz, M., Moorman, C., 2009. Avian response to microclimate in canopy gaps in a bottomland hardwood forest. *Southeastern Naturalist*, 8(1): 107-120.
- Chardon, N., McBurnie, L., Goodwin, K., Pradhan, K., Lambers, J., Angert, A., 2023. Variable species establishment in response to microhabitat indicates different likelihoods of climate-driven range shifts. *Ecography*, e07144.
- Coulson, B., Freeman, M., Conradie, S., McKechnie, A., 2025. Increases in humidity will intensify lethal hyperthermia risk for birds occupying humid lowlands. *Conservation Physiology*, 13(1).
- Criado, M., Myers-Smith, I., Bjorkman, A., Lehmann, C., Stevens, N., 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography*, 29(5): 925-943.

- Davis, K., Dobrowski, S., Holden, Z., Higuera, P., Abatzoglou, J., 2018). Microclimatic buffering in forests of the future: the role of local water balance. *Ecography*, 42(1): 1-11.
- Dobrowski, S., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, 17(2): 1022-1035.
- Eastman, J., Sangermano, F., Oliveira, E., Rogan, J., Anyamba, A., 2013. Global trends in seasonality of normalized difference vegetation index (NDVI), 1982–2011. *Remote Sensing*, 5(10): 4799-4818.
- Egli, M., Mirabella, A., Sartori, G., Giaccai, D., Zanelli, R., Plötze, M., 2007. Effect of slope aspect on transformation of clay minerals in alpine soils. *Clay Minerals*, 42(3): 373-398.
- Fa, J., Funk, S., 2007. Global endemicity centres for terrestrial vertebrates: an ecoregions approach. *Endangered Species Research*, 3: 31-42.
- Frenne, P., Lenoir, J., Luoto, M., Scheffers, B., Zellweger, F., Aalto, J., Hylander, K., 2021. Forest microclimates and climate change: importance, drivers and future research agenda. *Global Change Biology*, 27(11): 2279-2297.
- Frenne, P., Rodríguez-Sánchez, F., Coomes, D., Baeten, L., Verstraeten, G., Vellend, M., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46): 18561-18565.
- Frey, S., Hadley, A., Betts, M., 2016. Microclimate predicts within-season distribution dynamics of montane forest birds. *Diversity and Distributions*, 22(9): 944-959.
- Frey, S., Hadley, A., Johnson, S., Schulze, M., Jones, J., Betts, M., 2016. Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, 2(4).
- Giberti, G., Arx, G., Giovannelli, A., Toit, B., Unterholzner, L., Bielak, K., Wellstein, C., 2023. The admixture of Quercus sp. in *Pinus sylvestris* stands influences wood anatomical trait responses to climatic variability and drought events. *Frontiers in Plant Science*, 14.
- Gilliam, F., Hédl, R., Chudomelová, M., McCulley, R., Nelson, J., 2014. Variation in vegetation and microbial linkages with slope aspect in a montane temperate hardwood forest. *Ecosphere*, 5(5): 1-17.
- González-Gómez, P., Estades, C., Simonetti, J., 2006. Strengthened insectivory in a temperate fragmented forest. *Oecologia*, 148(1): 137-143.
- Gutiérrez-Jurado, H., Vivoni, E., Cikoski, C., Harrison, J., Bras, R., Istanbulluoglu, E., 2013. On the observed ecohydrological dynamics of a semiarid basin with aspect-delimited ecosystems. *Water Resources Research*, 49(12): 8263-8284.
- He, Y., D'Odorico, P., and Wekker, S., 2015. The role of vegetation–microclimate feedback in promoting shrub encroachment in the Northern Chihuahuan desert. *Global Change Biology*, 21(6): 2141-2154.
- He, Y., D'Odorico, P., Wekker, S., Fuentes, J., Litvak, M., 2010. On the impact of shrub encroachment on microclimate conditions in the Northern Chihuahuan desert. *Journal of Geophysical Research Atmospheres*, 115(D21).
- Jemal, Z., Girma, Z., Mengesha, G., 2020. Bird diversity in nensebo moist afromontane forest fragment, south eastern Ethiopia. *The Open Ornithology Journal*, 13(1): 1-9.

- Kang, S., Lee, D., Kimball, J., 2004. The effects of spatial aggregation of complex topography on hydro ecological process simulations within a rugged forest landscape: development and application of a satellite-based topo climatic model. *Canadian Journal of Forest Research*, 34(3): 519-530.
- Kim, H., McComb, B., Frey, S., Bell, D., Betts, M., 2022. Forest microclimate and composition mediate long-term trends of breeding bird populations. *Global Change Biology*, 28(21): 6180-6193.
- LeBrun, J., Thogmartin, W., Thompson, F., Dijak, W., Millspaugh, J., 2016. Assessing the sensitivity of avian species abundance to land cover and climate. *Ecosphere*, 7(6):
- Li, X., Burrows, G., Dong, N., Jordan, G., Kattge, J., Lenz, T., Wright, I., 2025. A thinner jacket for frosty and windy climates? global patterns in leaf cuticle thickness and its environmental associations. *New Phytologist*, 248(1): 107-124.
- Lin, H., 2006. Temporal stability of soil moisture spatial pattern and subsurface preferential flow pathways in the shale hills catchment. *Vadose Zone Journal*, 5(1): 317-340.
- Liu, S., Li, R., Deng, Y., Wang, Z., Feng, Y., Han, Z., Mou, C., 2025. RNA-seq revealed the effects of heat stress on different brain regions of *Leiocassis longirostris*. *Frontiers in Physiology*, 16.
- Lombaerde, E., Vangansbeke, P., Lenoir, J., Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., Frenne, P., 2022. Maintaining forest cover to enhance temperature buffering under future climate change. *The Science of the Total Environment*, 810: 151338.
- Mancuso, J., Messick, E., Tiegs, S., 2022. Parsing spatial and temporal variation in stream ecosystem functioning. *Ecosphere*, 13(8).
- Menge, J., Magdon, P., Wöllauer, S., Ehbrecht, M., 2023. Impacts of forest management on stand and landscape-level microclimate heterogeneity of European beech forests. *Landscape Ecology*, 38(4): 903-917.
- Moradi, N., Joger, U., Bafti, S., Sharifi, A., Sehhatisabet, M., 2024. Biogeography of the Iranian snakes. *Plos One*, 19(10): e0309120.
- Mulwa, R., Böhning-Gaese, K., Schleuning, M., 2012. High bird species diversity in structurally heterogeneous farmland in western Kenya. *Biotropica*, 44(6): 801-809.
- Murphy, B., Bradstock, R., Boer, M., Carter, J., Cary, G., Cochrane, M., Bowman, D., 2013. Fire regimes of Australia: a pyro geographic model system. *Journal of Biogeography*, 40(6): 1048-1058.
- Norris, C., Hobson, P., Ibisch, P., 2011. Microclimate and vegetation function as indicators of forest thermodynamic efficiency. *Journal of Applied Ecology*, 49(3): 562-570.
- Padmakumar, V., Joseph, S.P., 2022. Understanding the mangrove-associated avifauna and their conservation status in the Gorai Creek, Western Mumbai, Maharashtra, India: A Recent Study. *Environment*, 6(3).
- Padmakumar, V., Shanthakumar, M., 2023. The impact of human-wildlife conflict on biodiversity conservation in India. *Journal of Entomology and Zoology Studies*.
- Padmakumar, V., Silamabarasan, C., Joseph, S., 2020. Avifaunal diversity of mallathahalli lake in bangalore urban dt. Karnataka, India. *The Bioscan*, 15(2): 165-167.

- Pan, J., Liu, Y., Yang, Y., Cheng, Z., Lan, X., Hu, W., Feng, H., 2022. Slope aspect determines the abundance and composition of nitrogen-cycling microbial communities in an alpine ecosystem. *Environmental Microbiology*, 24(8): 3598-3611.
- Pandita, S., Kumar, V., Dutt, H., 2019. Environmental variables vis-a-vis distribution of herbaceous tracheophytes on northern sub-slopes in western Himalayan ecotone. *Ecological Processes*, 8(1).
- Pierce, S., Negreiros, D., Cerabolini, B., Kattge, J., Díaz, S., Kleyer, M., Tampucci, D., 2016. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31(2): 444-457.
- Pradhan, K., Ettinger, A., Case, M., Lambers, J., 2023. Applying climate change refugia to forest management and old-growth restoration. *Global Change Biology*, 29(13): 3692-3706.
- R Arx, G., Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *Journal of Ecology*, 101(5): 1201-1213.
- Regüés, D., Martí-Bono, C., Nadal-Romero, E., 2006. Badlands dynamics in the central Pyrenees: temporal and spatial patterns of weathering processes. *Earth Surface Processes and Landforms*, 32(6): 888-904.
- Roonjho, A., Muhamad, R., Omar, D., 2020. Determination of lethal and feeding deterrent activities of saponin from *Phaleria macrocarpa* against *Pomacea maculata*. *The Journal of Animal and Plant Sciences*, 31(4): 1070-1077.
- Rotenberg, E., Yakir, D., 2010. Distinct patterns of changes in surface energy budget associated with forestation in the semiarid region. *Global Change Biology*, 17(4): 1536-1548.
- Sankey, J., Law, D., Breshears, D., Munson, S., Webb, R., 2013. Employing lidar to detail vegetation canopy architecture for prediction of aeolian transport. *Geophysical Research Letters*, 40(9): 1724-1728.
- Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., Goßner, M., 2020. Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? *Journal of Applied Ecology*, 57(7): 1363-1375.
- Schwartz, T., Genouville, A., Besnard, A., 2020. Increased microclimatic variation in artificial nests does not create ecological traps for a secondary cavity breeder, the European roller. *Ecology and Evolution*, 10(24): 13649-13663.
- Smith, D., Willows-Munro, S., Smith, Y., Downs, C., 2021. Does anthropogenic fragmentation selectively filter avian phylogenetic diversity in a critically endangered forest system? *Bird Conservation International*, 32(4): 674-686.
- Sørensen, R., Zinko, U., and Seibert, J., 2006. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth System Sciences*, 10(1): 101-112.
- Spicer, M., Mellor, H., Carson, W., 2020. Seeing beyond the trees: a comparison of tropical and temperate plant growth forms and their vertical distribution. *Ecology*, 101(4).
- Stark, J., Fridley, J., 2022. Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography*, 31(3): 562-575.

- Suggitt, A., Gillingham, P., Hill, J., Huntley, B., Kunin, W., Roy, D., Thomas, C., 2010. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, 120(1): 1-8.
- Sunday, J., Bennett, J., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A., Morales-Castilla, I., 2019. Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B Biological Sciences*, 374(1778): 20190036.
- Svancara, L., Abatzoglou, J., Waterbury, B., 2019. Modeling current and future potential distributions of milkweeds and the monarch butterfly in Idaho. *Frontiers in Ecology and Evolution*, 7.
- Tewksbury, J., Levey, D., Haddad, N., Sargent, S., Orrock, J., Weldon, A., Townsend, P., 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences*, 99(20): 12923-12926.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M., Schwager, M., Jeltsch, F., 2003. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1): 79-92.
- Thorne, J., Boynton, R., Hollander, A., Flint, L., Flint, A., Urban, D., 2023. The contribution of microrefugia to landscape thermal inertia for climate-adaptive conservation strategies. *Earth S Future*, 11(6).
- Ulyshen, M., Adams, C., Adams, J., Adams, S.B., Bland, M., Bragg, D.C., Young, A.D., 2024. Spatiotemporal patterns of forest pollinator diversity across the southeastern United States. *Diversity and Distributions*, 30(8): e13869.
- Wolfe, J., Luther, D., Jirinec, V., Collings, J., Johnson, E., Bierregaard, R., Stouffer, P., 2025. Climate change aggravates bird mortality in pristine tropical forests. *Science Advances*, 11(5).
- Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S., Wulf, M., Frenne, P., 2019. Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*, 28(12): 1774-1786.
- Zellweger, F., Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in microclimate ecology arising from remote sensing. *Trends in Ecology and Evolution*, 34(4): 327-341.
- Zhu, Y., Britnell, J., Shi, J., Buuveibaatar, B., Shultz, S., 2025. Anthropogenic pressures lead to different patterns of niche contraction and protected area cover in three species *Procapra gazelles* on qinghai tibet plateau and mongolia. *Diversity and Distributions*, 31(1).