Title: A pattern-oriented simulation for forecasting species spread through time and space: A case study on an ecosystem engineer on the move

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Abstract

Modelling the spread of introduced ecosystem engineers is a conservation priority due to their potential to cause irreversible ecosystem-level changes. Existing models predict potential distributions and spread capacities, but new approaches that simulate the trajectory of a species' spread over time are needed. We have developed novel simulations that predict spatial and temporal spread, capturing continuous diffusion-dispersal with occasional long-distance leaps. We focused on the introduced population of Superb Lyrebird (*Menura novaehollandiae*) in Tasmania, Australia. Initially introduced as an insurance population, lyrebirds have become novel bioturbators, spreading across key natural areas and becoming "unwanted but challenging to eradicate". Using multi-scale ecological data, our research (1) identified broad and fine-scale correlates of lyrebird occupation and (2) developed a spread simulation guided by a pattern-oriented framework. This occurrence-based modelling framework is useful when demographic data are scarce. We found that the cool, wet forests of western Tasmania, with dense leaf litter and open understories, offer well-connected habitats for lyrebird foraging and nesting. By 2023, lyrebirds had reached quasi-equilibrium within a core range in southern Tasmania, and were expanding northwest, with the frontier reaching the western coast. Our model forecasts that by 2085, lyrebirds will have spread widely across suitable regions of western Tasmania. By pinpointing current and future areas of lyrebird occupation, we provide land managers with targeted locations to monitor the effects of their expansion. Our findings offer an evidence-based approach for future monitoring and provide a framework for understanding the dynamics of other range-expanding species with invasive potential.

Introduction

Introducing species to new areas, whether for conservation or by accident, often results in unforeseen ecological effects (Powell et al. 2011, Ricciardi et al. 2013). The invasive potential of such species varies between taxa and ecosystems, and across spatial scales (Davies et al. 2005, Guerin et al. 2018), necessitating case-specific assessments and tailored management strategies (Fridley et al. 2007, Januchowski-Hartley et al. 2018). Managing the impacts of rapidly spreading ecosystem engineers can be particularly challenging due to potentially irreversible ecosystem-level changes (i.e., hysteresis) and escalating monitoring and control costs as the species expands (e.g., Aschim and Brook 2019, Rodda and Savidge 2007). Effective decision-making thus relies on robust projections of species' distribution and spread across the new terrain.

Species are expected to spread and establish in areas where conditions are suitable, biotic pressures are low, and the terrain is accessible for dispersal (Kolar and Lodge 2001, With 2002, Guisan and Thuiller 2005). Spatially explicit population dynamics models are ideal for capturing detailed spread dynamics as they simulate key demographic processes, such as birth rates, mortality, and dispersal (Dunning Jr et al. 1995, Fordham et al. 2021). However, these models often lack the necessary data on population parameters, which typically require extensive long-term monitoring to obtain (Botterill-James et al. 2024). Occurrence-based spread simulations are employed as an alternative, as presence-absence patterns are ultimately the product of underlying demographic processes (Gormley et al. 2011).

Occurrence-based spread simulations capture continuous diffusion-dispersal, where individuals at the range edge colonise new areas via corridors of suitable habitats (e.g., Cucco et al. 2021) or where environmental resistance is low (e.g., Lovell et al. 2021). To this end, many models have been developed to predict the potential distribution and likely spread routes of introduced species (Gormley et al. 2011, Barbet-Massin et al. 2018). However, these species often have yet to reach biogeographic equilibrium, posing modelling challenges (Gallien et al. 2010). For example, one risk is underestimating the habitat suitability of new areas, as species may occupy a broader niche in new terrains (Fitzpatrick et al. 2007). Another challenge is identifying correlates for successful versus unsuccessful colonisation using presence-absence data, as unoccupied habitats might still be viable given enough time for the species to reach them (Gallien et al. 2012, Mainali et al. 2015). Additionally, more mobile species can also undergo jump dispersal or extreme long-distance dispersal—rare events where they "leap over" nearby unsuitable areas, bypassing them to reach suitable habitat (Wilson et al. 2009). These challenges are exemplified by the introduced population of the Superb Lyrebird (*Menura novaehollandiae)* - a prominent soil engineer on the move in Tasmania.

Native to the temperate forests of the southeast Australian mainland, the Superb Lyrebird (hereafter 'lyrebird') was translocated to Tasmania in the 1930s to safeguard it from mainland predators such as red foxes (*Vulpes vulpes*) and dingos (*Canis lupus dingo*) (Tassell 2014, Stobo-Wilson et al. 2021). Since then, lyrebirds have thrived, and spread across regions of high conservation value within the Tasmanian Wilderness and World Heritage Area (Tassell 2014). By raking soil and litter in search of invertebrates, foraging lyrebirds profoundly modify the forest floor (Maisey et al. 2021), introducing novel bioturbation to Tasmanian ecosystems that evolved without the process. Although they displace up to 155 tonnes/ha of leaf litter annually (Maisey et al. 2021), the full spectrum of lyrebirds' impacts on Tasmanian ecosystems—from beneficial nutrient cycling to disruptive community disassembly—remains poorly understood.

In mainland Australia, lyrebirds occupy wet forests or rainforests near creek lines, areas with deep leaf litter, and forest patches with complex mid- and high-strata vegetation (Ashton and

Bassett 1997, Maisey et al. 2019). These preferences imply that much of Tasmania, with its diverse forest landscapes, could offer suitable habitats for lyrebirds. However, the absence of biotic pressures such as predation and intra-specific competition (except in areas where the species has already established) on the island raises questions about how well lyrebirds' preferences translate to the Tasmanian environment. Despite being introduced for protection, lyrebirds are now categorised as second priority under the Tasmanian invasive species list (nre.tas.gov.au/invasive-species)—unwanted but difficult to eradicate. This scenario presents a conservation dilemma: managers must weigh the conservation value of the refuge population against potential impacts on the Tasmanian ecosystem. As such, the growing presence of lyrebirds in Tasmania warrants close monitoring if management is to be implemented.

This research uses multi-scale ecological data and advanced simulations to forecast the spread trajectory of the Superb Lyrebird in Tasmania. We draw habitat correlates from the species' native and introduced ranges, integrating data from lyrebirds' established mainland distribution with emerging patterns in Tasmania. Specifically, we ask: (1) What fine-scale habitat features influence the local occupancy of lyrebirds? (2) What regional/landscape factors facilitate the species' spread and distribution? (3) What currently unoccupied areas are most suitable for lyrebirds, and how long would it take to spread there? and (4) When will lyrebirds spread to reach an equilibrium within the Tasmanian environment? We build novel simulations that combine continuous diffusion-dispersal with occasional long-distance leaps, reflecting complex movement patterns. To accurately emulate lyrebird spread dynamics, we use a Pattern-Oriented Modelling (POM) approach (Grimm et al. 2005), fine-tuning our simulations to align with observed ecological patterns or 'targets'. By decoding these patterns, POM enables us to accurately parameterise the model, ensuring it represents the ecological processes of the lyrebird's spread.

By pinpointing current and future areas of lyrebird occupation, we aim to provide land managers with target locations to investigate the impacts of lyrebird expansion in Tasmania. Beyond the specific case of lyrebirds, this research offers a practical starting point for predicting the potential distributions of introduced species, and simulating future species spread despite limited data on demographic parameters. This approach equips researchers and managers with a predictive tool that can guide early intervention and management strategies.

Methods

Overview of the Modelling Framework

We used a sequential framework to model the fine- and broad-scale habitat preferences of lyrebirds and predict their future spread in Tasmania. We: (I) quantified species activity from camera-trap detections to model fine-scale habitat structure preferences within the current core range of lyrebirds in Tasmania (Figure 1a); (II) modelled broad-scale habitat correlates and projected habitat suitability maps using Species Distribution Models (SDMs) and citizen-science occurrence data across their mainland range, and camera-trap detections from their Tasmanian range (Figure 1b); and (III) used the habitat-correlate information from these models to build a two-phase simulation of lyrebird spread. In the first phase, we developed a Parameter Calibration Model (PCM) to trace the species' spread following the introductions in the 1930s. To validate this model, we anchored the target (presence-absence) predictions to both current observations and habitat models, a key step in parameter search using Pattern-Oriented Modelling (POM). Then, the selected parameters from POM were used to project the spread of lyrebirds up to the year 2085.

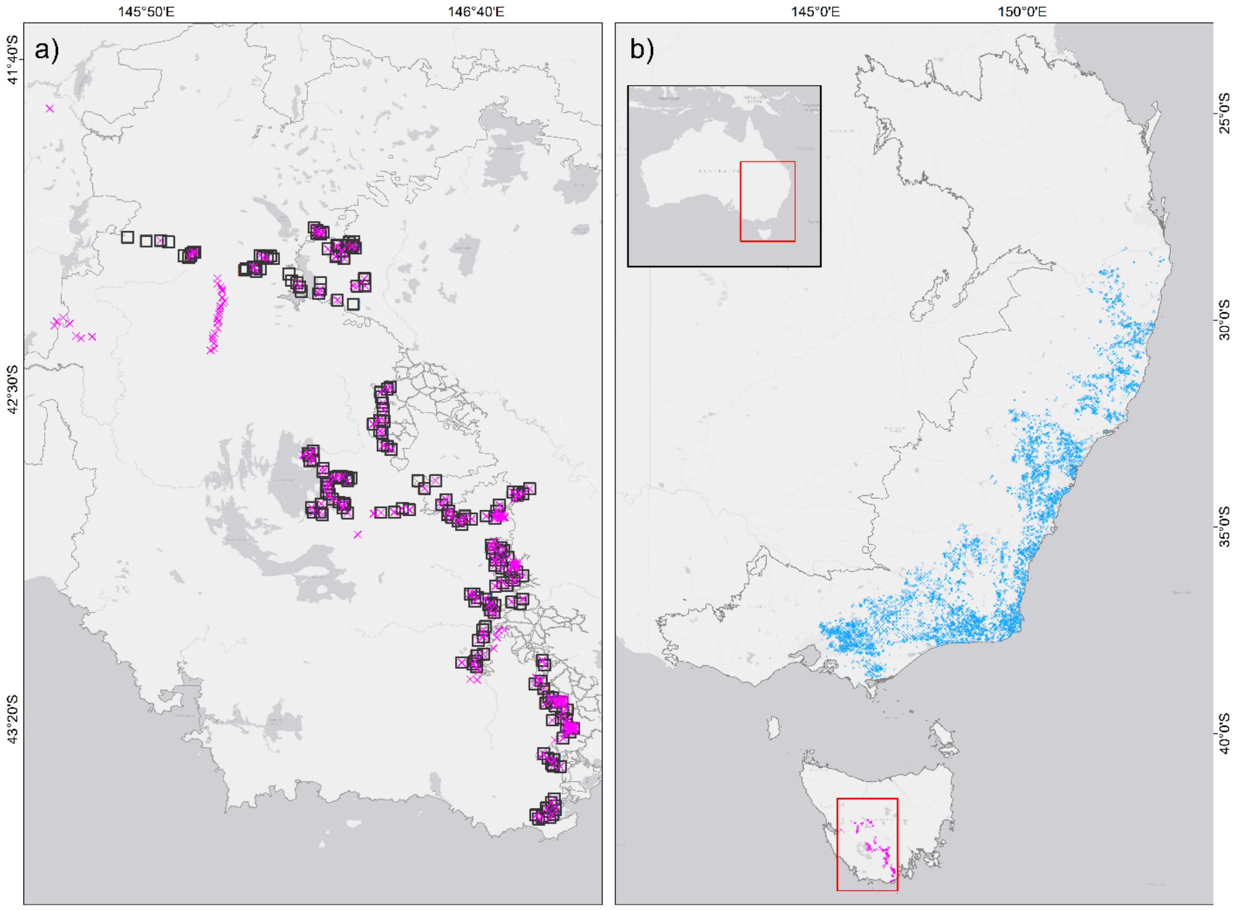

Figure 1. Data sources for modelling the habitat preferences and spread of the Superb Lyrebird (*Menura novaehollandiae*) in Tasmania. Panel (a) shows the distribution of camera-trap detections (red crosses) of lyrebirds within Tasmania. The black squares highlight the specific field sites where fine-scale habitat-structure data were collected to inform the models of lyrebird habitat preferences within their current core range. The dark grey boundary defines the Tasmanian Wilderness World Heritage Area. Panel (b) shows a map of Australia indicating the lyrebird presence across their native mainland range (from the Atlas of Living Australia database; blue crosses), complemented by camera-trap detections in Tasmania (red crosses). The dark grey boundary delineates the perimeter of all thirty-four of the Interim Biogeographic Regionalisation for Australia (IBRA) regions that were included in the study (full list in Table S1), with the red extent box marking the detailed study area within Tasmania.

I. Fine-scale Habitat Preferences of the Superb Lyrebird in Tasmania

Camera Survey and Data Pre-processing

We used lyrebird detections from a camera network set across Tasmania for a large-scale continuous wildlife-monitoring program from 2018 to 2023. These data included 497 unique camera stations within the lyrebird's occupied range (Figure 1a), operating over a total of 226,031 camera nights (531 average operational days per camera). The Cuddeback Xchange (model 1279) cameras were unbaited and set 30-40 cm above ground, positioned either on trails or in off-trail bushland, and spaced 0.5 to 5 km apart to encapsulate diverse habitat types. To ensure independent observations, we retained one lyrebird detection per 30-minute sampling period. We considered this the appropriate duration to infer lyrebird activity patterns considering their usual rate of movement through a landscape while occupying a given area (e.g. while foraging or searching for mates) (Lill 1996). The lyrebird activity index was then calculated as the number of independent observations per operating day for each camera site.

Station-Level Habitat Structure Modelling

Fine-scale habitat structure data was documented from 211 camera sites in Tasmania (Figure 1a), concentrating on areas where lyrebirds have been present for decades—indicative of a potentially stable equilibrium range. We used the camera-detection rate for lyrebirds across the multi-year sampling period to delineate this range, where camera regions with consistent lyrebird records (i.e., more than two records per camera across the sampling period) were considered viable for fine-scale assessments. At each camera, we quantified litter cover, the abundance of rotting logs, and the density of grasses, herbaceous understorey, woody understorey, and trees. To do this, we photographed four images of the vegetation, one facing each cardinal direction (east, west, north, and south) at each site. Habitat structure was then classified by calculating the proportion of the image covered by each vegetative layer by overlaying a 3 × 3 grid over each image. The images were taken using a camera with a 35 mm focal length, and the grid size was adjusted to match the image aspect ratio to ensure coverage from the ground layer to the tree line (see Fig S1). The relative density of each vegetation layer was calculated as the ratio of the number of cells where a layer is present to the available nine cells. The scores for all four images were averaged for each layer and used to classify the density of each vegetative layer into dense (average score > 0.5) or sparse (< 0.5).

II. Broad-scale Habitat Preferences and Habitat Suitability Mapping

Range-wide Species Data Collection and Processing

We sourced lyrebird occurrence data from the Atlas of Living Australia, collected between 1970 to 2023, across their mainland equilibrium range (downloaded at: doi.org/10.26197/ala.4744a2de-99ec-4cfb-9a0d-2a52d0f1dd5e, accessed on 06 April 2023; Figure 1b). To control for data quality, we only included records from quality-controlled sources, such as NSW Wildlife, Victorian Biodiversity Atlas, NSW Bird Atlassers, eBird, and Birdlife Australia. In Tasmania, the long-term camera-trap data (see above) provided a reliable indication of lyrebird absence, but such data were not available for their mainland range. Therefore, we generated effort-controlled pseudo-absence data for the mainland by inferring lyrebird absence in locations where at least three other land-bird species had been reported (indicating sampling effort for birds) but not lyrebirds. This process was applied to all land-bird species records from the same sources, collected between 1970-2023 (downloaded from Atlas of Living Australia: DOIs available in Table S2). To minimise duplicates, we converted both presence and pseudo-absence data into 1 km² grid presences, retaining only one record per grid and filtering out spatial anomalies. We implemented a 2 km buffer zone around presence grids to account for localised movement and positional errors. Pseudo-absence sampling was confined within a 50 km radius from presence grids to avoid ecological irrelevance from locations too distant from known occurrences (VanDerWal et al. 2009). To address spatial bias common in citizen-science surveys, we applied spatial thinning based on Nearest-neighbour Minimum Distance *NMD* (Pearson et al. 2007, Barve et al. 2011), adjusted to human activity levels, following Amin et al. (2021).

For Tasmania, we prioritised camera-derived presences over citizen-collected data in grids where they overlapped. Given that lyrebirds are still expanding their range in Tasmania; to define their current range, we created an 80% Kernel Density Estimate (KDE) contour around Tasmanian presences. Within this contour, we included only camera-derived absences, thus avoiding potential biases from adding suitable but yet-to-be-reached habitats. Consequently, the final dataset comprised 10066 presences and 9762 absences across the entire lyrebird range.

Mapping Suitable Habitats and Potential Distribution

We selected 17 environmental-raster layers to predict the broad-scale habitat use and distribution of lyrebirds, chosen for their ecological relevance. These included bioclimatic (climate and weather) and landscape (e.g., land-use and vegetation type) rasters (complete list in Table S3). The layers were rescaled to a 1 km^2 resolution to match the species-occurrence grids and cropped to Interim Biogeographic Regionalisation for Australia (IBRA) regions relevant to the lyrebird range across southeast Australia (full list in Table S1; Figure 1b). All continuous raster layers were centred and normalised before analysis. We checked for collinearity among variables and removed highly inter-correlated predictors ($|r| > 0.7$). To avoid model overfitting due to overly nuanced layer classification, vegetation and land use type were both aggregated into four major categories: rainforests, wet forests, dry woodland, and other (e.g., grasslands) for vegetation; and protected, modified native, plantation, and farmland for land use.

For the habitat suitability modelling, we initially explored five different model algorithms: Generalised Linear Models (GLM), Generalised Additive Models (GAM), Random Forests (RF), Gradient Boosted Machines (GBM) and an unweighted ensemble (see Table S4). Subsequently, the Random Forest classifier was selected as the final modelling method for its superior performance and was fit using the R package `caret` (Kuhn et al. 2020). The data were split into a 75% validation set for training and tuning and a 25 % hold-out set for performance evaluation. The Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) values guided model refinement (variable selection/rejection), with only the most accurate and parsimonious predictor set retained—this step used default tuning parameters (1000 number of trees *ntrees*; 7 number of randomly drawn candidate variables *mtry*). After selecting the most relevant predictor set, we used k-fold cross-validation ($k = 25$)

and grid search for hyperparameter tuning. The selected tuning parameters and predictor set were then used in the final model to evaluate predictive performance and create response curves. We used the AUC of ROC and True Skill Statistic (TSS) as metrics to assess model performance. While AUC allows threshold-independent assessment of model performance, TSS requires the conversion of probabilities to class predictions (Allouche et al. 2006). To address the slight class imbalance (i.e., unequal representation of presences and absences) in our data, we refined our threshold using F1 scores, chosen for their emphasis on the minority class and ability to navigate the trade-off between Precision and Recall.

Given that our research focuses on the future spread of lyrebirds, modelling their potential distribution under climate change scenarios was crucial. Ideally, this would incorporate forecasts of both climate change and habitat conversion, but only future climate projections were available. Consequently, to model future change in climatic suitability for lyrebirds, we used mean projections for 2085 from three Global Climatic Models (GCMs) under Representative Concentration Pathway (RCP) scenario 4.5: GFDK-CM21, MRI-CGCM232A, and UKMO-HADCM3, selected for their robustness in downscale scenarios (accessed via ecocommons.org.au; Di Virgilio et al. 2022).

Predicting the Timing of Future Spread

Spread Model Concept

We developed a raster-based spread model at a 5 km^2 resolution (selected for computational efficiency) that combines local diffusion to adjacent cells and infrequent leap events. Our discrete-time grid-cell approach was chosen to avoid the complexities of predicting individual-based spread, which requires detailed mechanistic knowledge about species behaviour. While similar grid-based diffusion models have been successfully applied to model disease spread in the Tasmanian devil (*Sarcophilus harrisii*) (Cunningham et al. 2021), we have advanced this approach to incorporate more complex mechanisms of local diffusion and leap events, reflecting nuanced spread pathways and species dynamics.

At each time step in the simulation, spread probability (P_{spread}) was calculated for each occupied cell to determine whether spread occurs. Then, for each spreading cell, leap probability (P_{leap}) dictated whether to diffuse to adjacent areas or to perform a long-distance leap (skipping adjacent areas). We used an additional parameter, layer coefficient (λ), to determine how likely a cell is to successfully leap at different distances. These coefficients are tied to conceptual 'expansion rings' (R2, R3, R4), which represent increasing distances from the occupied cell. The first ring, R1, covers the immediate neighbouring cells, while R2, R3, and R4 cover progressively farther zones. The coefficients for each ring were calculated using a trigonometric function, given the parameter θ as (Eq. 1, 2, 3):

$$\lambda_{R2} = \frac{1}{2} \times (1 + \sin\theta) \qquad (1)$$

$$\lambda_{R3} = \frac{1}{2} \times (1 + \cos\theta) \qquad (2)$$

$$\lambda_{R4} = 1 - \lambda_{R2} - \lambda_{R3}. \qquad (3)$$

Then, we derived normalised layer coefficients (Eq. 4, 5, 6):

$$\lambda_a = \frac{\lambda_{R2}}{\lambda_T} \qquad (4)$$

$$\lambda_b = \frac{\lambda_{R3}}{\lambda_T} \qquad (5)$$

$$\lambda_c = \frac{\lambda_{R4}}{\lambda_T} \qquad (6)$$

where $\lambda_T = \lambda_{R2} + \lambda_{R3} + \lambda_{R4}$. The normalised coefficients (Eq. 4, 5, 6) effectively adjust the probability of leaping to each ring based on its distance, ensuring distance-based likelihood is appropriately scaled in the model.

For the post-diffusion establishment, assuming the cell in which the dispersing lyrebird arrived was unoccupied, we used logistic regression to calculate the probability of establishment success ($P_{\text{establish}}$): the log odds Y following dispersal were calculated as (Eq. 7):

$$\log(Y) = \beta_1 + \beta_2 \times Habitat\ Suitablity \tag{7}$$

where β_1 was the intercept, and β_2 was the coefficient weighting the influence of habitat suitability at the destination cell. The probability of establishment was estimated by converting log odds into probability using the logistic function $\exp(Y)/(1+\exp(Y))$. For leap events, a cell was randomly selected from one of the expansion rings (R2, R3, or R4). The probability of a successful establishment in this selected cell is then calculated (using the logistic regression above), adjusting for the distance of the leap. This adjustment is made using the appropriate layer coefficient (λ) for the selected ring, modifying the base establishment probability as follows: $P_{\text{leap}} = P_{\text{establish}} \times \lambda$. This formulation accounts for the likelihood of successful establishment with changing leap distance, reflecting the challenges of colonisation at farther ranges.

This process was repeated at each timestep, charting species spread over time. The model's inherently stochastic nature was addressed by running multiple simulations, wherein the median spread timeline was used to predict expansion patterns.

Pattern-oriented Parameter Search and Simulation of Future Spread

We applied a pattern-oriented framework to parameterise the spread model. Pattern-oriented modelling provides a systematic, data-driven approach to calibrate complex simulations (Grimm et al. 2005, Grimm and Railsback 2012). Using Latin Hypercube Sampling (LHS), we explored a parameter space encompassing 15,000 combinations of parameter values, including spread probability (P_{spread}), leap probability (P_{leap}), the logistic regression intercept (β_1), the coefficient measuring the weight of habitat suitability (β_2), and the layer coefficient control parameter (θ). Then, we employed Approximate Bayesian Computation (ABC) to estimate posterior distributions by comparing the simulated outcomes with target patterns. We configured ABC to the neural network approach to improve the model's ability to learn complex patterns from the data. We implemented this in the `abc` package in R (Csilléry et al. 2012), with 200 neural networks, each with 8 nodes, and allowing a maximum of 1000 iterations for network training. Our primary objective for this step was to align the model's predictions with the observed range, using binary entropy loss as a metric for validation using POM. The binary entropy loss was calculated as (Eq 8):

$$Loss = -\sum_i (T_i \times \log(P_i + \in) + (1 - T_i) \times \log(1 - P_i + \in)) \tag{8}$$

where T_i represents the presence or absence value in the target raster for a cell, and P_i is the predicted probability for that cell. We added a small value, ε (= $1e$-15), to the probabilities to avoid numerical issues with *log(0)*. This adjustment ensured that the probabilities remain within valid range for the logarithm function.

We applied a Parameter Calibration Model (PCM) to map the spread of lyrebirds in Tasmania, from their introduction at Hastings Caves and Mt. Field in the 1930s through to 2023. The PCM identified the optimal parameter set, aligning the model's predictions with a carefully constructed target raster (Figure S2). This raster used current observational data and habitat preferences at broad and fine scales. Rigorous calibration ensured that the PCM accurately reflected the observed patterns of lyrebird presence, absence, and spread boundaries up to 2023, minimising mean binary entropy loss. We then used the selected parameters to project the species' spread from the 2023 distribution in Tasmania to 2085.

Results

Fine-scale habitat correlates of the lyrebird

Lyrebirds were more active in areas of Tasmania with dense litter (mean activity index ($\overline{ai}$) = 0.17, std. error (se) = 0.03) and many decaying logs ($\overline{ai}$ = 0.16, se = 0.03). They also preferentially used patches with sparse grass ($\overline{ai}$ = 0.12, se = 0.02), woody ($\overline{ai}$ = 0.13, se = 0.02), and herbaceous understoreys ($\overline{ai}$ = 0.11, se = 0.02; Figure 2). We found no effect of tree density on lyrebird activity, highlighting the importance of understorey composition in their habitat preferences (Figure 2).

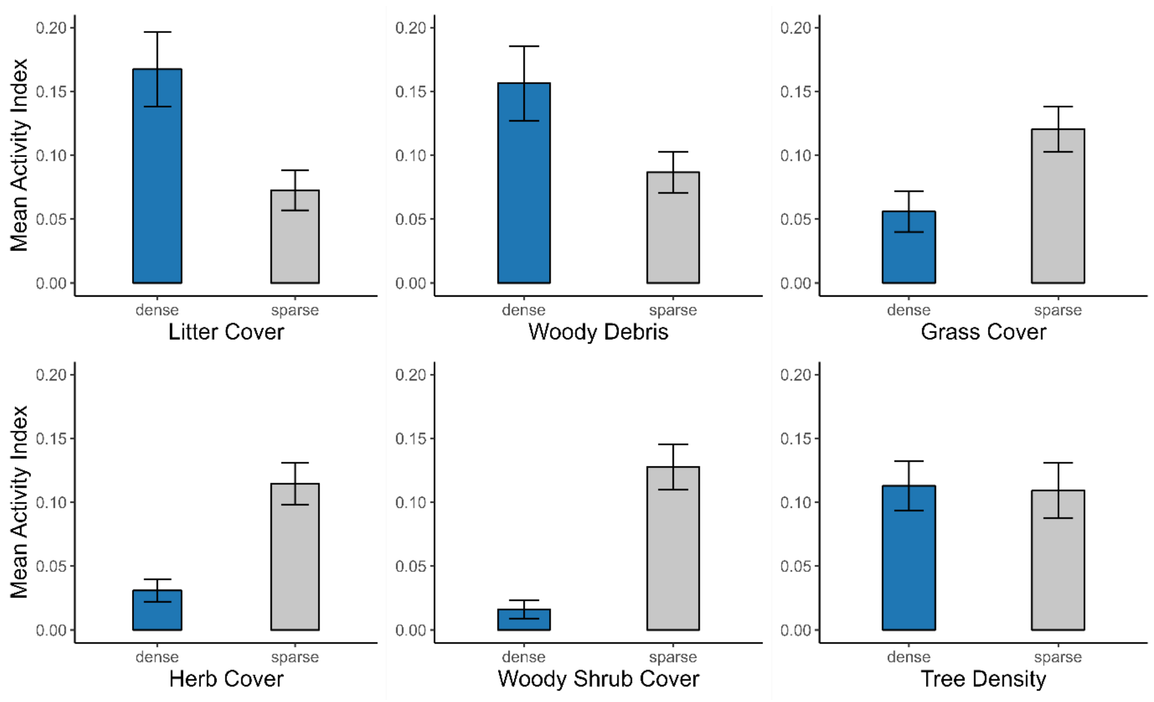

Figure 2. Change in mean activity index of Superb Lyrebirds (*Menura novaehollandiae*) with habitat structure. This plot shows the activity index of lyrebirds across six habitat-structure variables in Tasmania. The variables include relative density (classed as dense or sparse) of litter cover, woody debris, grass cover, herb cover, woody shrub cover, and tree density. Data

were gathered from 211 camera-station sites, with the activity index calculated as independent observations per number of camera operating days. Error bars represent standard error generated using bootstrapping with 10,000 iterations.

Potential distribution of lyrebird

At the broader scale, lyrebirds were found to prefer lower daily temperatures, and rainforest and wet forests (Figure 3a, c). Here, tall forest stands with lower photosynthetic activity—indicative of mature ecosystems—provided ideal habitat for the lyrebirds (Figure 3b, c). Conversely, the widespread conversion of native forests into farmlands and non-native plantations constrained lyrebird occupancy (Figure 3d).

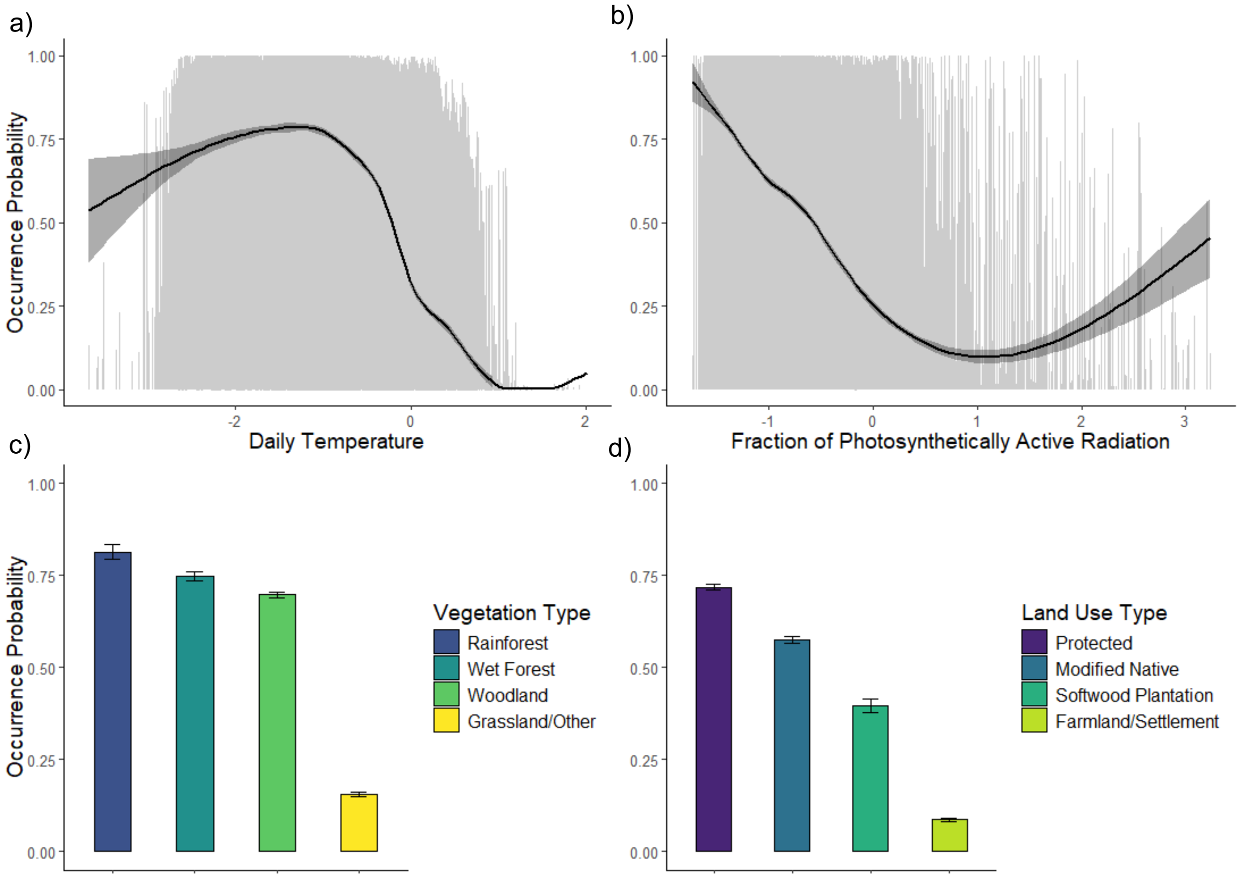

Figure 3. The relationship between Superb Lyrebird (*Menura novaehollandiae*) occurrence probability and environmental factors from the Random Forest model: (a) daily temperature, and (b) fraction of Photosynthetically Active Radiation (fPAR) of vegetation canopy, as well as categorical habitat characteristics: (c) vegetation type, and (d) land use type. Continuous variables are standardised (z-transformed), shown on the x-axis, to depict their relative influence on the y-axis probability of occurrence. The bars represent 95% confidence intervals, providing a visual gauge of model's uncertainty.

Our habitat suitability model for lyrebirds effectively mapped the species' preference for cool, temperate forests of southeast Australia (Figure 4b). The model had robust predictive power, with an AUC of 0.9 (TSS = 0.65 at a threshold of 0.54). The model predicted approximately 33,936 km^2 of the Tasmanian landscape to be conducive to lyrebird occurrence, with extensive availability of suitable habitats across the western and northeastern forests of the island (Figure 4a). Our model identified a vast corridor of lyrebird habitat with a high suitability index (> 0.8) extending about 350 km from southwest to northwest Tasmania (Figure 4a). This corridor, free from natural landscape barriers, will be important in facilitating the species' movement. Despite the availability of suitable habitats, lyrebird spread to the northeast is likely to be impeded by the agricultural midlands and drier lands of part of the east. In the southwest, large areas predominantly covered by button-grass plains and scrublands were also of low to only moderate suitability (Figure 4a).

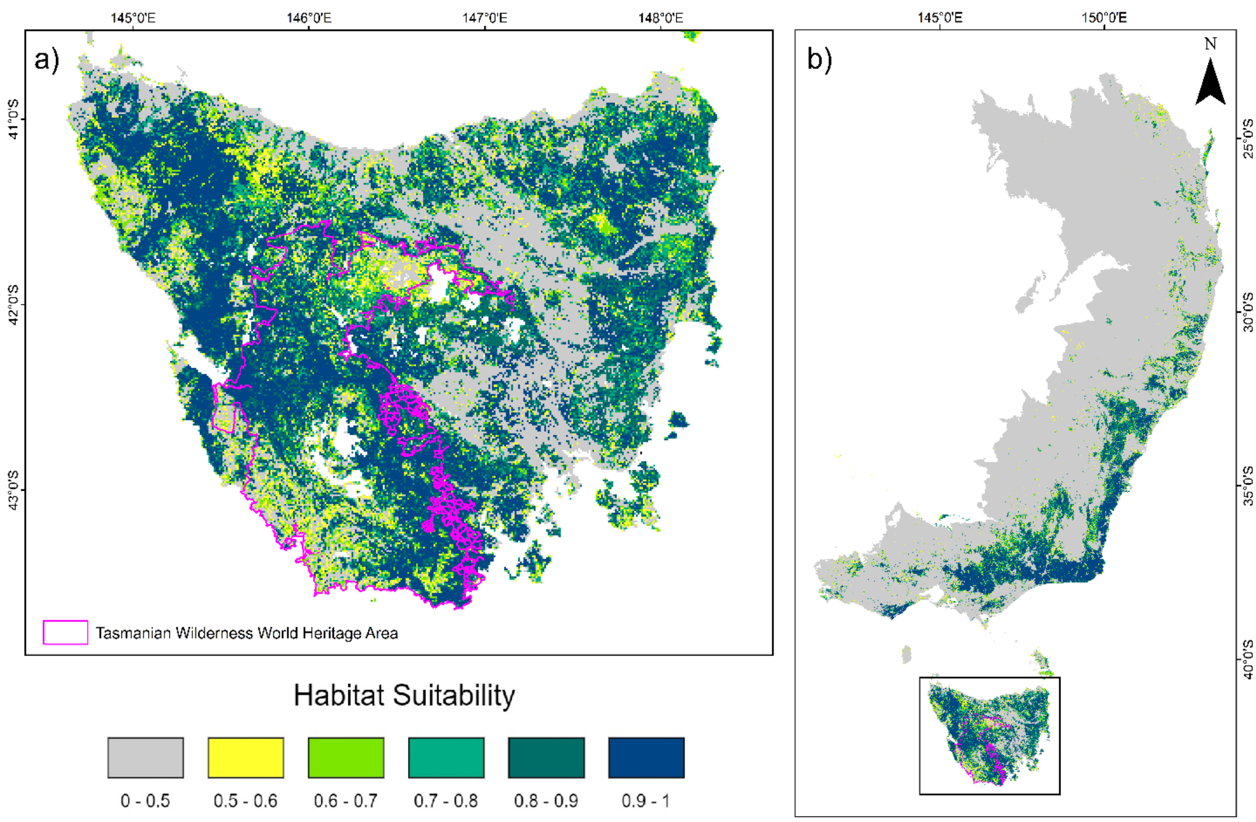

Figure 4. Habitat suitability for the Superb Lyrebird (*Menura novaehollandiae*), modelled using Random Forests (RF). Panel (a) displays the range of suitability within Tasmania, ranging from low (yellow) to high (blue) habitat suitability. Panel (b) shows the modelled habitat suitability across southeastern Australia, demarcating areas supporting the mainland lyrebird populations across its native range. The inset map shows Tasmania's position relative to the identified suitable habitats in the broader region. The magenta boundary defines the Tasmanian Wilderness World Heritage Area.

Timing of future spread

The PCM model, fine-tuned with current lyrebird observations, robustly mapped the species' expansion range in Tasmania in the year 2023 (mean binary loss = 0.72; Figure 5). The model successfully excluded the button-grass regions of the far southwest and the drier, human-impacted midlands from lyrebird occupancy, meeting the target exclusion criteria. Notably, it successfully captured the northwestern verified detections of lyrebird (Figure 5).

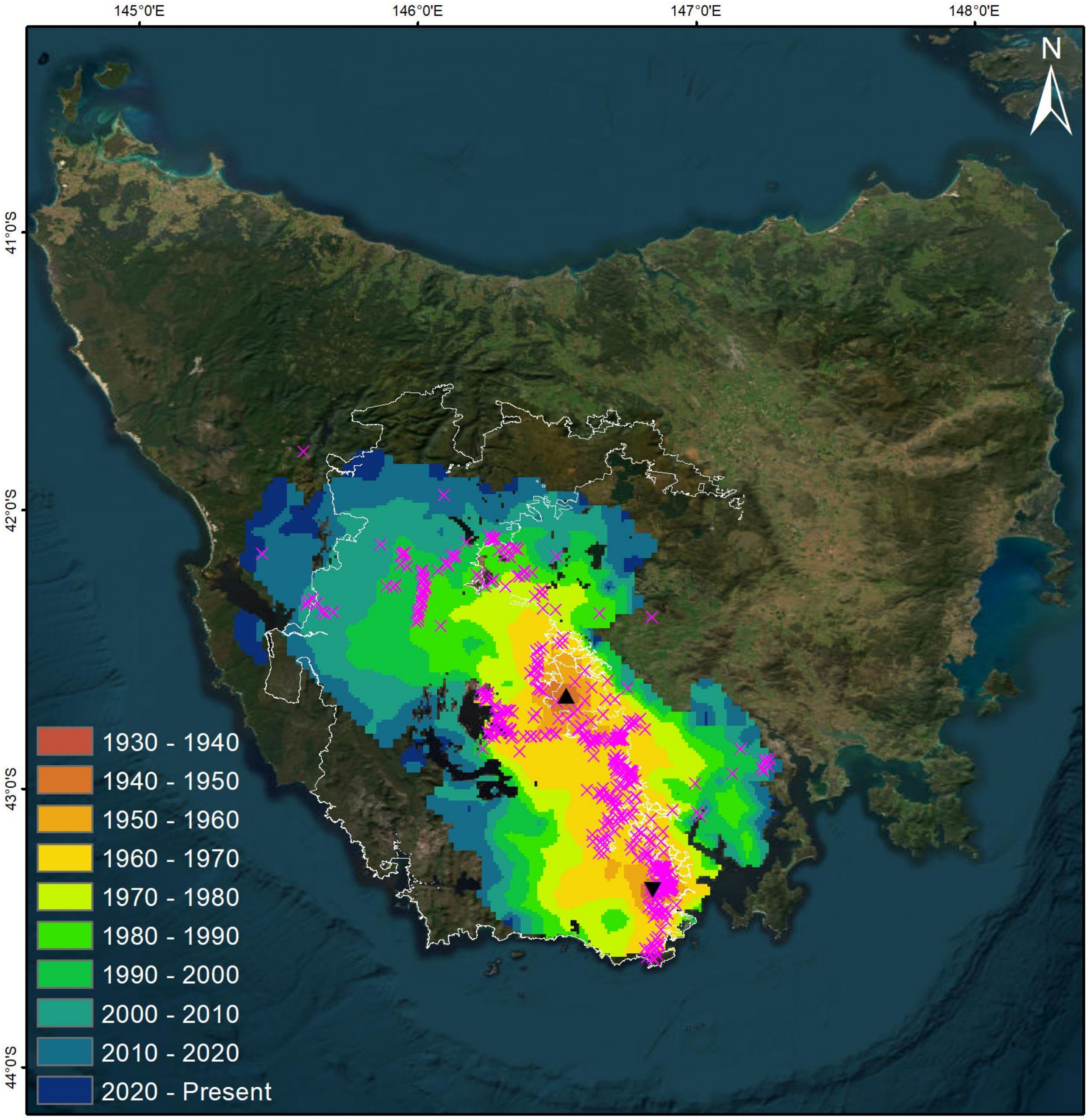

Figure 5. Modelled potential timing of the spread of the Superb Lyrebird (*Menura novaehollandiae*) in southern and central Tasmania, from initial introduction to present-day (2023) distribution. The spread simulation (illustrated by coloured, time-coded contours) is calibrated using pattern-oriented modelling and illustrates the lyrebird's capacity for range

expansion over 89 years. Spread started from two introduction sites at Hastings Caves State Reserve (down black triangle) and Mt. Field National Park (up black triangle) in 1934, with magenta crosses marking lyrebird detections by the year 2023. The white boundary defines the Tasmanian Wilderness World Heritage Area.

The projected lyrebird distribution forecasts an ongoing expansion in Tasmania, with a bias towards the northwest of the state. By the year 2085, the model predicts that lyrebirds will have spread across most of the suitable habitat in the west except the far northwest tip of the island (Figure 6). Despite the presence of suitable habitats in the northeast, their spread to these areas is expected to be limited by unsuitable habitat in the midlands and on the southeast coast. In addition, the button-grass regions of the far southwest are predicted to remain uninhabited (Figure 6), reflecting the strong preference of lyrebirds for cool, temperate forests. The eastern, western, and south boundaries of the suitable habitats are expected to remain relatively stable from 2023 to 2085, indicating that these areas may already be saturated. However, within these boundaries, future spread will result in increased density and infilling of less densely populated areas, especially towards the northwest (Figures 5 and 6).

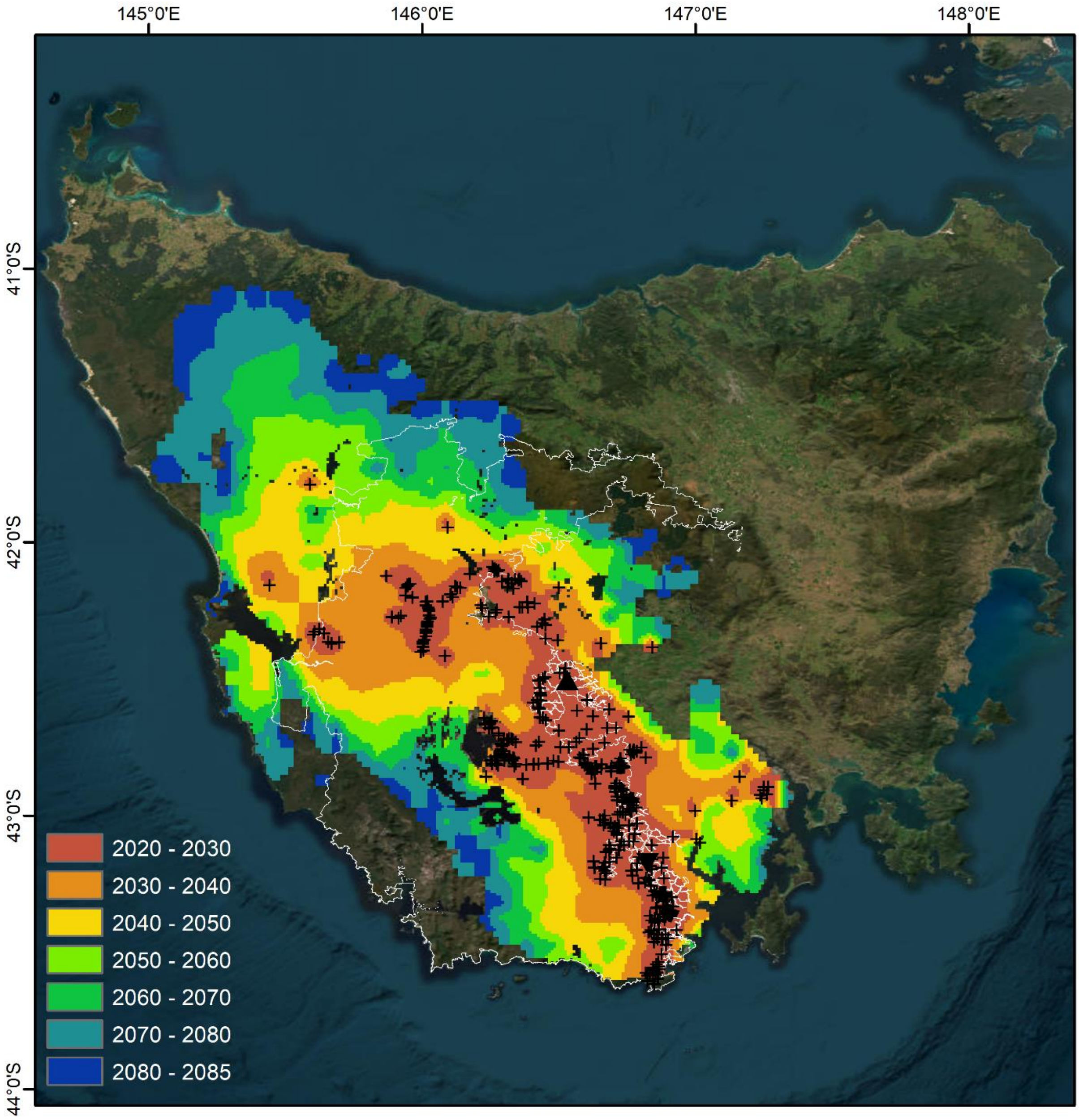

Figure 6. Simulated ongoing spread of the Superb Lyrebird (*Menura novaehollandiae*) throughout Tasmania, from their current occurrence in 2023 (black crosses and red shading), projected at ten-year intervals until 2085 (coloured time-coded contours), as determined by a habitat-constrained stochastic dispersal-diffusion model. The white boundary outlines the Tasmanian Wilderness World Heritage Area.

Discussion

The projected expansion of Superb Lyrebird (*Menura novaehollandiae*) in Tasmania reveals a critical combination of ecological adaptation and invasive potential, with the species growing in presence through the island's temperate forests. Using advanced spread simulations calibrated with multi-scale ecological data, we project a continued spread towards the western coast by the end of this century, underscoring the need for improved knowledge of the effects of lyrebirds upon Tasmanian ecosystems, and targeted conservation management strategies in these well-connected habitats.

The fine-scale habitat models found lyrebird activity to be closely associated with open areas within forests that had abundant leaf litter. This habitat selection in Tasmania mirrors their preferences in their native range on the mainland, suggesting consistent ecological requirements across both regions. As ground-foraging insectivores, lyrebirds thrive in environments rich in decomposing logs and leaf litter, home to a variety of invertebrates they feed upon, such as earthworms and insect larvae (Tassell 2014; Maisey et al. 2019). Dense understorey vegetation, in contrast, poses navigational challenges and reduces foraging efficiency, explaining their preference for more open habitats (Maisey et al. 2019).

Within their native range, lyrebirds prefer habitats with complex mid-stratum vegetation, such as small trees and large shrubs, which provide necessary camouflage from predators and facilitate breeding (Lill 1979; Maisey et al. 2019). This preference for vegetative concealment, due to their lower nesting attentiveness compared to other birds, is crucial for their reproductive success (Lill 1979). Similarly, in Tasmania, lyrebirds favour rainforests and wet-eucalypt forests with old-growth trees and dense mid-strata (Buettel et al. 2017), environments that our models confirm as ideal areas of occupancy. Lyrebird's preference for cooler climates is likely due to an evolutionary trait for successful egg incubation at lower temperatures (Lill 1979) and a predictable food supply (Maisey et al. 2019).

Based on these habitat preferences, it is clear that the national parks and reserves in western and northeast Tasmania contain extensive areas of habitat conducive to lyrebird spread. The prevalence of lyrebirds throughout south-central Tasmania can be attributed to the wide availability of connected habitats, at the sites of lyrebird introduction to the state. The two introduced populations, at Hastings Caves State Reserve and Mt. Field National Park, have now merged, facilitating gene flow and potentially enhancing their adaptability and capacity to spread across the island. The camera data showed high prevalence within these regions, indicating successful long-term establishment. The westward spread of lyrebirds to areas like the Macquarie Harbour region, albeit at a lower density, suggests an early stage of invasion, potentially entering a lag phase of colonisation (Crook 2002). With the Tasmanian Wilderness World Heritage Area and over half of the Tasmanian mainland predicted to be suitable for lyrebird habitation in our modelling, the species appears poised for further expansion.

Our spread simulations project an extensive future range expansion of lyrebirds, particularly across western Tasmania's suitable but currently unoccupied habitats. By the end of this century, the species is forecast to colonise the west-central highlands, northern slopes, and northwestern Tasmania. However, the periphery of the northwest is not likely to be reached within a century due to the patchy nature of suitable forests there. Human and natural barriers, such as cultivated lands, drier climates, and unsuitable vegetation, will also likely block any expansion to the otherwise highly suitable northeast unless an introduction (accidental or malicious) is attempted there. Any detection in the northeast should be rapidly addressed by conservation and management interventions if lyrebirds are to be kept permanently out of that region. More broadly, given the projected spread of lyrebirds in Tasmania, especially in the wet, temperate forests of the west, focused ecological monitoring is crucial. We recommend prioritising areas such as the Macquarie Harbour region and adjacent open-temperate forests near Rosebery, which our models identify as likely frontiers for future lyrebird spread. Using habitat information and suitability maps from our study, targeted monitoring should add further on-ground data to investigate the lyrebirds' spread dynamics and ecological impacts from the invasion front.

In this context, what ecological risks does the species pose? Tassell (2014) found no long-term evidence for their impacts on native invertebrate assemblages across spatial scales. One possible biological reason for the apparent lack of lyrebird impacts on their food resource is a time lag between the first introduction and measurable effects (Crooks 2005). Such prolonged lags can result from low initial population density or other stochastic demographic processes (Crooks 2005). Concurrently, systematic studies are needed to assess their influence on soil composition, forest structure, and native species interactions. These studies should aim to understand to what degree lyrebirds, as ecosystem engineers, are facilitating ecological benefits (e.g., nutrient cycling (Maisey et al. 2021) and fire-risk suppression (Nugent et al. 2014)) versus posing threats to the Tasmanian fauna and the structuring of its forest communities (e.g., through excessive bioturbation) (Tassel 2014).

As the Superb Lyrebird adapts to its new habitats in Tasmania, it is imperative to consider the broader challenges the species faces. Recent catastrophic events, such as the ‘Black Summer’ mega-fires of 2019-2020, have resulted in loss of crucial lyrebird nesting habitats across mainland Australia (Hughes et al. 2023; Maisey et al. 2023). The early 20th-century relocation to Tasmania has played an important role in safeguarding the lyrebird's future amidst escalating environmental threats. This creates a paradox where the introduced population holds conservation value but may require strategies to limit its future spread.

While our models offer robust predictions, there are limitations, particularly associated with the broad-scale vegetation data. For instance, the absence of detailed understorey characteristics in our habitat suitability predictions may lead to an overestimation of suitable habitats, as lyrebirds require open understorey—a feature not adequately represented in the available datasets. This constraint is particularly important for oligotrophic regions of western Tasmania, which support a dense, complex understorey that makes lyrebird foraging difficult. In addition to these data constraints, factors such as climate change, habitat alteration, and unforeseen ecological interactions could influence lyrebird distribution and impacts in ways that are not currently understood. Future work could also incorporate population data into spread models, but this will require more detailed spatio-temporal monitoring to better track lyrebird demographics and environmental impact. Additionally, exploring the indirect effects of lyrebird activities, such as their influence on fire regimes and nutrient cycling in Tasmanian forests, would provide much-needed insight into the ecological trade-offs they influence.

Conclusion

Our research underscores the Superb Lyrebird's adaptability and potential for range expansion in Tasmania's southern and central temperate forests. The extensive, interconnected habitats in the west and northwest are primed for species' future spread. In the broader context, the stable and growing population in Tasmania is significant, as Hughes et al. (2023) argue that lyrebirds face greater risk than their current IUCN status of 'Least Concern' indicates. Despite being introduced for conservation, the species is now listed as unwanted in Tasmania, presenting a conservation dilemma. For managers, this involves a delicate balance between protecting this iconic species in a range-wide context, while also managing their unintended effects on new ecosystems. Key to this is continuous monitoring at the expanding range front, ensuring that any interventions are timely and based on current data. Leveraging predictive models, our research equips conservation managers with information to identify options for targeted monitoring and potential interventions. Our findings not only address the specific narrative of the lyrebird in Tasmania, but also offer a methodological blueprint, combining detailed habitat analysis and flexible forecasting tools, for modelling the future spread of translocated vertebrate species in broader contexts.

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