Individual-Based Modelling of Species' Dynamic Resource Use

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Abstract

Understanding the current and future distribution of species is a critical facet of biodiversity conservation, and species distribution models (SDMs) are a powerful framework for achieving this, applying a correlative approach between distributional observations and a set of geospatial environmental predictors. Despite the vast potential of SDMs to address an array of challenges, they can be greatly improved by incorporating metrics that are developed based on spatial simulation. In this research, an individual-based model was used to simulate the dynamic relationship between movement and biotic resources (e.g. food sources) for oilbirds in Venezuela, in order to generate a new environmental variable for use in model calibration. This environmental layer represented the sustainability of a neighbourhood, based on connectivity, accessibility, and viability of biotic resources, and this dynamic variable greatly improved the accuracy and ecological realism of the SDM projection compared to other commonly applied SDM scenarios. Furthermore, this research advanced recent studies that have attempted to develop simulations based on quantitative analysis of real movement observations.

Keywords: Species distribution modelling, movement analysis, spatial simulation.

1. Introduction

By understanding the factors that define a species' geographic range, more precise estimations of resilience, range dynamics, and extinction can be made. Species distribution models (SDMs) are a widely accepted framework for achieving this, applying a correlative approach and extrapolating species-environmental relationships in space as well as time (Franklin 2009). However, the consideration of the different environmental factors that could influence a species distribution, and subsequent selection of these variables with which to train the model is an enduring issue (Guisan and Zimmermann 2000).

To illustrate the individual and joint effects of the three factors deemed most important in determining species distributions, Soberón and Peterson (2005) developed the heuristic 'BAM' framework (Figure 1). In this framework, biotic factors (**B**) represent interactions with other species (i.e. competition, food sources), abiotic factors (**A**) represent the physiological tolerances of a species (i.e. temperature, precipitation) and movement (**M**) refers to the area that has been or will be accessible to a species within a certain timeframe (i.e. dispersal, connectivity). While the importance of all three factors is well recognised in SDM research, the incorporation of movement has lagged. When movement has been incorporated in SDM, its almost exclusive conceptualization has been to couple the statistical model with a measure of dispersal in response to climate change or invasive spread (Miller and Holloway 2015), or as a measure of accessibility with which to select the appropriate spatial extent for model calibration (Qiao et al. 2015). The reasons for animal movement are vast, and movement patterns range from dispersal into unknown landscapes to daily movements such as foraging and homing. These finer scale movement behaviours have yet to be incorporated alongside SDM, despite the important role they play in the maintenance of a mobile species distribution.

Furthermore, the relationship between biotic factors and movement is dynamic, as movement can greatly impact the biotic resources of an area. When organisms traverse through a landscape, biotic resources deplete while the individual is in the area (e.g. herbivory) and replenish while the individual is absent. Daily consumption of resources can substantially alter the configuration of the landscape within a short period, and as such, it is not sufficient to consider accessibility (**M**) of biotic resources (**B**) as a static relationship. A species distribution could therefore be better explained by an ecological factor that integrates the dynamic relationship between ambulatory movements and biotic factors.

1.1. Spatial Simulation

Spatial simulation has been used extensively to investigate the movement and dispersal of plants and animals across a landscape, with a suite of approaches used including system models, cellular automata, and individual-based modelling (Tang and Bennett 2010). Due to their potential to incorporate the inherent relationship between movement and the environment, spatial simulation models are increasingly being used to understand animal movement and plant dispersal, and are beginning to be observed within the SDM framework.

In this paper, I will explore how step-selection function (SSF - a powerful spatial modelling approach that uses telemetry data to analyse movement patterns and resource use based on the underlying environment) can be used as a basis for spatial simulation. The use of SSF in generating bias estimates has not yet been implemented despite the vast potential to accurately and reliably inform animal-environment movement decisions. This model will inform the development of an environmental variable which will represent the dynamic relationship between biotic resources and movement, which can then be used within the species distribution modelling framework. This will provide researchers with an improved understanding of the relationship between biotic and movement factors, something that has been absent in previous studies, as well as an improved understanding of which factors contribute to a species distribution.

2. Methodology

The oilbird (*Steatornis caripensis*) is a nocturnal avian frugivore that inhabits northern South America, roosting in caves or crevices during the day, and foraging for fruit at night. With an extensive home range (mean foraging distance of 44km - Holland *et al.* 2009), an individual oilbird most likely utilizes several areas of biotic resources, making this a useful species to explore the integration of a dynamic movement-resource spatial simulation model in SDM. Maximum entropy (MaxEnt) was chosen as the statistical method to model the species-environment relationships. Five different BAM scenarios were analysed: A, B, BA, Classic BAM (cBAM), and Dynamic BAM (dBAM) (Table 1).

3. Results & Discussion

The inclusion of a variable which accounts for the dynamic relationship between movement and biotic resources improved the accuracy (when measured as the Boyce Index) of the SDM (Table 2) compared to other commonly implemented BAM scenarios. The Boyce Index is considered the most robust presence-only accuracy metric due to its ability to measure the monotonic increase in the predicted-to-expected frequency ratio with increasing habitat suitability, with a higher value representative of a more valid model. The Boyce Index was highest for the dBAM model, suggesting that incorporating a variable that measured the relationship between M and B was advantageous to the SDMs projection capacity.

This argument is furthered by the fact that this layer had the highest relative contribution of all the 'BAM' variables used the final model (37.6%), or in other words the most influence on the projected environmental and geographic distribution of oilbirds. The use of a dynamic environmental layer of biotic resources and movement removed the assumption of homogeneity across the distribution of food species, and delineates between accessible and sustainable areas of biotic resources from isolated and unsustainable areas. This resulted in a better indicator of the relationship between biotic resources and movement, and removed some of the uncertainty introduced by source and sink populations for mobile species.

The incorporation of SSF within a spatial simulation model was novel, and the results suggest that this is a method that performs well. The movement trajectories of the individual oilbirds were characteristic of several short steps followed by a long one. The benefit of using SSF within a random walk framework over other implementations is that it includes the results of conditional logistic regression. As movement is simulated using a statistical model generated from observed movements, more realistic movement behaviours are simulated compared to a model specified solely on subjective assumptions, and results better illustrate the influences of the environment on actual movements.

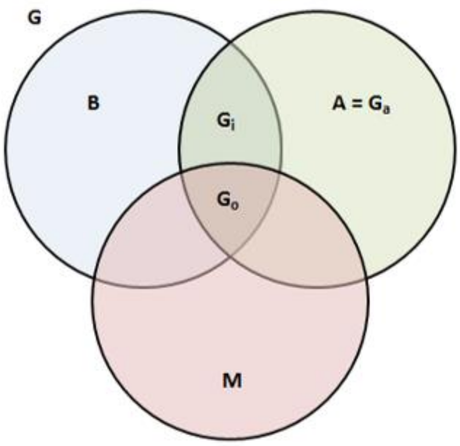


Figure 1: The 'BAM' Framework, which depicts the interaction between biotic (**B**), abiotic (**A**), and movement (**M**) factors. **G** is the geographic space in which the analysis occurs, $\mathbf{G_a}$ represents the abiotically suitable area, $\mathbf{G_i}$ s the invadable (abiotic and biotic) suitable area. Finally $\mathbf{G_o}$ represents the occupied (abiotic and biotic) suitable area and is therefore the actual distribution. Modified from Soberón (2007).

Table 1: BAM Scenarios used to explore oilbird distributional patterns.

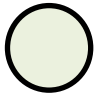
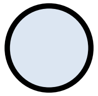
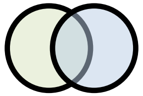
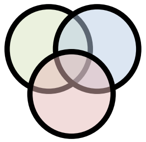
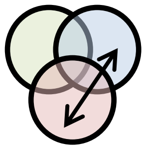
BAM Scenario	Explanation
A 	Abiotic factors (**A**) represent the physiological tolerances of a species (i.e. temperature, precipitation). Here, the 19 bioclimatic variables were considered as the abiotic factors.
B 	Biotic factors (**B**) represent interactions with other species (i.e. competition, food sources). A categorical variable representing presence or absence of the five species within the 10km observation were used as the biotic factors.
BA 	This scenario projects the invadable distribution ($\mathbf{G_I}$) in the classic BAM framework. The 19 bioclimatic variables and the five presence absence maps of the food species were used as the input variables.
Classic BAM (cBAM) 	Movement factors (**M**) refer to the area that has been or will be accessible to a species within a certain timeframe. The presence or absence of the five fruit-bearing tree species will be identified within a focal area of 50km for each 10km observation. This will be represented by a categorical binary representation of presence / absence within a focal area of 50km, and the 19 bioclimatic variables.
Dynamic BAM (dBAM) 	Spatial simulation will be used to create a variable which summarizes the dynamic relationship between movement and biotic factors within the 50km focal area. The survival rate of 1000 oilbirds will be the input layer representing BM, and the 19 bioclimatic variables representing A. Full Overview, Design Concepts and Details are available here.

Table 2: The three accuracy metrics of the five BAM scenarios: Lowest possible threshold (LPT), minimum predicted area (MPA), and the Boyce index (BI).

	LPT	MPA	BI
A	0.0002	0.0197	0.8210
B	**0.0172**	**0.0296**	0.0580
BA	0.0001	0.0256	0.7600
cBAM	0.0004	0.0220	0.6350
dBAM	0.0002	0.0271	**0.8920**

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