

# Predictive movement ecology using spatial simulations

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## Code and data availability

We created a website to host the code used to explore movement data for the presence of temporal dynamics, fit basic models and plot response curves, and assess extrapolation in environmental space: [https://swforrest.github.io/predictive\\_movement\\_ecology/](https://swforrest.github.io/predictive_movement_ecology/).

## Author contributions

MAC, DN, and SWF conceived the initial idea for the paper. MAC and SWF wrote the original draft, with conceptual direction from DDH, NJK, JRP, TM, JF, JS, RM, LB, and DN. DDH provided the text and figures for the African wild dog case-study, MAC provided the northern quoll figures, and SWF provided the water buffalo figures. All authors contributed to manuscript revision and editing.

## Generative AI statement

ChatGPT was used to generate some of the individual icons in Figure A7. Generative AI was not used at any stage for generating ideas or for the writing of this manuscript. Perplexity and Claude were occasionally used to check for literature that may not have been found using typical search procedures. Claude Code (Opus 5) was used to generate the initial version of the ‘Predictive SSF Walkthrough’ notebook on the website, based on code from [https://github.com/swforrest/dynamic\\_SSF\\_sims](https://github.com/swforrest/dynamic_SSF_sims), which was manually edited and verified by SWF.



# Abstract

The active movement of animals is fundamental to the structure and function of ecosystems globally. In recent years, reductions in the size and cost of animal tracking equipment have precipitated an explosion of interest in movement ecology, accelerating our understanding of the causes and consequences of animal movement. Until recently, movement ecology was largely a descriptive science. However, recent developments signal that the field is shifting toward a more predictive lens, facilitated by a surge in the availability of data and analytical tools. Here, we review recent advances in predictive movement ecology and clarify promising future directions for the field. We particularly focus on predictions generated with spatial simulations from step-selection functions, but cover topics relevant to other predictive approaches. We first provide an overview of key concepts in predictive movement ecology, before presenting a detailed summary of a predictive movement ecology workflow from study conceptualisation to the final presentation of outputs. At each step of the workflow, we summarise current and emerging methods and highlight key sources for technical details. We offer guidance for predictions made within the same domain as the collected data, as well as those projected into novel locations, times or landscape configurations. We distinguish between animal-centric predictions, which quantify prediction metrics specific to a single simulated animal, and landscape-centric predictions, which predict quantities that are tied to spatial locations. To accompany our review of concepts, applications, and methods for predicting animal movement, we include a detailed case-study of African wild dogs (*Lycaon pictus*) that steps through each decision-point in a predictive movement ecology study. We finish by outlining future directions for predictive movement ecology, emphasising the need for continued development to enhance the accuracy and ecological realism of simulations. Overall, we aim to summarise the progress of an emerging field, which will guide the next generation of predictive movement models and their application for conservation management and environmental decision-making under global change.

## Keywords

Predictive movement ecology, predictions, spatial simulations, step-selection functions, domain, interpolative, extrapolative, forecasting, explanatory, conservation

# 1 Introduction

## 1.1 Animal movement ecology

Movement is a defining characteristic of the animal kingdom, allowing organisms to locate resources, avoid threats, and persist in dynamic environments (Nathan et al., 2008). Movement links animal behaviour, population dynamics, and ecosystem processes (Morales et al., 2010), thereby shaping ecosystem structure and function at multiple temporal and spatial scales (Hanski, 1998; Turchin, 1998). Movement makes animals vulnerable to anthropogenic disturbance (Pay et al., 2025), but is also a key component of their capacity to behaviourally adapt under shifting ecological conditions (Kokko & López-Sepulcre, 2006; Doerr et al., 2011). As such, understanding and predicting animal movement is central to conserving animal biodiversity in the 21st century (Allen & Singh, 2016; Gomez et al., 2025).

Animal movement ecology seeks to explain the causes, mechanisms, patterns, and consequences of animal movement (Nathan et al., 2008; Rutz & Hays, 2009; Kays et al., 2015; Beltran et al., 2024). Several factors have hastened its development since the early 2000s. First, rapid advancements in biologging and animal tracking technology (e.g. Global Positioning System, GPS) have increased the range, accessibility, and volume of fine-scale animal movement data, while reductions in the size and weight of devices allow smaller animals to be tracked (Tomkiewicz et al., 2010; Williams et al., 2020; Wild et al., 2022, 2023; Beltran et al., 2024). Second, advances in remote sensing have yielded unprecedented volumes of fine-scale data from satellites and aerial systems, offering detailed characterisations of spatially and temporally dynamic environmental conditions that affect animal movement (Toth & Józków, 2016). Finally, statistical methods have emerged that leverage increased computational power to link animal movement data with remotely sensed data, providing novel insights into animal movements and the decisions that govern them (Hooten et al., 2017; Patterson et al., 2017; Northrup et al., 2022; Florko et al., 2025).

In combination, these new data sources and technologies have enabled researchers to ask how and why organisms move and make use of their surroundings (Joo et al., 2022), providing insights into themes such as foraging ecology, population connectivity, and the role of movement in ecological networks (Adriaensen et al., 2003; Elliot et al., 2014). To date, much of the research within movement ecology has been descriptive. Most studies have sought to describe and explain the patterns of animal movement that have been observed through biologging and animal tracking technologies by, for instance, relating patterns of movement to environmental variables. However, movement ecology has recently begun to transition from a predominantly descriptive science to a predictive one (Gomez et al., 2025; Hacker et al., 2026). This mirrors similar transitions in other areas of ecology (Hobbs & Morton, 1999; Mouquet et al., 2015; Houlahan et al., 2017; Maris et al., 2018; Hacker et al., 2026).

## 1.2 From description to prediction in movement ecology

Scientific fields and subfields often begin by describing phenomena, usually informed by case studies. As the number and quality of case studies grow, recurring patterns may become apparent, giving rise to hypotheses that seek to explain them. Through this inductive reasoning, general theories grounded in underlying mechanisms can emerge (Maris et al., 2018). These theories can be tested in a variety of ways. Qualitative predictions are common in ecology and movement ecology

is no exception; for instance, the human shield hypothesis predicts that human disturbance reduces the activity of dominant predators, thereby increasing activity of a subordinate species (Gaynor et al., 2025). While such predictions are valuable and can guide management decisions, they do not provide a quantitative measure of the magnitude of change (Houlahan et al., 2017). Quantitative predictions, on the other hand, do more than indicate the nature of change - they specify how much change to expect under defined conditions (Hacker et al., 2026). This capacity allows scientists to construct testable hypotheses, quantify uncertainty, and forecast future scenarios to guide decision-making (Maris et al., 2018).

A notable example of prediction in ecology is the development of species distribution models, which transformed species distribution research from describing patterns to making quantitative predictions that now underpin conservation decision-making globally (Sofaer et al., 2019). Given the lack of consideration of animal movement in global disturbance planning (Bergès et al., 2020), the appetite for predictive movement ecology is clearly present (Thurfjell et al., 2014; Williams et al., 2020; Gomez et al., 2025; Fredston & Beltran, 2026; Hacker et al., 2026; Oliver, Hébert, et al., 2026; Speaker et al., 2026). As with progress in species distribution models, the shift to predictive movement ecology allows ecologists to quantitatively test movement theories while informing conservation decision-making.

Animal-movement predictions can be generated using a range of modelling frameworks that differ in their level of mechanistic detail and the processes they represent. Correlative habitat- and distribution modelling approaches, such as resource-selection functions and species distribution models, can predict patterns of occurrence or space use, but do not generally represent the movement decisions that generate those patterns (Northrup et al., 2022; Florko et al., 2025). By contrast, movement-process models, including discrete- and continuous-time stochastic movement models, state-space and hidden Markov models, and individual- or agent-based simulations, explicitly describe trajectories or their underlying behavioural processes, although they vary in their treatment of habitat selection, behavioural state, and interactions among individuals (Auger-Méthé et al., 2021; Florko et al., 2025). Among these, step-selection models have become popular because they jointly model movement and habitat selection at the scale of individual movement decisions. A step-selection function (SSF) parameterises a discrete-time movement model that then can be simulated to generate a number of prediction outputs including [utilisation distribution \(UD\)s](#), [landscape connectivity](#), and responses to landscape and anthropogenic features, while being able to incorporate behavioural processes such as temporal dynamics, memory, and social interactions (Signer et al., 2017; Hooker et al., 2021; Potts & Börger, 2022; Potts, Börger, et al., 2022; Hofmann et al., 2023; Signer et al., 2023; Cowan et al., 2025; Forrest et al., 2025). Given their flexibility, technical accessibility, and potential for further development with emerging statistical and computational tools, we focus this review on step-selection models.

In this review, we chart the ongoing progression of movement ecology from a descriptive to a predictive science. We describe a general workflow for movement ecologists to transition from descriptive to predictive approaches, giving details on each of the key steps in a predictive simulation-based application and presenting core concepts in predictive movement ecology (Section 3). We include figures from several studies, including from a predictive movement case-study of African wild dogs (*Lycaon pictus*), which is presented in full to outline decisions that were made for an applied example in the Supplementary Materials (Section A). Finally, we outline considerations, limitations, and future work in simulation-based predictive movement ecology (Section 4). This review is intended to serve as an introduction to predictive movement ecology tools and concepts, while also providing sufficient detail to be a useful reference for experienced practitioners.

## 2 Predictive movement ecology using spatial simulations: Core concepts

### 2.1 Step-selection functions

A step-selection function (SSF) defines an animal selecting a ‘step’ from candidate possibilities in their surrounding environment at some future time, with respect to their movement behaviour and habitat selection preferences (Fortin et al., 2005; Potts et al., 2014; Avgar et al., 2016). SSFs have been the subject of several review papers over the years so we do not provide an exhaustive description here. Instead, we refer readers to Thurfjell et al. (2014), Fieberg et al. (2021), and Northrup et al. (2022) for details on how to fit SSFs and interpret the estimated parameters, and here we focus on using a fitted model to predict animal behaviour. An SSF models the probability density function for an animal to move to a location  $s_{t+1}$ , given its current location is  $s_t$  and its previous location was  $s_{t-1}$ , with the following functional form

$$p(s_{t+1}|s_t, s_{t-1}; \beta, \theta) = \frac{\phi(s_{t+1}, s_t, s_{t-1}; \theta, \mathbf{X}(s_t))\omega(\mathbf{X}(s_{t+1}); \beta)}{\int_{q \in S} \phi(q, s_t, s_{t-1}; \theta)\omega(\mathbf{X}(q); \beta) dq}. \quad (1)$$

where  $\mathbf{X}(s_t)$  is a column vector of covariates at  $s_t$ . The  $\phi$  term denotes the selection-free movement kernel, which typically encodes step length and turning angle distributions, and may also include some of the covariates  $\mathbf{X}(s_t)$  if they are hypothesised to influence selection-free movement behaviour. The  $\omega$  term denotes the relative selection of  $s_{t+1}$ , a location at the next time-step, and  $\beta_i$  is the coefficient that quantifies the relationship between the animal’s behaviour and the associated habitat covariate  $X_i$  associated with location  $s_{t+1}$ . Positive coefficient values are interpreted as indicating a relative preference for higher values of the associated covariate, and negative coefficient values suggest relative avoidance (Fieberg et al., 2021). If required, it is straightforward to include quadratic responses, and explicitly specify interactions between covariates, as well as non-linear and time-varying coefficients (Forester et al., 2009; Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024; Forrest et al., 2025). The denominator is a normalising constant that ensures the probability density integrates to 1, and  $S$  is the spatial domain that the animal can access. In practice this integral is typically approximated by sampling from a proposal distribution (Michelot et al., 2024). This Monte Carlo approximation avoids evaluating the integral directly, and allows the SSF to be estimated by conditional logistic regression (CLR) if the numerator is expressible as the exponential of a linear function of the predictor variables (Forester et al., 2009). As such, sampling distributions from the exponential family are most common, but are not necessary if the user is willing to use a bespoke likelihood function rather than CLR (Michelot et al., 2024). Figure 1 gives an example plot of the function  $p$  (Panel C), which is the product of the selection-free movement kernel,  $\phi$  (Panel A), and the habitat selection function,  $\omega$  (Panel B), illustrating how the movement and habitat selection processes combine to shape animal movement.

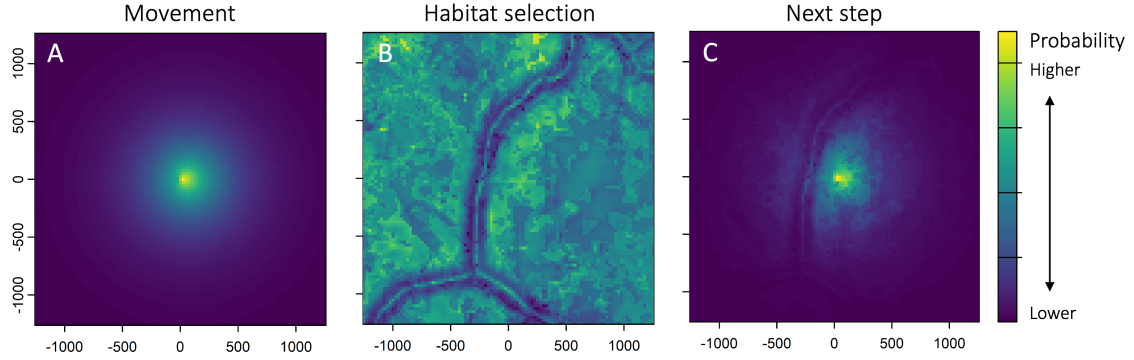


Figure 1: The (A) movement and (B) habitat selection surfaces ( $\phi$  and  $\omega$  from Equation 1 respectively) are combined into a (C) next-step probability surface ( $p$  in Equation 1 respectively) which we can sample from directly to generate simulations, or approximate using random proposal steps (Michelot et al., 2024).

We note that typical step-selection models still currently have a number of limitations, notably the scale-dependence relating to the sampling resolution and the computational cost for generating simulations. Additionally, these discrete-time methods usually require regularly sampled location data with low error (but see Hofmann, Cozzi, and Fieberg (2024)), and naturally point towards terrestrial and some aquatic studies. In comparison, continuous-time models relax the requirement of regular location sampling, and reduce the scale-dependence that is inherent to discrete-time step-selection models (Hanks et al., 2015; Wilson et al., 2018; Michelot et al., 2019; McClintock & Lander, 2024; Michelot, 2024; Dupont et al., 2026), which is discussed further in Section 3.5.5.

## 2.2 Generating predictions from step-selection functions

A benefit of step-selection models is the range of outputs they can produce. Much can be learned simply by interpreting the parameter estimates (coefficients) of step-selection models, especially when these parameters are contrasted across different individuals and environmental conditions (Fieberg et al., 2021; Northrup et al., 2022; Florko et al., 2025; Gerber et al., 2025). However, predicting from step-selection models also allows one to ‘scale up’ the movement model, in both space and time, to generate landscape-scale predictions of space use or connectivity (Potts & Börger, 2023). This scaling up typically requires simulating from the model (Equation 1), generating probability surfaces through time (Potts & Börger, 2023), or using the estimated parameters to create a permeability surface. Here, we briefly describe the process, benefits and limitations of various methods for projecting Equation (1) through time to understand broad-scale space use patterns. Due to their generality and flexibility, we have focused the predictive movement ecology workflow in Section 3 on generating predictions using spatial simulations, but we mention other approaches where relevant.

### 2.2.1 Spatial simulations

A simple way to simulate from a fitted SSF is to propose potential steps from the estimated movement kernel,  $\phi$ , and choose one of the steps with probabilities proportional to the value of the habitat selection kernel  $\omega$  at their endpoints, as shown in Figure 2 (possibly also integrating information at the start or along each step) (Signer et al., 2017; Signer et al., 2023). The process then repeats at each new location until a trajectory is generated. This approach is often referred

to as a spatial simulation, or as a stochastic individual- or agent-based model (IBM/ABM; Potts and Börger, 2023; Rogers et al., 2025). Simulating from a fitted SSF is straightforward, as one only needs to extract the covariate values pertaining to each step and estimate the selection weights based on the estimated coefficients. This simplicity allows for the inclusion of more complicated processes such as temporal dynamics, memory, and social interactions, as the covariate values can be updated step-by-step (Cowan et al., 2025; Forrest et al., 2025). Software such as the `amt` R package (Signer et al., 2019) make this straightforward by having functions that help to prepare data, fit, and simulate from SSFs (Signer et al., 2017; Signer et al., 2023).

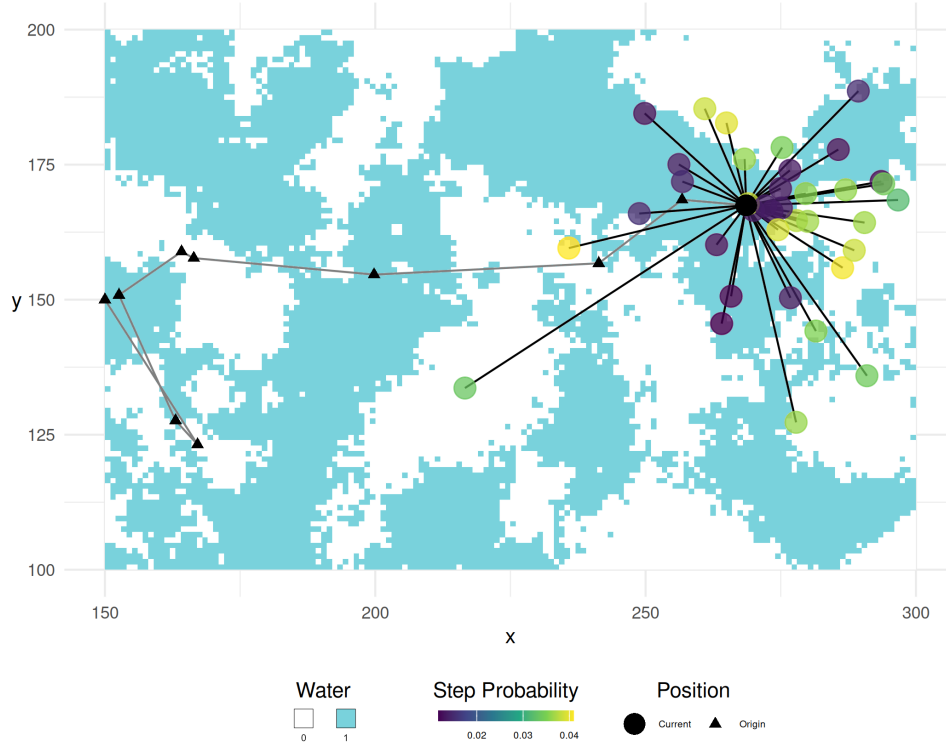


Figure 2: A simulated trajectory (black line with triangles) showing proposed steps from the current location (black circle), with probability weights given by movement and habitat selection parameters, which are illustrated by colour of the circles at the end of each step. In this example, water bodies are avoided.

### 2.2.2 Probability surfaces

An alternative to stochastically simulating individual trajectories is to solve directly for the probability distribution of an animal’s location through time, avoiding the need to simulate many individual movement paths. This avoids Monte Carlo sampling error and can therefore produce more precise estimates, often with greater computational efficiency. This can be done, for example, using an integro-difference equation formalism (sometimes called a ‘master equation’), which describes how the probability of an animal’s location changes over time (Barnett & Moorcroft, 2008; Merkle et al., 2017). The ‘how to’ paper of Potts and Börger (2022) gives an overview of this approach. If space is represented as a set of discrete locations rather than as a continuous landscape, the integral becomes a sum, and Equation (1) can be expressed as a transition matrix denoting how the utilisation distribution changes from one time step to the next. The eigenvector of this transition matrix is therefore the steady state utilisation distribution (which is noted in the SSF context by Potts and Börger (2022, Supplementary Appendix E)). Rogers et al. (2025) and Ellison-Neary et al. (2026) took up this idea to provide methods for predicting long-term space

use from a fitted SSF. In certain circumstances, these approaches can be faster than agent-based simulations to compute utilisation distributions. However, they are less flexible: movement and selection parameters are typically assumed constant through time (though it is possible to use these models to explore transient dynamics), and the methods have only been used to predict the steady-state utilisation distribution so far, if it exists, but not yet transient distributions.

### 2.2.3 Landscape connectivity

SSFs can be used to predict landscape permeability - the relative ease with which an animal is expected to move through different parts of the landscape - by projecting estimated habitat selection onto spatial covariates across a landscape using the habitat selection function,  $\omega(\mathbf{X}(s); \boldsymbol{\beta})$  (Zeller et al., 2012; Diniz et al., 2020). Such permeability surfaces are widely used as inputs for functional landscape connectivity models, which assess the degree to which the landscape facilitates or impedes movements among resource patches. Common approaches include least-cost path analysis (LCPA; Adriaensen et al., 2003; Etherington, 2016), randomised shortest paths (RSP; Panzacchi et al., 2016; Dorber et al., 2023), and circuit theory (CT; McRae, 2006; McRae et al., 2008). LCPA assumes a start and end point, and perfect knowledge of what is in between, while CT has no goal and assumes random walks. These issues of perception are avoided using RSPs, which have a parameter that controls the ‘knowledge’ of the environment, and therefore randomness of movement (Panzacchi et al., 2016). A key limitation of all these approaches, however, is their reliance on a static permeability surface, which is an unconditional prediction (see Signer et al., 2017) and ignores temporal variation in both animal behaviour (e.g. circadian rhythms) and landscape conditions (e.g. seasonality or climate change) (Hofmann, 2024). Spatial simulations address these limitations, obviating the need for a permeability surface while allowing for dynamic behaviour and landscapes, predicting where movement is conditional on the animal’s current location, and also accommodating behavioural processes such as memory and social dynamics (Diniz et al., 2020; Hofmann et al., 2023; Hofmann, 2024). Even though such spatial simulations are typically more computationally expensive, they provide a more comprehensive view of connectivity that quantifies metrics such as [connectedness](#); the degree to which different patches or habitats within a landscape are functionally connected, [conductance](#); the degree of movement or flow that the landscape allows, and [betweenness](#); the importance of landscape cells in facilitating connectivity (Hofmann, 2024).

| Approach                                                       | Can predict                                                                                               | Pros                                                                                                                | Cons                                                                                                 | Key references                                                                                                    | Some examples                                                                                                                                                                                                   |
|----------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b>SSF coefficients and relative selection strength (RSS)</b>  | Relative responses to habitat covariates and movement interactions                                        | Fast and straightforward                                                                                            | Ignores the movement process when generating spatial predictions                                     | Avgar et al. (2016, 2017) and Fieberg et al. (2021)                                                               | Fortin et al. (2005), Mawer, Bruneel, Pauwels, et al. (2023), Chatterjee et al. (2024), and Cowan et al. (2024)                                                                                                 |
| <b>Spatial (agent-based) simulations</b>                       | Approximate utilisation distributions, functional landscape connectivity, responses to landscape features | Highly flexible: can include temporal dynamics, behavioural states, memory, social interactions                     | Computationally costly to simulate over large landscapes                                             | Signer et al. (2017), Potts, Börger, et al. (2022), Hofmann et al. (2023), and Signer et al. (2023)               | Whittington et al. (2022), Aiello et al. (2023), Sells et al. (2023), Ellison, Potts, Strickland, et al. (2024), Cappello et al. (2025), Cowan et al. (2025), Forrest et al. (2025), and Westaway et al. (2025) |
| <b>Probability surfaces via integro-difference equations</b>   | Exact utilisation distributions                                                                           | Generates a complete, exact, summary of all possible stochastic trajectories at once, can include temporal dynamics | Can be computationally intensive, both speed- and memory-wise                                        | Barnett and Moorcroft (2008) and Potts and Börger (2023)                                                          | Merkle et al. (2017, 2018)                                                                                                                                                                                      |
| <b>Probability surfaces via partial differential equations</b> | Approximate utilisation distributions                                                                     | Opens the gateway to a wealth of mathematical theory on spatial pattern formation and tipping points (bifurcations) | Non-exact: involves various limiting approximations                                                  | Moorcroft and Barnett (2008), Potts and Schlägel (2020), and Potts and Börger (2023)                              | Potts and Lewis (2019), Ellison et al. (2020), Ellison, Potts, Boudreau, et al. (2024), and Arnold et al. (2026)                                                                                                |
| <b>Calculating the eigenvector of a transition matrix</b>      | Exact steady-state utilisation distributions                                                              | Gives the exact steady-state probability distribution                                                               | Only calculates steady state so does not allow for temporal dynamics                                 | Potts and Börger (2023), Rogers et al. (2025), and Ellison-Neary et al. (2026)                                    |                                                                                                                                                                                                                 |
| <b>Resistance-based landscape connectivity</b>                 | Functional landscape connectivity                                                                         | Faster than spatial simulations                                                                                     | Requires creating a permeability surface and making assumptions about animal movement and perception | Zeller et al. (2012), Etherington (2016), Panzacchi et al. (2016), Diniz et al. (2020), and Hofmann et al. (2021) | Etherington et al. (2014), Zeller et al. (2016), Brennan et al. (2020), Brennan et al. (2022), and Dorber et al. (2023)                                                                                         |

Table 1: Predictive outputs that are possible from a fitted step-selection function by using different approaches, and their benefits and limitations.



### 3 Predictive movement ecology workflow

The process of predictive movement ecology roughly follows the nine steps shown in Figure 3: 1) outline and define the research aim(s), 2) collect movement data, 3) prepare environmental data and other covariates, 4) explore data, 5) build and fit movement model(s), 6) generate (e.g., simulate) in-domain predictions from fitted models, 7) validate in-domain predictions against withheld data (looping iteratively from step 5 to 7 as required), 8) if generating out-of-domain predictions, create covariates and simulate under those conditions, and 9) interpret outcomes based on research aims. We determined these steps for applied predictions, but a similar workflow could also be used for explanatory predictions to further understand a study system. Given their flexibility and generality, we also focus primarily on spatial simulations, but highlight where other prediction approaches would be beneficial. We structure the remainder of the paper according to these steps by devoting one section to each. The workflow is illustrated with figures created using data from Asian water buffalo (*Bubalus bubalis*), northern quolls (*Dasyurus hallucatus*), and African wild dogs (*Lycaon pictus*), with a full case-study of African wild dogs in the Supplementary Materials (Section A), which highlights decisions that were made during a real predictive movement study.

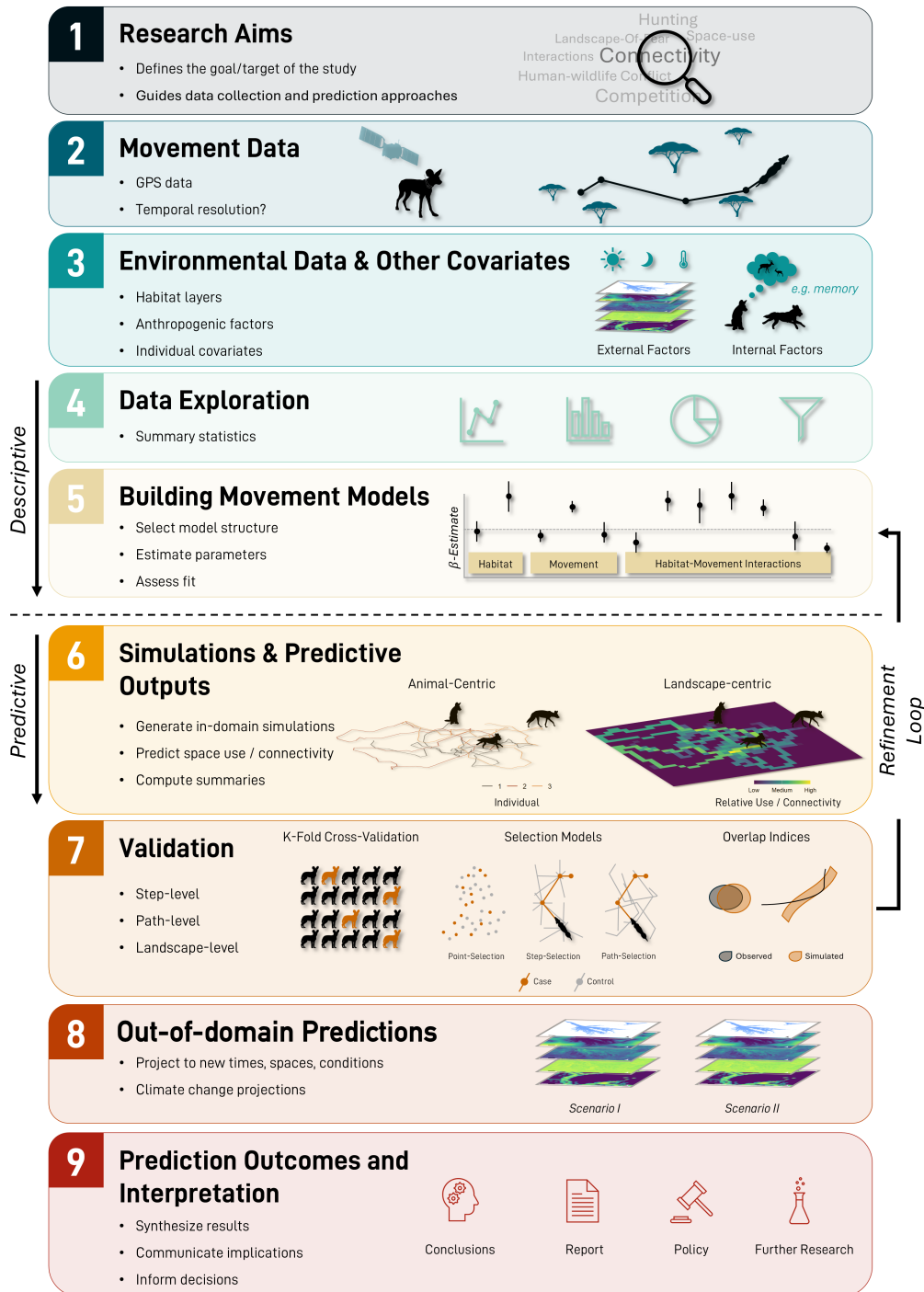


Figure 3: Conceptual workflow for predictive movement ecology. (1) The researcher first defines the research aim(s). (2) These determine the type and spatio-temporal characteristics of the required data, including (2) animal movement data and (3) environmental covariates describing internal and external drivers of movement. (4) Movement and environmental data are then explored and (5) jointly analysed to infer movement behaviour and habitat–movement relationships. (6) The fitted movement model is used to simulate trajectories and generate predictions, from which animal-centric or landscape-centric metrics can be derived. (7) Predictions are validated at multiple levels (e.g., step, path, or landscape) using withheld data, with results informing iterative model refinement. (8) If generating out-of-domain predictions, spatial covariates representing novel scenarios (e.g. space, time or landscape configuration) should be created, and predictions generated for these conditions, and compared to the in-domain predictions under the current conditions. (9) Finally, predictions are interpreted to address the research aim(s) and inform ecological understanding or decision-making.

### 3.1 Research aims

Clear research aims outline the goal of the study and guide researchers towards specific pipelines that inform data collection, model selection, validation, and interpretation. For predictive movement ecology, the research aim dictates the type of movement data required (e.g. GPS locations, accelerometry) and whether such data might already exist, and helps identify the covariates that best represent hypothesised drivers of movement. As different aims demand different data resolutions and extents, the temporal (e.g., second, minutes, weeks) and spatial scale of interest must also be established early. Researchers should also determine i) whether the research is **explanatory** or **applied**, and whether the predictions will be **in-domain** or **out-of-domain**, ii) whether an **animal-centric** or **landscape-centric** perspective (or both) is most appropriate, and iii) what the predictive quantities are that must later be validated. Most importantly, clearly defined research aims, along with appropriate subsequent methods, allow results to be interpreted and linked to priority conservation decisions that benefit the species of interest. One way to ensure that predictive methods are suitable for the research aims is to engage statisticians, modellers, and land managers early in the planning process, to ensure that methods and anticipated data can be applied for that purpose (Gomez et al., 2025). This upfront planning can ensure that data collection is targeted and efficient, while reducing the negative welfare impact on animals by ensuring data are usable and effective.

#### 3.1.1 Purpose, domain and environmental space of predictions

Choices made when predicting with spatial simulations must be guided by the intended purpose of the predictions. Drawing on previous work (Elith & Leathwick, 2009; Mouquet et al., 2015; Maris et al., 2018), we distinguish two broad classes of simulation-based predictions in movement ecology: explanatory and applied. **Explanatory predictions** (also called corroboratory predictions by Maris et al., 2018) test hypotheses from theoretical frameworks and aim to validate or refine hypotheses by comparing predictions against observed data (Mouquet et al., 2015). In movement ecology, simulation-based explanatory predictions have addressed questions such as how species differ in their foraging abilities (Spiegel et al., 2013), how spatial memory and social interactions shape the long-term space use of animals (Moorcroft et al., 2006; Merkle et al., 2017, 2019; de Guinea et al., 2021; Potts, Giunta, & Lewis, 2022; Ranc et al., 2022; Ellison, Potts, Strickland, et al., 2024), and how seed dispersal for different birds affects carbon sequestration outcomes across a fragmentation gradient (Bello, Crowther, et al., 2024; Bello, Dent, & Crowther, 2024). In other cases, simulations represent null models that intentionally omit the process of interest, allowing researchers to assess its influence on observed patterns (Abrahms et al., 2019; de Guinea et al., 2021; Zeller et al., 2021; Picardi, Abrahms, et al., 2022; Dejeante et al., 2025).

In contrast, **applied predictions** from movement models often assume the validity of underlying hypotheses and focus instead on what can be learned from simulations, particularly as it relates to decision-making and conservation. They have been used to investigate the effects of disturbance or conservation actions on wildlife movement (Whittington et al., 2022; Aiello et al., 2023; Cowan et al., 2025), and to forecast the impacts of climate change on animal space use and connectivity (Hofmann, Behr, et al., 2024). While simulation-based explanatory predictions will continue to advance our fundamental understanding of animal movement, we envision a step-change for predictive movement ecology toward robust applied predictions from realistic models that can inform evidence-based biodiversity conservation (Gomez et al., 2025; Oliver, Hébert, et al., 2026). We thus focus our attention on applied predictions for the remainder of this review, noting that many

of the topics are still relevant for explanatory predictions.

Alongside a model’s overarching purpose, two characteristics of a study are important to consider in simulation-based predictions. The first is the **domain**, which refers to the conditions (i.e., spatial extent, time period, landscape configuration, and taxa) in which the training data were collected. **In-domain predictions** are made within the bounds of the observed conditions for which a model was trained (i.e., where and when the observed movement data were collected). Common in-domain predictions in movement ecology include utilisation distributions (Sells et al., 2022; Dulude-de Broin et al., 2025; Forrest et al., 2025), measures of landscape connectivity (Hooker et al., 2021; Hofmann et al., 2023; Sells et al., 2023; Westaway et al., 2025), and maps of mortality risk from anthropogenic features (Cappello et al., 2025). In-domain predictions may be the final goal of a study focused on the sampled area, or may be used to internally validate the predictive performance of models prior to generating out-of-domain predictions. **Out-of-domain predictions** (also called model transfer; Yates et al., 2018) focus on making predictions beyond the domain of training data in any of the above dimensions, for example by 1) forecasting future states of ecological systems (Hofmann, Behr, et al., 2024), 2) predicting to geographically-separated landscapes (Hooker et al., 2021), or 3) testing scenarios of landscape or environmental change with counterfactuals, interventions, or hypothetical reconfigurations of covariates (Whittington et al., 2022; Aiello et al., 2023; Cowan et al., 2025).

Additionally, there is an important interplay between the domain and the **environmental space** of both the training conditions and those that are being predicted into (i.e., the ‘target’ conditions) that must be considered in simulation-based movement studies. The environmental space is a multi-dimensional space defined by covariate values (Elith & Leathwick, 2009; Matthiopoulos et al., 2015) and can differ quite substantially both within and between the training and target domains. Figure 4 illustrates this difference across a spatial domain, but similar principles apply for time, landscape configuration, and taxa. Where the training and target domains overlap and an in-domain prediction is made (e.g., spatial interpolation, Figure 3 A-B), predictions can be made to environmentally similar ‘analogous’ conditions (e.g., similar ecosystem types), or environmentally distinct ‘novel’ conditions (e.g., unique microclimates within a study area). The equivalent can occur for out-of-domain predictions (e.g., spatial extrapolation/transfer; Figure 3 C-D), where non-overlapping locations can either occupy similar environmental conditions (e.g., cover similar ecosystem types), or not. The **environmental distance** between the training and target domain determines the extent to which a movement model must **interpolate** or **extrapolate** in environmental space when simulations are produced. Environmental extrapolation has been studied for more than a decade in the context of species distribution modelling, with evidence suggesting an important, albeit complex, impact of environmental distance on model predictive performance (Elith & Leathwick, 2009; Zurell et al., 2012; Mesgaran et al., 2014; Sequeira et al., 2018; Yates et al., 2018; Liu et al., 2020; Meyer & Pebesma, 2021; Rousseau & Betts, 2022; Patterson et al., 2025). Tools have been developed to assess the gradient from interpolative to extrapolative in environmental distance for a target domain, usually quantified as a continuous value from 0 to  $\infty$  based on training conditions (illustrated in Figure 4).

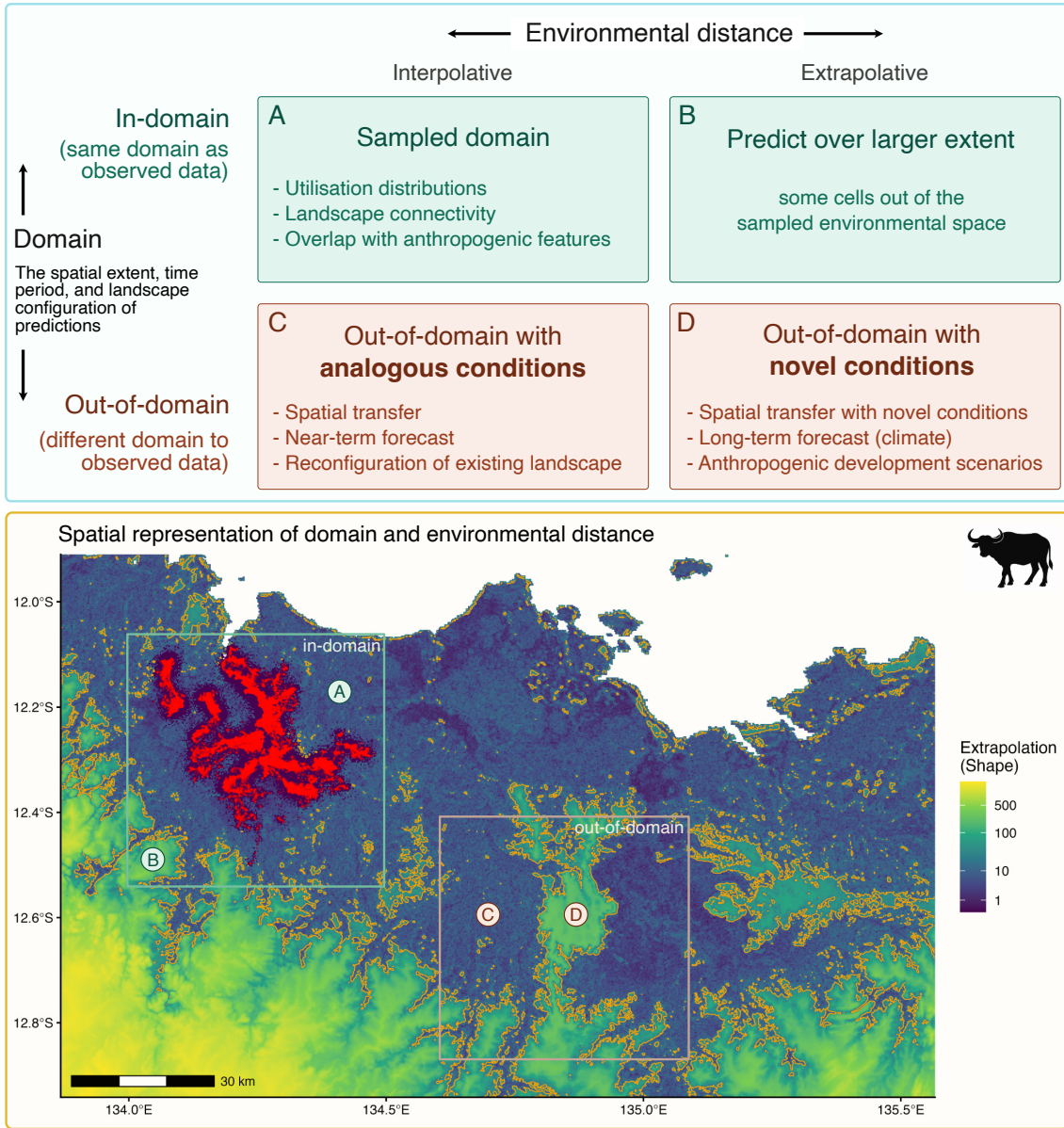


Figure 4: Interplay between the domain and environmental distance of the predictions. In the upper panel, between the rows, in-domain predictions have the same domain (space, time, landscape configuration and taxa) as the observed data, and out-of-domain predictions are different to the observed data in one or more factors, here in geographic space. Across the columns, interpolative predictions have analogous environmental conditions, whereas extrapolative predictions have novel environmental conditions. In the lower panel, we show a spatial representation of environmental distance compared to observed locations (shown as red points) for 14 water buffalo (*Bubalus bubalis*) in northern Australia, as measured by the Shape method (viridis colours, scaled by  $\log(1 + \text{Shape})$ ) (Velazco et al., 2024). We display an illustrative threshold to delineate between interpolative and extrapolative predictions (orange contour). As we show here, a given domain may include both environmentally interpolative and extrapolative cells.

### 3.1.2 Animal-centric and landscape-centric predictions

**Animal-centric** predictions (analogous to Lagrangian; Turchin, 1998; Hooten and Johnson, 2017) focus on the movement behaviour of individual animals in response to a given landscape, such as their distance travelled, home range sizes, energetic expenditure (Cowan et al., 2025), number of intersections with anthropogenic structures like roads (Zeller et al., 2021), or passes around riverine barriers (Mawer, Pauwels, et al., 2023; Mawer et al., 2025). The predicted quantities of

animal-centric predictions are typically not tied to particular spatial locations and result in a single value per trajectory, allowing for the predicted values from multiple simulations to be aggregated into distributions and compared to the observed data, or between different hypothetical scenarios, using statistical tests (Cowan et al., 2025).

**Landscape-centric** predictions (analogous to Eulerian; Turchin, 1998; Hooten and Johnson, 2017), by contrast, focus on a particular part of the landscape, aiming to predict how changes to that part of the landscape might affect animal movement within and through it. Landscape-centric predictions are typically calculated per pixel of the landscape that was simulated over. Examples might be how likely we are to see an individual in a particular pixel (or set of pixels), or, on the population level, how many individuals we are likely to see in that same place at a particular time, i.e., a heatmap (Sells et al., 2022; Dulude-de Broin et al., 2025; Forrest et al., 2025). Other examples might include measures of landscape connectivity such as betweenness (Hofmann et al., 2023; Cowan et al., 2025; Westaway et al., 2025) or inter-patch connectivity (Whittington et al., 2022; Hofmann et al., 2023), or how the construction of anthropogenic structures might affect movement or mortality risk of animals at a location (Aiello et al., 2023; Cappello et al., 2025).

As demonstrated by Cowan et al. (2025), the same or similar model fit and process of simulating trajectories may be used to calculate animal-centric and landscape-centric predictions. We illustrate these concepts using in-domain predictions of northern quolls (*Dasyurus hallucatus*) in an existing mining landscape (Cowan et al., 2025) in Figure 5. Out-of-domain predictions were also generated for this study (not shown in the figure), where alternative hypothetical mining scenarios were generated and the animal- and landscape-centric predictions were compared between scenarios (Figure A8).



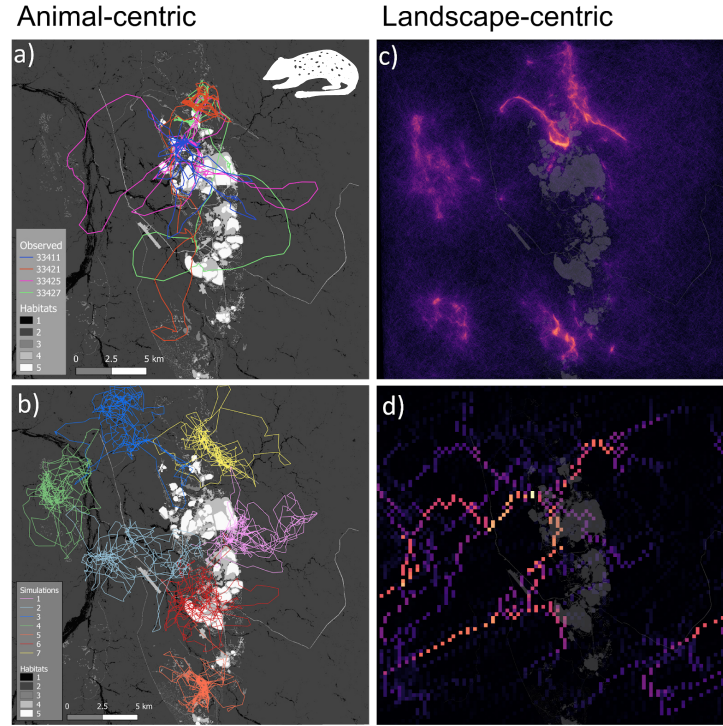


Figure 5: Animal-centric (left) and landscape-centric (right) predictions of northern quolls (*Dasyurus hallucatus*) in an existing mining landscape (Cowan et al., 2025). Observed GPS data are shown in (a), and in (b), a sub-sample of seven simulated trajectories are shown that were used to assess space use, energetic costs, and number of habitat revisitations in the existing mining landscape. Landscape-centric predictions of trajectory location counts per cell (c - heatmap of relative occurrence), and landscape connectivity (d - betweenness) were calculated from 50 simulated trajectories ( $n = 438,000$  steps) and used to assess how landscape context changes through the lens of northern quoll movement. When the animal-centric and landscape-centric predictions were considered together and compared under different mining and non-mining landscape scenarios, a picture appeared of higher energetic costs, reduced habitat connectivity, and altered movement pathways in mining landscapes, with the strongest negative impacts coming from the current mining landscape. Reproduced with permission from Cowan et al. (2025). The northern quoll icon was created by Gabriela Palomo-Munoz, and downloaded from PhyloPic under the <https://creativecommons.org/licenses/by-nc/3.0/> license.

### 3.2 Movement data

The collection of new animal movement data should be driven by the research aim (Figure 6). That is, the type, resolution, and duration of data collection must align with the biological process that the study seeks to capture. At a minimum, parameterising a predictive animal movement model requires sequential, timestamped location data that are, ideally, regularly spaced in time. However, continuous-time models (Hanks et al., 2015; Michelot et al., 2019; McClintock & Lander, 2024; Dupont et al., 2026) may relax the requirement of regularity. There also exists massive amounts of animal tracking data from open databases such as Movebank (Kays et al., 2022), which can be checked for suitable data that may address the research aim.

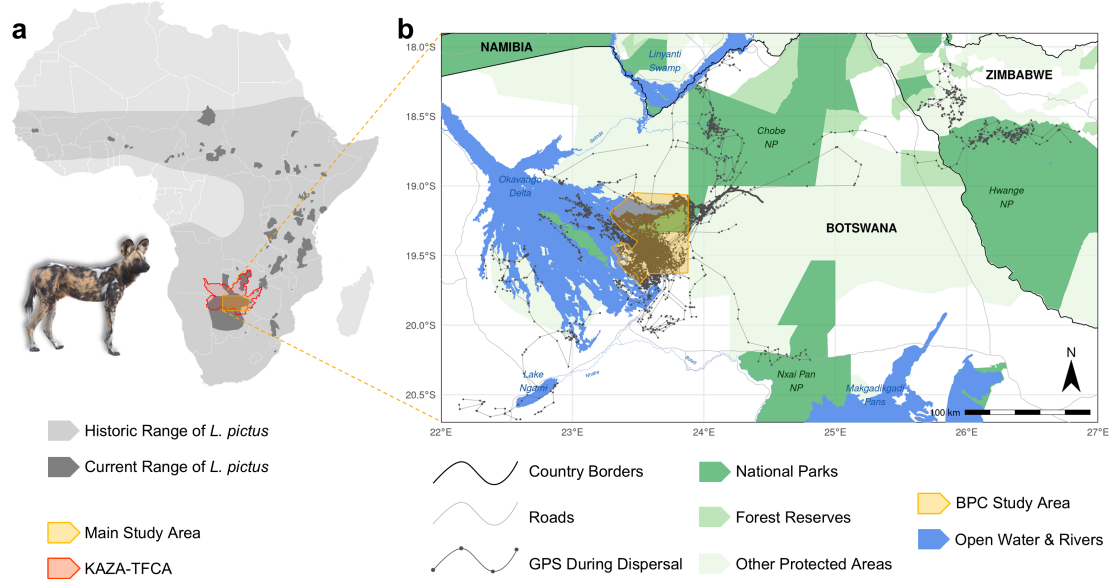


Figure 6: **(a)** The current and historic range of the African wild dogs, and study area and tracking data from the case study in northern Botswana, representing a major stronghold for the species (full details in Supplementary Materials Section A). The area forms part of the Kavango-Zambezi Transfrontier Conservation Area, which encompasses over 520,000 km<sup>2</sup> and spans the countries of Angola, Namibia, Botswana, Zimbabwe, and Zambia. **(b)** Researchers from the Botswana Predator Conservation Program operate in the western part of the Okavango Delta and monitor the local population. Under this program, potential dispersers are equipped with GPS satellite collars and their dispersal trajectories are recorded, thus providing the foundation for simulating dispersal movements using step-selection functions.

### 3.2.1 Temporal resolution

The parameters of discrete-time models depend on the temporal resolution at which movement data are collected (Northrup et al., 2016; Schlägel & Lewis, 2016; Bastille-Rousseau, Murray, et al., 2018; Mitchell et al., 2019; Florko et al., 2025; Signer et al., 2025). In some cases, data can be collected at very high frequencies, sometimes more than once per second (Williams et al., 2020; Nathan et al., 2022). This introduces scale and dependence challenges for predictive modelling due to highly autocorrelated locations, but creates an exciting opportunity for building models based on the precise places animals make decisions to change direction (Potts et al., 2018) using some careful pre-processing and adjustments to the more common discrete-time techniques (Munden et al., 2021; Gupte et al., 2022; Hofmann, Cozzi, & Fieberg, 2024; Alharbi et al., 2025; Forrest, 2026). With such data it is, in principle, possible to infer quite fine-grained details about movement decisions (Gunner et al., 2026). Higher frequency data can also provide a buffer against missing locations, present more opportunities for multi-scale analyses, and can be used to assess the sensitivity of parameter estimates to temporal frequency (Gupte et al., 2022). Conversely, low-frequency data (several hours to days) may extend logger battery life, but often reflect broader-scale space use and habitat-selection patterns. If data are too sparse, there may be little information about the movement process and movement interactions with habitat - which may be critical for predictive targets such as landscape connectivity. In such cases, these targets may be difficult to estimate, leading to important ecological relationships being missed or interpreted inaccurately (Nathan et al., 2022). The balance between capturing temporally-appropriate movements, accounting for the scale of environmental covariates, and obtaining a suitable deployment duration is context-dependent, based on species traits, landscape heterogeneity, technology capacity (e.g. battery



life), and the research aim (Signer et al., 2025).

### 3.2.2 Sampling periods and the representation of behaviours

An additional consideration relates to the behaviours that are captured within the recorded movement data. Recording of locations across all hours should capture periods of movement as well as periods of inactivity, whereas only the periods of movement may be necessary for prediction. Modelling data that contains inactive periods, without properly accounting for them, can obscure species-habitat relationships (Roever et al., 2014), and mischaracterise movement behaviour, as a model’s parameters will reflect averages across the different behaviours. Instead, it may be beneficial to collect data only when the species is active, thereby also preserving battery capacity (such as in Cowan et al., 2025), or to filter data to movement periods (e.g. Dulude-de Broin et al., 2025) using movement rules or behavioural state classification models such as hidden Markov models (HMMs) (Langrock et al., 2012; McClintock et al., 2012). We discuss behavioural state classification, and its use for partitioning data or for direct inclusion in predictive models, in Section 3.5.

## 3.3 Environmental data and other covariates

Questions related to movement data often require characterisation of the movement determinants through spatial covariates (also referred to as predictors, descriptors, explanatory variables, features, or inputs), or interactions with non-spatial covariates (see 3.3.4). These covariates may include measurements of landscape features, such as vegetation types, altitude, or weather; variables related to animal interactions, such as movement costs or the locations of conspecifics, predators, or prey (Ellison, Potts, Boudreau, et al., 2024; Ellison, Potts, Strickland, et al., 2024; Webber et al., 2024); and/or a spatial representation of the animal’s cognitive map (Merkle et al., 2014; Rheault et al., 2021; Kim et al., 2024). Such covariates characterise the spatial makeup of the landscape and contextualise animal movement decisions. They also form the underlying ‘canvas’ upon which movement predictions can be made under observed or novel domains. We do not provide an exhaustive list of spatial covariates here, but provide conceptual considerations for preparing spatial data and how that can affect predictions.

### 3.3.1 Quantifying landscape features

Spatial covariates can be derived from remotely sensed data, such as that from Landsat, Sentinel-2, or other satellites (Wehner et al., 2025), which can facilitate classification of vegetation indexes (e.g., Normalised Difference Vegetation Index [NDVI]) and habitat types. Spatial layers can also be developed from field-collected data, producing layers depicting anthropogenic activity (Oliver et al., 2024; Oliver, Yanco, et al., 2026), landscape feature density (e.g., animal refuges, food resources), and physical (e.g., topography, wind speed, water flow velocity) or climatic variables (e.g., surface temperature, rainfall) (Abrahms et al., 2019; Mawer, Pauwels, et al., 2023; Mawer et al., 2024). Spatial proximity covariates may also be created by measuring the distance of each cell to linear or discrete vectorised features such as fire scars (e.g. Mahood et al., 2022; Pike et al., 2026), rivers, roads, or buildings (Masolele et al., 2026; Potts et al., 2026). Such covariates allow the fitted movement model to estimate whether the animal is ‘attracted’ to or ‘repelled’ from those features (Cowan et al., 2025; Westaway et al., 2025; Masolele et al., 2026). Interacting distance-to

covariates with temporal dynamics can also allow for goal-orientated or flexible behaviour, such as nightly returns to dens by northern quolls (Figure 5, panels a and b (Cowan et al., 2025)). Cost and energy surfaces can also be used as covariates in simulations to assess how the predicted cost of movement affects movement patterns or energy expenditure (Klappstein et al., 2022). Spatial covariates are usually represented as rasters – i.e., they have discrete spatial cells that cover the spatial and temporal extent of the tracking data. The spatial resolution (cell size) of rasters should relate to the scale of movement (including spatial error), such that both successive and randomly sampled steps mostly fall into cells with different values. Examples of satellite-derived and modelled spatial covariates is shown in Figure 7.

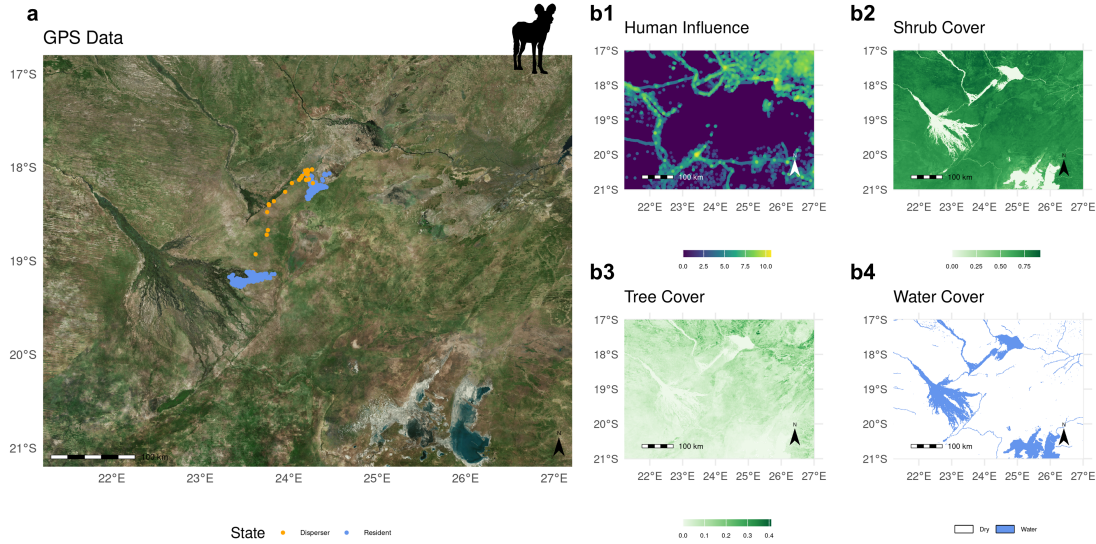


Figure 7: Visualization of spatial data used in the African wild dog case study (see Supplementary Materials Section A). (a) a track of one African wild dog is shown here. Only data during dispersal (orange portion) were assumed pertinent to connectivity and thus considered for further analyses. (b) Observed dispersal movements were linked to the environment via a series of spatially mapped covariate layers, including data on human influence, shrub and tree cover, as well as water cover. Some layers were prepared as time-series layers to capture seasonal dynamics. The water cover layer (b4), for instance, was updated every week using remote sensed MODIS imagery to obtain accurate representations of the distribution of surface water in the ecosystem. Besides the depicted spatial layers, non-spatial covariates, such as temperature and light availability, were also used.

### 3.3.2 Memory and social interactions

Spatial raster layers may be created directly from the observed tracking data of the focal individual or its neighbouring individuals. The density of previous space use (Avgar et al., 2013, 2015; Merkle et al., 2017; Rheault et al., 2021; Thompson et al., 2022) and time-since-last-visit (to that cell; Schlägel and Lewis, 2014) can be used to approximate memory (Kim et al., 2024), and the space use (Potts, Giunta, & Lewis, 2022; Ellison, Potts, Boudreau, et al., 2024; Ellison, Potts, Strickland, et al., 2024), proximity (Webber et al., 2024), and alignment (Merkle et al., 2024) with conspecifics can describe the spatial-social interface (Webber et al., 2023; Albery et al., 2024). Inclusion of such covariates enables simulations to better mimic home-ranging behaviours, dispersal, or intra-species interactions captured by the observed data. Predominately, the inclusion of covariates that represent memory and social interactions have been used for explanatory purposes, but there are recent examples of their use in applied predictive applications (Cowan et al., 2025; Pollock et al., 2026). A consideration when simulating with a memory process is that the memory covariate (e.g., previous space use) must be continuously updated, which presents technical and computational

challenges, and for social interactions, concurrent individuals would need to be simulated. Using a lattice-based version of the model (Potts, Börger, et al., 2022) may be useful here, as animals may detect conspecifics at any point along a step, rather than just at the end locations which are typically simulated (Ellison, Potts, Boudreau, et al., 2024).

### 3.3.3 Spatial non-locality

Many studies extract covariates at the raster’s native resolution at point locations, which assumes that an animal selects its next step based on the local habitat type at that point. However, animals may select for some features based on the broader landscape context around it – e.g., forest being embedded in a large, integrated patch vs. a small, isolated fragment, or for soaring birds that respond to broad-scale landscape features such as mountain ranges or habitat composition (Pay et al., 2025). Topographic Position Index (TPI), which calculates the relative elevation of a pixel compared to others within an enclosing buffer, is an example of a covariate that is often explored at different scales. The effects of spatial scale and non-locality, and multi-scale models, have been explored for habitat selection (Mayor et al., 2009; Zeller et al., 2014; McGarigal et al., 2016) and species distribution modelling (Riva et al., 2024), but there have been fewer applications for movement models (but see Bastille-Rousseau, Murray, et al., 2018; Masolele et al., 2026). Some modelling structures naturally incorporate multiple spatial scales of selection (Michelot et al., 2019; Michelot, 2024), while others use model structures such as convolutional layers to accommodate the broader landscape context beyond single raster cells (Forrest et al., 2026).

### 3.3.4 Dynamic and non-spatial covariates

The environment that animals inhabit is constantly changing. Some variables can be considered constant across some time-scales (e.g., elevation), but others like daily temperature averages or monthly NDVI will change seasonally. It is therefore vital to match the covariates to the period over which data were collected, and to the spatio-temporal scale at which the studied process unfolds. Covariates that vary across time rather than space can capture large changes in an animal’s movement behaviour, either directly or through associations with other, unmeasured variables. Across a diel cycle, there are changes in light and temperature that drive predictable rhythmic behaviour in many animals (Ouled-Cheikh et al., 2020; Richter et al., 2020; Toro-Cardona et al., 2023). This variability can be accounted for by including time of day (or solar time) as a proxy (Richter et al., 2020; Forrest et al., 2025). For variables that change seasonally (e.g., NDVI, snowpack), it can be straightforward to directly include the covariate as it changes across the year (Merkle et al., 2016; Bowersock et al., 2023), although interacting the time of year (e.g., day of year, month, season) with spatial covariates may capture unobserved variability in other factors across the yearly cycle, such as a dynamic relationship to elevation across seasons (John et al., 2024). It should be noted that any non-spatial variables such as time will be constant within a set of used and random steps (a ‘strata’), meaning that parameters can only be estimated by interacting them with spatial covariates. We provide more information on fitting models with temporal dynamics in Section 3.5.

### 3.3.5 Predictive accuracy and interpretability

Predictive accuracy describes how closely predictions match observed data, and interpretability (or explainability) is the ability to understand why the model gave those predictions. Often, there exists a trade-off between predictive accuracy and interpretability (Breiman, 2001b; Shmueli, 2010), which is a product of both the structure of the model and the complexity of the covariates. For instance, complex deep learning models fitted to raw satellite bands (Sentinel-2 satellite contains 13 bands/layers of different spectral wavelengths) can provide high predictive accuracy (Forrest et al., 2026), but the ‘black box’ nature of these models, which include many modelled interactions, can make it difficult to understand the ecological mechanisms responsible for the predictions (Leblanc, 2023). On the other hand, other satellite-derived covariates can be more intuitive, such as NDVI, which captures ‘environmental greenness’, with higher values indicating higher productivity (Reed et al., 1994; Pettorelli et al., 2011). A simple SSF fitted to only NDVI will provide an interpretable coefficient indicating the animal’s response to environmental greenness, but the information that was contained in the other bands is lost by excluding them. Additionally, layers created using field-collected data, such as the locations of tree cavities or daily temperature, may provide very useful and interpretable insights into a species’ behaviour, but have high collection effort and can often only be predicted for the space and time that data for those covariates have been collected, limiting their applicability for out-of-domain predictions. We can therefore consider a conceptual (and approximate) relationship between how much information the covariates contain, which will reduce as they are processed into simpler layers, and how interpretable the model’s responses will be (Figure A7).

## 3.4 Data exploration

Data exploration, including cleaning and preparation for modelling, is a vital step in any analytical protocol (Zuur et al., 2010). For predictive movement ecology, data exploration can be used to build intuition about movement and habitat processes that may help to guide model development and match predictions to observed data, noting that some data should be withheld such that it can remain unseen and be used for model validation and testing (see Section 3.7). Much can be learned about the data by plotting it spatially using R or GIS software, or by creating movement animations using tools like `moveVis` (Schwalb-Willmann et al., 2020), `ECODATA` (Missik et al., 2025) or `trajVis` (<https://internetofelephants.github.io/trajvis/>). Data exploration allows missing locations and irregularities to be identified and the steps taken to account for them; for instance, splitting tracks into sequences of temporally regular locations (called ‘bursts’) when fitting the model to account for irregular sampling or missed locations, or interpolating or imputing missing locations (McClintock, 2017; Hofmann, Cozzi, & Fieberg, 2024). Movement data should also be cleaned to remove spurious locations and ensure data quality. Methods differ, but to facilitate SSFs for prediction, data cleaning should be robust and reproducible, discarding major location errors while retaining valid movement information (Bjørneraas et al., 2010; Shimada et al., 2012; Forrest et al., 2022; Gupte et al., 2022).

Further exploration, including assessment of step length and turn angle distributions, can also reveal behavioural patterns, such as multimodality in step lengths that imply multiple behavioural states, and can help determine which distributions are appropriate for modelling step length and turn angles (Figure 8) (Signer et al., 2019). Visualising correlations between step lengths and turn angles can help to assess whether the correlation between them needs to be explicitly modelled

(Hodel & Fieberg, 2022), or if a flexible movement kernel would be appropriate (Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024; Arce Guillen et al., 2025). Assessing the distribution, mean, and quantiles of step lengths and/or covariate values (against the background distribution) at different temporal scales (i.e. within days or between months) can also reveal temporal patterns, from fine-scale daily patterns to seasonal changes in movement or habitat selection (Richter et al., 2020; Forrest et al., 2025). The added context that data exploration allows means that movement predictions are more likely to incorporate biologically meaningful information that may help to ensure realistic predictions, but users should be wary of overfitting.

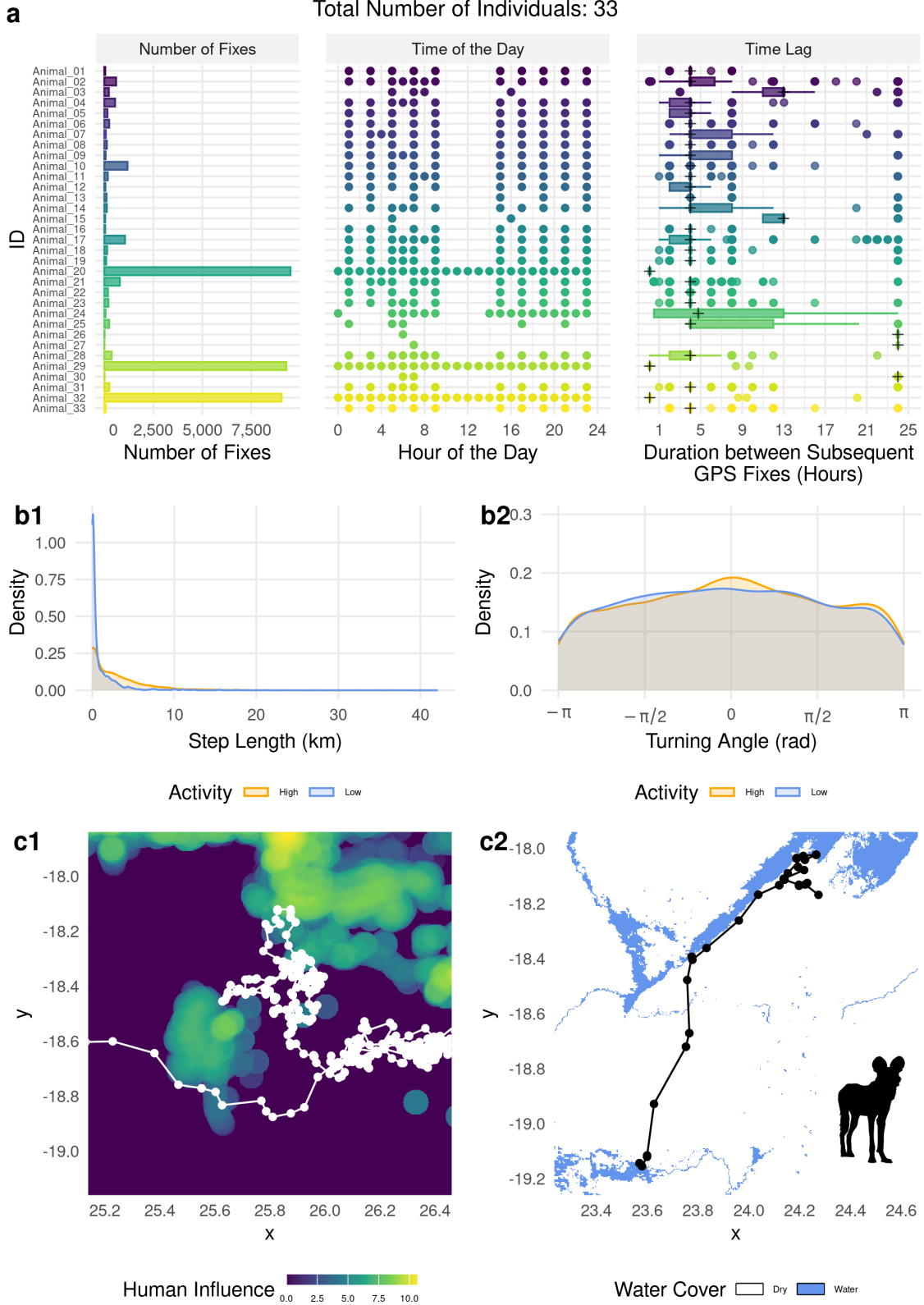


Figure 8: (a) GPS data from collared African wild dogs were examined to determine the number of fixes per animal, time of day at which GPS fixes were obtained, and the duration between subsequent fixes (see Supplementary Materials Section A). (b) Based on the regularized data, movement metrics, such as step lengths (b1) and turn angles (b2) were derived, providing initial insights into the movement characteristics of dispersing wild dogs. (c) Overlaying observed dispersal paths with environmental covariates facilitated an intuition for preferred and avoided covariates, e.g. avoidance of human settlements (c1, dispersal path in white) and water (c2, dispersal path in black).



### 3.4.1 Data preparation for model fitting

In step-selection frameworks, model fitting is usually achieved by comparing observed movement steps to randomly sampled proposal steps (often called ‘available’ steps), allowing the model to learn how movement decisions are shaped by factors such as directional persistence, habitat selection, behavioural processes, and environmental variability (Thurfjell et al., 2014; Fieberg et al., 2021; Michelot et al., 2024). Once proposed steps have been sampled for movement modelling, there are choices about whether to extract covariate values at the start, end, or along each observed/proposed step, and how constraints such as barriers and inaccessible habitat can be included. Typically, for independent estimation of the movement kernel and habitat selection process, it is sufficient to sample covariate values only at the end of each step, but for movement-habitat interactions (described in Section 3.5.2), covariate values are usually extracted at the start of each step, as it is the animal’s current location that influences how the animal will move. It is also possible to extract covariate values along each step (noting that the true path between locations is unobserved), which allows for the inclusion of features that might act as barriers (Signer et al., 2023), and can also be used to relate a movement cost or penalty to each step, which may be particularly important for generating realistic and accurate estimates of landscape connectivity. For example, Hofmann et al. (2023) computed averages of each habitat covariate along each step, resulting in slower movements when traversing areas that were inundated with water. Furthermore, the `permeability` package presents an alternative approach to estimating the permeability of potential barriers by allowing for a movement kernel to be distorted to varying degrees (Barbour et al., 2026).

## 3.5 Building movement models

The goal at this stage is to combine the processed animal movement data with the environmental covariates to build a movement model that describes how animals move through landscapes and respond to a range of environmental conditions. Once parameterised, these models can be used to simulate realistic movement trajectories and predict ecological outcomes across space and time. Building on the description of step-selection models in Section 2.1, there are a number of conceptual and practical considerations to help ensure that predictions address the question of interest. The same covariates can be formulated and included in a movement model in various ways, most of which will influence simulated trajectories and the resulting prediction outputs. Different approaches may therefore be better suited to specific applications.

Model parameterisations may include quadratic or smooth non-linear covariate terms (Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024), temporal variability (Forrest et al., 2025), or multiple behavioural states (Klappstein et al., 2023; Pohle et al., 2024). These additions increase model complexity and degrees of freedom, thereby enabling more flexible representations of the relationship between the animal and its environment, and potentially improving the realism of simulated trajectories (Figure 9). However, given their increased complexity, these model formulations typically require more data, can make the models more challenging to fit in terms of computation and statistical convergence, and increase the risk of overfitting - where the model learns behaviours that are specific to particular individuals, populations or environmental contexts that do not generalise to unsampled domains. We discuss these considerations in Section 3.5.1, but recommend exploring different model formulations, and stress the importance of validating each model’s predictions, particularly by using withheld individuals (see Section 3.7 for more details).



Animal movement and habitat selection vary depending on the behavioural mode that individuals exhibit. As described in Section 3.2.2, tracking data can also capture periods of inactivity, which can be filtered out, or alternatively modelled as periods with little movement, explicitly accounting for behavioural heterogeneity. Directly modelling inactive behaviours can be achieved by incorporating temporal dynamics to allow continuous behavioural variability across time (Richter et al., 2020; Forrest et al., 2025), or by modelling discrete behavioural states (Klappstein et al., 2023; Pohle et al., 2024). For instance, Dulude-de Broin et al. (2025) used an HMM to filter out inactive data, resulting in bursts of active movement data, to which an SSF was fitted and then used for prediction, whereas Klappstein et al. (2023) fitted and simulated from an SSF that estimated the parameters for multiple behavioural states. We discuss this in more detail in Section 3.5.4.

### 3.5.1 Movement and habitat selection formulations

There are a number of ways to specify the relationship between the animal and its surrounding environment (represented as covariates), which can affect predictions. These different relationships can be captured via response curves, particularly in relation to their shape and flexibility of the response across the range of a (continuous) covariate. The simplest and most common response is a log-linear term, which for a single covariate (e.g. NDVI) is specified as  $\omega(s_{t+1}) \sim \exp(\beta_{ndvi} X_{ndvi}(s_{t+1}))$ , and the coefficient is interpreted as selection for higher values of NDVI when there is a positive coefficient (and vice versa). A more flexible parameterisation is a quadratic term, specified as  $\omega(s_{t+1}) \sim \exp(\beta_{ndvi} X_{ndvi}(s_{t+1}) + \beta_{ndvi^2} X_{ndvi}^2(s_{t+1}))$ . A quadratic response can account for situations where animals tend to select for or against intermediate values of a covariate (if  $\beta_{ndvi^2} < 0$  or  $\beta_{ndvi^2} > 0$ , respectively). To provide more flexibility in the response curve, smooth terms can also be applied for non-linear relationships, allowing for responses such as multimodal peaks within the range of a covariate (Klappstein, Michelot, Fieberg, Pedersen, Field, & Flemming, 2024). Smooth terms comprise of a number of basis functions that are summed, and can be specified using the `mgcv` package using  $\omega(s_{t+1}) \sim s(X_{ndvi})$  (Wood, 2011; Klappstein, Michelot, Fieberg, Pedersen, Field, & Flemming, 2024). Smooth terms can also be applied to produce flexible movement kernels, relaxing the need for parametric distributions and also allowing for correlation between step lengths and turn angles (Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024; Michelot et al., 2024; Arce Guillen et al., 2025). An additional benefit of using smooth terms is that they can be used as a spatial random effect to account for spatial variability that otherwise is not accounted for by the covariates included in the model (Arce Guillen et al., 2023; Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024). This may lead to less biased parameter estimates, thereby improving prediction accuracy when generating extrapolative predictions (Dormann, 2007; Kühn, 2007; Patterson et al., 2025), but care needs to be taken to ensure that the spatial random effect does not confound the effect of the covariates, masking the true effect (Hodges & Reich, 2010; Hui et al., 2024).

In Figure 9, we show choices of different formulations for a single covariate, NDVI, that was fitted to the GPS tracking data of a single water buffalo (*Bubalus bubalis*) and how the different response curves affect selection patterns.

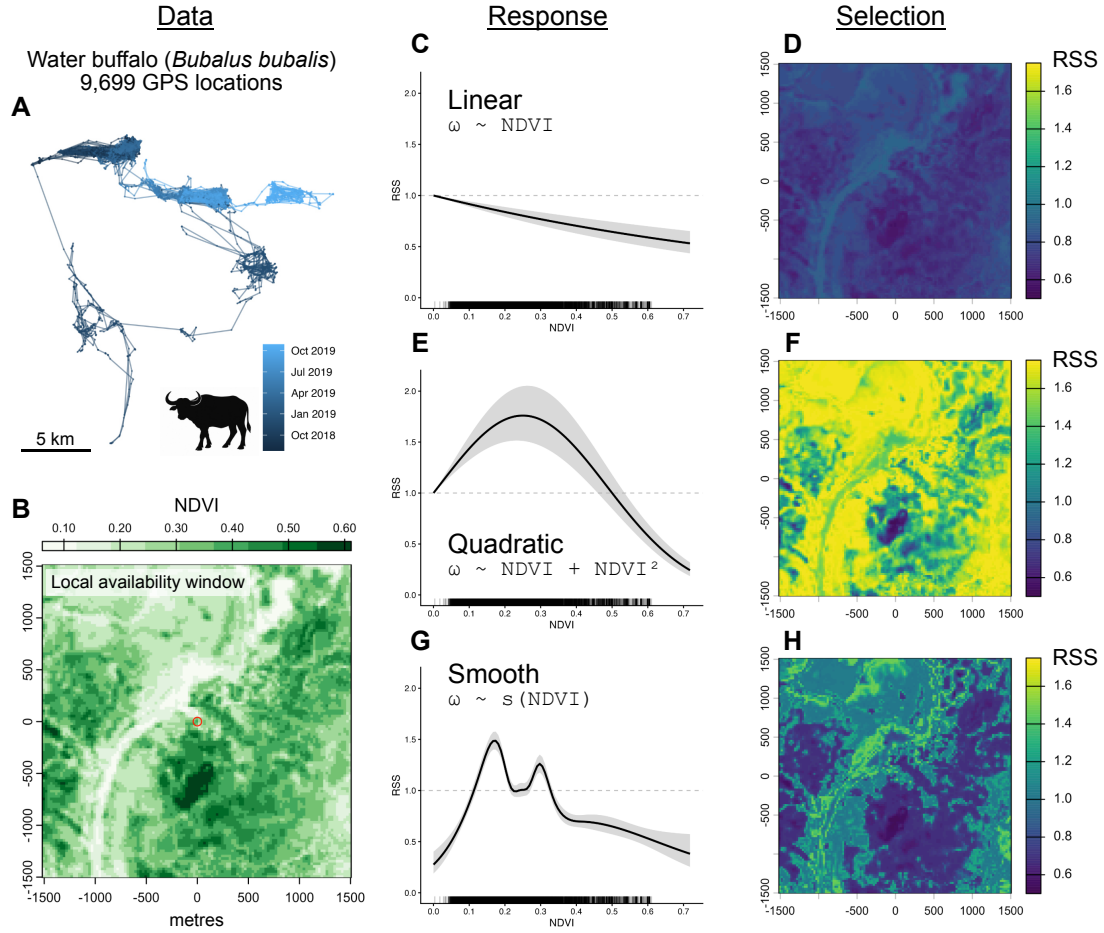


Figure 9: Different formulations of the habitat selection process for a single covariate, Normalised Difference Vegetation Index (NDVI), and how that affects Relative Selection Strength (RSS; Avgar et al., 2017). We show NDVI included as a linear, quadratic, or smooth term fitted to hourly GPS tracking data of a single water buffalo (*Bubalus bubalis*) (Panel A), with the response curve and the habitat selection predictions for the next step. In Panel B we show the NDVI values of the local availability window for a single step, which is analogous to Panel B in Figure 1. The linear response (Panels C and D) shows selection for lower values of NDVI, whereas the quadratic response (Panels E and F) shows selection for intermediate values centred around  $\text{NDVI} = 0.25$ . The more flexible smooth response (Panels G and H) shows peaks of selection around  $\text{NDVI} = 0.2$  and  $\text{NDVI} = 0.3$ . The different response curves will result in different predictions, highlighting the importance of validation for assessing prediction accuracy across individuals. In Panels C, E and G we include rug plots to show the distribution of the GPS data across the range of NDVI. We provide the code used to fit these models and generate the figures at [https://swforrest.github.io/predictive\\_movement\\_ecology/](https://swforrest.github.io/predictive_movement_ecology/).

To give even more flexibility, deep learning approaches have recently been used to model the response curves in SSFs, with multilayer perceptrons allowing for highly flexible and non-linear functions that naturally model interactions between the covariates (Fronville et al., 2026). Convolutional layers have been used to capture landscape features that are comprised of multiple pixels (i.e. non-local effects) (Forrest et al., 2026), and transformers to better represent autocorrelation in movement (Cířka et al., 2023). Deep learning models have the additional benefit of requiring minimal *a priori* specification of the functional forms, and will learn to replicate patterns present in the observed data, including hitherto difficult-to-model behaviours such as multi-scale temporal dynamics (e.g. daily cycles that vary seasonally). In species distribution modelling, high predictive performance has been gained from fitting an ensemble of models, which combine the different structural properties of each model (Valavi et al., 2022). A similar process could be followed for the habitat selection process of an SSF, and potentially also the movement kernel if models are

fit using customised likelihoods that explicitly account for how the random points were generated. The same set of observed and proposed locations could be used to fit and predict from a number of models, possibly including machine learning approaches (Rieber et al., 2024), including random forests (Breiman, 2001a) and extreme gradient boosting, XGBoost (Chen & Guestrin, 2016), which are very common for species distribution models but are currently underutilised in movement ecology.

### 3.5.2 Interacting movement and habitat selection parameters

An animal’s observed movement behaviour can be viewed as the result of two intertwined behavioural processes: the animal’s movement kernel and its habitat-selection function (Avgar et al., 2016; Signer et al., 2023). While early movement models often treated these processes as independent when estimating parameters (e.g. Fortin et al., 2005), later frameworks introduced methods to incorporate their interdependencies, allowing for more realistic movement behaviour which can influence animal space use (Potts et al., 2014; Avgar et al., 2016). SSF models are able to incorporate interactions between habitat covariates and movement parameters, such as those defining step lengths and turn angles, describing the influence of external factors on movement behaviour (i.e. slower movement through deep snow, or faster and more directed movement in grassland compared to forest; Fieberg et al., 2021; Pike et al., 2026). This interaction will affect space use predictions (Potts et al., 2014) and may be particularly relevant to connectivity studies. For example, Hofmann et al. (2023) demonstrated that dispersing African wild dogs exhibit slower and more tortuous movements when traversing areas inundated by water, which significantly affects their dispersal propensity and the time required to move between areas.

### 3.5.3 Temporal dynamics

Animal movement and habitat-selection behaviour may change through time (Ouled-Cheikh et al., 2020; Richter et al., 2020; Toro-Cardona et al., 2023), and incorporating temporal dynamics may be important for simulating realistic behaviours. Forrest et al. (2025) showed that for water buffalo, incorporating fine-scale (i.e., hourly) temporal dynamics on the movement and habitat-selection processes allowed for hourly utilisation distributions of buffalo, potentially enabling more targeted management practices, which also resulted in more accurate long-term predictions (as temporally dynamic behaviours were not being averaged out across the day). Computing independent utilisation distributions for each time period from a fitted selection model (e.g. using an analytic approach; Potts and Börger, 2023; Rogers et al., 2025; Ellison-Neary et al., 2026) may not yield correct time-specific utilisation distributions, because habitat availability is conditional on the animal’s locations in preceding periods. In this case, it is straightforward to simulate trajectories with temporal variability in the parameter estimates, which can be used to produce time-specific UD<sub>s</sub> (noting that many simulations may be required, as the predictive outputs need to converge for the time of interest). Additionally, for predictions of landscape connectivity, capturing cyclic temporal changes across daily timescales may ensure that simulated paths go through landscapes that would otherwise be ignored when using a static model (Cowan et al., 2025).

Temporal dynamics can be incorporated into SSFs in several ways. Time can interact with movement parameters, spatial covariates relating to external environment or social interactions (such as to model fission-fusion dynamics), internal processes such as memory (Cowan et al., 2025), or all of the above. There are also multiple choices for how they are incorporated, such as by interacting

movement and/or habitat-selection covariates with harmonics (pairs of additive sine and cosine terms) (Forester et al., 2009; Forrest et al., 2025), or by using smooth terms (Klappstein, Michot, Fieberg, Pedersen, & Mills Flemming, 2024). In Figure 10, we show different approaches of incorporating temporal dynamics on the habitat selection of a single covariate. A similar process can be followed to include temporal dynamics on the movement parameters, allowing for dynamic movement kernels which change across time as the animal’s movement behaviour changes (Forrest et al., 2025).

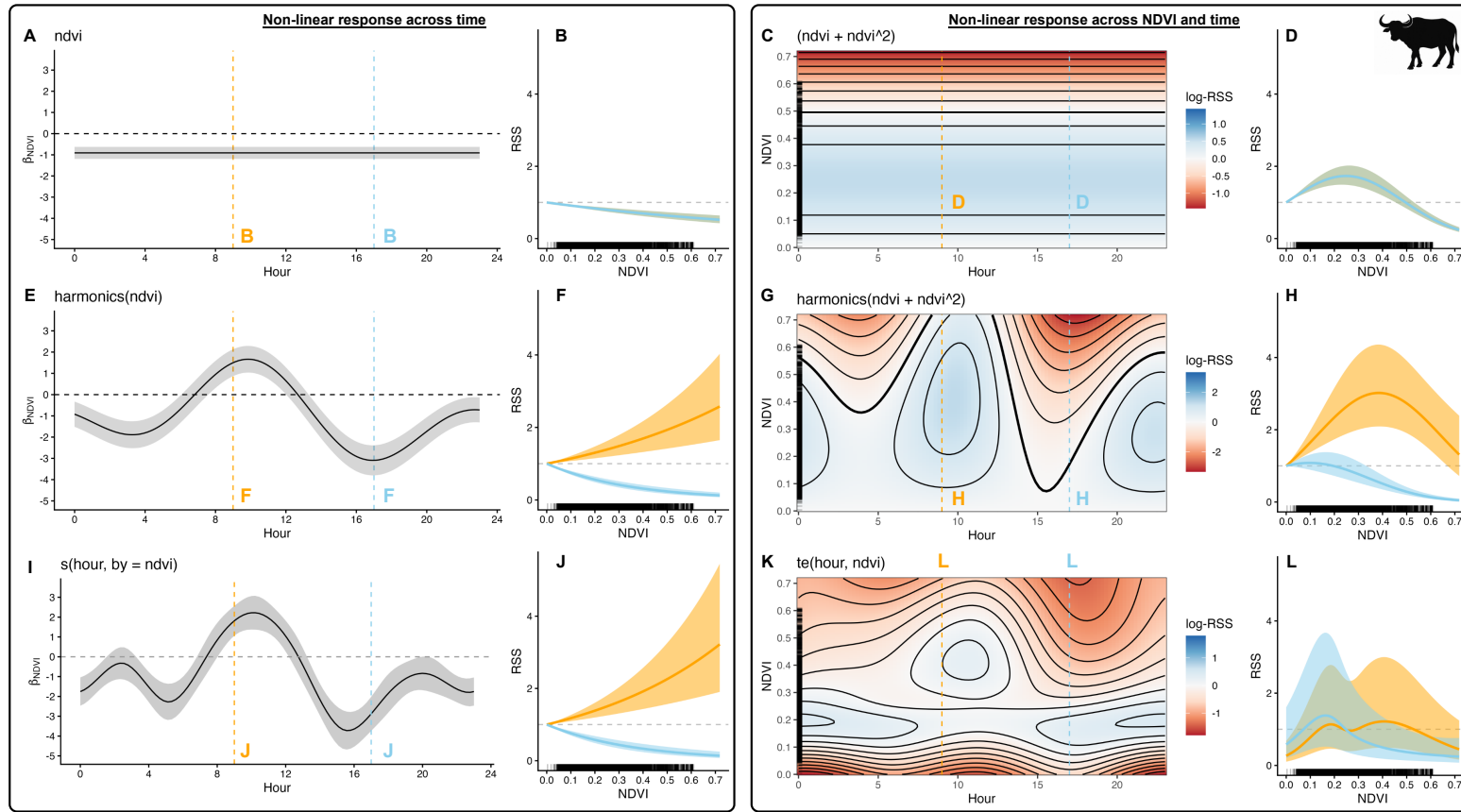


Figure 10: Different formulations of temporal dynamics for selection of a single covariate, Normalised Difference Vegetation Index (NDVI), fitted to the same data as in Figure 9. The top row of plots (A, B, C, D) does not have temporal dynamics, the middle row (E, F, G, H) incorporates temporal dynamics using harmonic terms, and the bottom row (I, J, K, L) by using time-varying smooth with cyclic cubic regression splines ( $\text{bs} = \text{"cc"}$ ). To interpret these plots, we can read across the hours of the day, with continuously changing response curves. The plots with the orange and blue curves are realisations of the RSS at hour = 9 (orange) and 17 (blue). The left block of plots have non-linearity only across the time axis (except for A), resulting in linear response curves. The right block of plots have non-linearity across time and across the range of NDVI, such as in Figure 9E and 9G. Panels C and G use quadratics across NDVI, and K uses a tensor smooth for the hours of the day ( $\text{bs} = \text{"cc"}$ ) and across the range of NDVI ( $\text{bs} = \text{"cr"}$ ). The selection surfaces in C, G and K give a log-RSS value for each NDVI-hour combination, with blue values indicating selection and red values indicating avoidance. Overall, there was positive selection for NDVI in the middle of the day for all models except for those that ignore temporal dynamics (top row), and avoidance of higher values at other times of the day. The selection for NDVI is smoothed by the static model to the average response across the day (Panel A), obscuring inference and reducing predictive accuracy. We provide the code used to fit these models and generate the figures at [https://swforrest.github.io/predictive\\_movement\\_ecology/](https://swforrest.github.io/predictive_movement_ecology/).

### 3.5.4 Step-selection models with discrete behavioural states - HMM-SSFs

Movement and habitat selection varies due to the behaviour that the animal is exhibiting (Roever et al., 2014; Abrahms et al., 2016; Suraci et al., 2019). These behaviours may vary continuously and predictably with time, which we could capture with temporal dynamics (Forrest et al., 2025), or there may be well-defined and discrete behaviours, such as encamped and exploratory movements (Morales et al., 2004), which we might model with **behavioural states**. In this case, it would be appropriate to use a model that allows for state-switching dynamics, such as a hidden Markov model (HMM) (Langrock et al., 2012; McClintock et al., 2012). However, in their typical implementation, habitat covariates are incorporated into HMMs via the state-switching probabilities (i.e. the state-transition matrix) or by influencing the movement parameters within each state. Simulated trajectories from HMMs therefore do not have a bias component (there are no proposal steps to be selected from), and simulations do not add any novel information that cannot be obtained analytically. But, it is possible to combine SSFs with state-switching dynamics, such that there are different sets of movement and habitat selection parameters for each behavioural state (Nicosia et al., 2017; Prima et al., 2022; Klappstein et al., 2023; Pohle et al., 2024).

There are multiple approaches to incorporating state-switching dynamics into movement models. It is possible to use a two-step process, where behavioural states are inferred from the movement information alone (typically the distributions of step lengths and turn angles), and then separate SSFs are fitted to the data of each behavioural state (Roever et al., 2014; Abrahms et al., 2016; Suraci et al., 2019; Picardi, Coates, et al., 2022; Beumer et al., 2023). This approach may be preferable when there is only a single state that is of interest for generating predictions, such as when an animal is actively moving (Dulude-de Broin et al., 2025). Another approach is to employ HMM-SSFs and estimate the state transitions and selection coefficients jointly (Nicosia et al., 2017; Prima et al., 2022; Klappstein et al., 2023; Pohle et al., 2024), which allows habitat selection behaviour to influence the state classification (e.g. courtship behaviour and foraging may have similar movement characteristics, but occur in different habitats) and also incorporates the state-classification uncertainty into the SSF component (Klappstein et al., 2023; Pohle et al., 2024). This approach allows for a more integrated approach to generating predictions that captures all aspects of behaviour that were recorded during tracking, potentially allowing for simulated trajectories to have more realistic behaviours. Klappstein et al. (2023) exemplified behaviour-aware space use by simulating trajectories from an HMM-SSF to generate a UD for both behaviours combined, which could also be separated into state-specific UDs.

### 3.5.5 Movement models in continuous-time

The interpretation of discrete-time movement models, such as step-selection functions, is tied to the time interval of the locations. Simulating from such a model over a long time period can somewhat attenuate this limitation, as the prediction outputs can provide insights at larger spatio-temporal scales than the scale of observation (e.g. long-term distributions). Continuous-time models circumvent this problem altogether, as their parameters are independent of timescale. In continuous time, it is also straightforward to simulate at a finer (or coarser) resolution than the observation interval, which can be important if fine-scale events are of interest (e.g. close contact between two individuals). Although we do not elaborate here, there have been many valuable contributions to fitting and predicting from continuous-time movement models (Hooten et al., 2010; Hanks et al., 2011, 2015; Blackwell et al., 2016; McClintock & Lander, 2024; Dupont et al., 2026), and earlier work is described in Hooten et al. (2017). In general, continuous-time models of

habitat selection have been under-utilised, but recent work has proposed using diffusion processes from physics, such as Langevin diffusion or switching Ornstein–Uhlenbeck processes, to model animals’ movement decisions in response to their environment (Michelot et al., 2019; Wang et al., 2019; McClintock & Lander, 2024; Michelot, 2024; Dupont et al., 2026).

### 3.6 Simulations and predictive outputs

As described in Section 2.2.1, once a model has been fitted, it is typically straightforward to generate simulations, but there are a number of choices to consider. These general recommendations apply to both in-domain and out-of-domain predictions, although more consideration regarding the degree of extrapolation may be required for out-of-domain predictions.

The typical process for simulating from an SSF is that a starting location is selected and proposal steps are randomly sampled using the same process as was used to generate the proposal steps prior to model fitting, i.e. using the same sampling distribution (e.g., gamma/von Mises for importance sampling, or a disc for uniform sampling), and the same number of proposal steps. To match with model fitting, covariate values are extracted at the start, end, or along each step, and each step is assigned a selection weight based on the model’s formula and estimated coefficients. It is also possible to sample the proposed steps from the movement kernel that has been ‘updated’ following model fitting (Avgar et al., 2016; Fieberg et al., 2021; Klappstein, Michelot, Fieberg, Pedersen, & Mills Flemming, 2024), and then ignore the movement coefficients when calculating the probability weights. One step is probabilistically selected based on these weights, which becomes the starting point for the next step. The process repeats until a trajectory of specified length has been generated. There are functions in the `amt` package (Signer et al., 2019; Signer et al., 2023) for generating simulations, although more complicated models may need custom code.

#### 3.6.1 Simulation parameters and considerations

##### Prediction domain

The prediction domain is the space and time that are simulated over. In-domain predictions will cover the spatial extent, time period, and landscape configuration that the data were collected from, and most of the domain should be interpolative (in environmental space - see Section 3.1.1). If the spatial or temporal extent extends to be larger than what the data were collected from, predictions in some areas or times may be considered extrapolative. We discuss approaches for assessing the degree of extrapolation, and other information for generating out-of-domain predictions, in Section 3.8.

##### Boundary conditions

Boundary conditions denote what happens when simulations reach the edge of the prediction extent. Common boundary conditions are **hard/reflective**, where any proposal steps that fall outside the prediction extent are assigned zero probability of selection (Cowan et al., 2025); **wrapped/toroid**, where any proposal steps wrap to the other side of the landscape (Forrest et al., 2025); or a **buffer**, where the prediction extent is expanded, and the added area receives randomised covariate values, such that agents can leave and return to the study area (Koen et al., 2010; Hofmann et al., 2023).

##### Starting locations



Depending on the aims of the study and predictions, starting locations may be sampled from the observed data, or randomly from across the prediction extent. Where the simulations are attempting to replicate the observed data, such as home range sizes under different scenarios, it makes sense to start at the focal individual's first location. For landscape-centric predictions that attempt to fill the prediction domain, randomly distributed starting points across the landscape should ensure coverage. If the starting locations are random, then the simulated trajectories may require a 'warm-up' (also called 'burn-in') period (typically several hundred locations), which are then discarded, to reduce any bias towards the starting locations.

### **Number of simulated trajectories**

The number of simulated trajectories will vary widely depending on the question, spatial extent and resolution, and whether animal-centric or landscape-centric predictions are being targeted. More trajectories will typically be required for landscape-centric predictions, as the predicted value in each cell needs to converge, so it may be preferable to simulate the probability surfaces instead of using stochastic agent-based simulations. Some processes, such as memory, will have a stronger dependence on the starting locations, and if the goal is for the simulated individuals to fully explore a landscape, there may need to be more simulations from more starting locations to ensure coverage.

### **Number of steps per trajectory**

The number of steps within each trajectory may relate to the number of steps in the observed data, such as if the simulations are attempting to replicate observed patterns or cover a discrete time period, such as a year to cover seasonal variability. Otherwise, the number of simulated locations per trajectory is arbitrary. A benefit of simulating a large number of trajectories with fewer locations (as opposed to few trajectories with many locations), is that many trajectories can be run in parallel (unless there are social interactions).

### **Convergence**

Convergence is achieved when adding new simulated locations does not change the predicted quantities within some tolerance threshold. For animal-centric predictions, this may be the average home range size under a given set of conditions or average energetic expenditure per trajectory. For landscape-centric predictions, convergence may be assessed using randomly distributed checkpoints (Hofmann et al., 2023). Allowing for the considerations mentioned above, convergence may be achieved by adding more simulated trajectories and/or running each trajectory for longer, or alternatively, directly simulating a probability surface.

## **3.6.2 Computational considerations**

A considerable constraint for generating simulations is the amount of computation time required. Simulating movement over large spatial extents at high spatial resolution will impose much heavier computational requirements than a study looking at small areas with coarse spatial resolution. A higher number of simulated locations will also be required when targeting temporally dynamic or state-specific predictions, as the predictions need to converge for each time period or behavioural state of interest. It will vary based on the study system and predictive quantities being targeted, but for landscape-centric predictions, an average of 10s to 100s of simulated locations may be required for each raster cell in the spatial prediction extent: a 10 km x 10 km extent at 25 m x 25 m cell resolution has 160,000 raster cells, which may then require millions of simulated locations. These requirements will be much less for animal-centric predictions, but the computational cost

should be carefully considered. Given that, there are approaches to reduce the computational burden, such as using kernel-based (KDE/AKDE; Worton, 1989; Fleming et al., 2015) methods on the simulated locations to estimate UD, or aggregating the simulated locations to a coarser spatial resolution (after simulating) when calculating landscape connectivity metrics. If aggregated to 100 m cells, the number of cells in the above example would reduce by a factor of 16 for a much more manageable total of 10,000 cells. In some cases, such as when generating utilisation distributions for a model without temporal dynamics or behaviour states, it may be preferable to adopt a more computationally efficient prediction approach using the fitted SSF, such as presented in Table 1, or use a different modelling approach altogether (Calabrese et al., 2016; Scharf et al., 2017; Wilson et al., 2018; Michelot et al., 2019; McClintock & Lander, 2024; Michelot, 2024; Dupont et al., 2026).

### 3.6.3 Generating predictive outputs

A number of predictive outputs can be generated from the same set of simulated trajectories. For animal-centric research aims, predictions would be calculated for each simulated trajectory, such as the mean home range size or the total number of road crossings for different scenarios, which may then be used to generate a distribution to compare to the observed data (Cowan et al., 2025). For landscape-centric predictions, the simulated trajectories would typically be aggregated such that each cell in the simulated landscape receives a value. Landscape connectivity metrics such as landscape betweenness, or betweenness centrality, measure the number of simulated steps passing through a raster cell relative to the total number of steps in the landscape, indicating the cell's significance for connectivity within the landscape network (Bastille-Rousseau, Douglas-Hamilton, et al., 2018; Hofmann et al., 2023; Hofmann, Behr, et al., 2024). Maps showing a population-level UD, betweenness, and interpatch connectivity are shown for the African wild dogs in Figure 11.

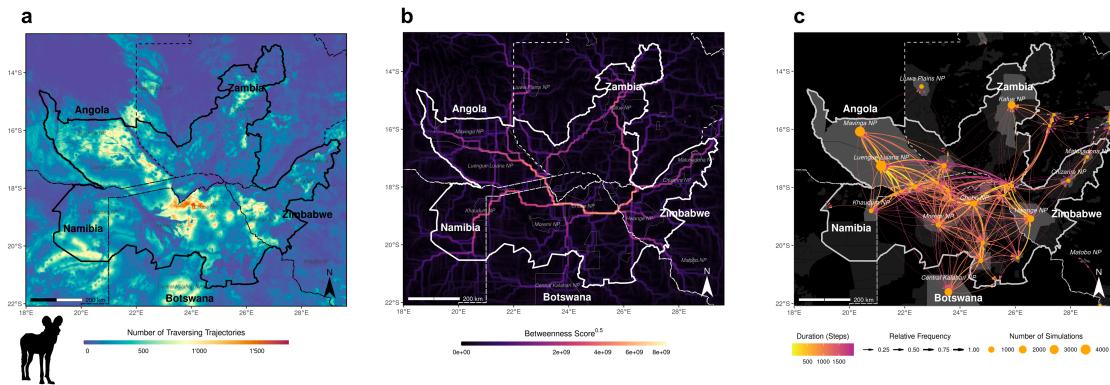


Figure 11: Landscape-centric predictive outputs derived from dispersal simulations across the entire extent of the Kavango-Zambezi Transfrontier Conservation Area (border indicated by the thick solid line) (see Supplementary Materials Section A). (a) A utilisation distribution (heatmap), (b) a corridor map, and (c) a map of inter-patch connectivity. Figure adapted from Hofmann et al. (2023).

### 3.6.4 Accounting for parameter uncertainty and individual variability

The fitting of any model is subject to multiple types of uncertainty, which arise from data collection, the model that was used, and the inherent stochasticity of the process itself. This uncertainty is captured in the model's estimated parameters, which include a coefficient estimate for each

parameter (the mean effect) and a variance-covariance matrix which describes the uncertainty in the parameters, including how the parameters co-vary with one another. Additionally, hierarchical (i.e. mixed/random-effects) models (Muff et al., 2020; Chatterjee et al., 2024) and two-step (Craiu et al., 2016) modelling approaches are often used to account for differences between individuals. These models can account for individual variability in any of the movement, habitat selection, memory and/or social dynamic processes (Muff et al., 2020; Chatterjee et al., 2024; Cowan et al., 2025; Forrest et al., 2025).

To ensure that the simulated individuals cover the range of behavioural variability estimated by the model, simulation parameters may be drawn from distributions created using the fitted model. When fitting a hierarchical model, the random effects will give a distribution of parameters. Therefore, for each simulated individual, it may be beneficial to sample the parameter values from those distributions, rather than using mean (‘population-level’) values. In a frequentist setting, population-level parameters representing coefficient means and variances across individuals can be drawn from their estimated asymptotic sampling distribution (often multivariate normal for means, perhaps log-normal for variance parameters), and conditional on those values, individual-specific parameters can be sampled from the assumed population distribution. When using a Bayesian sampling approach, one can take draws from the posterior predictive distribution for the individual-specific coefficients.

### 3.7 Validation

Validating movement models and their predictions is essential for ensuring both their reliability and interpretability (McClure et al., 2016; Laliberté & St-Laurent, 2020). Given the complexity of these models, a wide range of properties can be validated. Except for information-based criteria such as AIC or BIC, validation should be calculated on data that has been withheld from model fitting, and the specific data withheld should relate to the intended use of the models. In most cases, withheld data should ideally be from different individuals, to ensure that the model is not overfitting to individual behaviours. For out-of-domain predictions, withheld validation data should capture novelty in the dimension of interest (i.e. the time, space, or environmental conditions). For example, if the goal is to predict movement in unsampled space, the withheld data should be in novel regions of the sampled area, such as for spatial (or environmental) block cross-validation (Roberts et al., 2017; Valavi et al., 2019). Although there are no fixed rules about the amount of withheld data, a typical rule-of-thumb is to use ~80% of data for fitting models, with the remainder used for validation. In the case of limited movement data, validation data may be withheld during model development to determine the model structure and covariates, but once the final model and covariates have been selected, using all of the data to fit the model and generate predictions.

While there are a number of tools available for validating predictions generated using spatial simulations, there are a number of challenges. These tools will also differ depending on whether predictions are animal- or landscape-centric. Animal movement is high-dimensional and stochastic, meaning that simulated trajectories cannot be directly compared to the observed ones, and often require validation to be conducted at multiple levels, such as at the step-level and the path-level. These levels correspond to different predictive goals: from short-term movement decisions to emergent space-use patterns. Good performance at one level does not guarantee accurate predictions at another, and validation should ideally consider several complementary approaches and be in alignment with the research aims of the study.

Validation can also leverage independent data sources that reflect movement or connectivity over broader spatial or temporal scales. Genetic data, for example, can reveal long-term functional connectivity among habitats, while occurrence data from aerial surveys, camera traps, spoor surveys, or conflict records can indicate spatial patterns of habitat use (Vasudev et al., 2023). Such datasets provide valuable external benchmarks for assessing predictions derived from movement models.

### 3.7.1 Model selection

Information-based criteria, such as AIC or BIC, assess in a relative sense how well the model describes observed movement patterns at the scale of the next step, which is penalised by the number of estimated parameters in the model. These metrics provide a quantitative measure of model fit, helping identify the most suitable model among competing alternatives. However, information criteria do not indicate the accuracy of the model (Mac Nally et al., 2018), and even if the model performs well at the scale of the next step, this does not necessarily indicate how well the simulations can capture the longer term or emergent properties that we are interested in. We therefore can (and should) also assess how well the model can generate the predictive quantity of interest, such as the home range sizes, connectivity pathways, or utilisation distributions (Nicosia, 2026).

### 3.7.2 Step-level validation

Step-level validation evaluates predictive accuracy for the next movement step given an animal’s current location. This tests whether the model correctly captures local movement decisions and habitat selection. A common approach is k-fold cross-validation, in which the model is trained on a subset of the data and evaluated on withheld steps (Figure 12b1 and 12b2) (Fortin et al., 2009; Hofmann et al., 2023; Pike et al., 2026). While strong step-level predictions indicate that movement processes are well represented, they do not necessarily guarantee that longer-term movement paths or emergent spatial patterns will be reproduced correctly. Additionally, the results of k-fold cross-validation depend on the distribution of randomly proposed steps used for model fitting, i.e. a model will have better ‘performance’ when selecting steps from a uniform disc compared to importance sampling, as many of the uniformly proposed steps are unlikely. It is therefore still hard to interpret the outputs of k-fold cross-validation as a measure of the overall quality of the model, but with the same set of proposed steps it is a useful indicator of relative model performance.

### 3.7.3 Path-level validation

Path-level validation evaluates predictive quantities pertaining to entire movement trajectories or dispersal paths. Primarily for animal-centric predictions, summary statistics such as step length and turn angle distributions, total path length and sinuosity, home-range size, and the mean and quantiles of habitat selection, act to reduce the dimension of the observed and simulated trajectories, allowing for comparison (Abrahms et al., 2017; Fieberg et al., 2018; Kays et al., 2023; Fieberg et al., 2024; Cowan et al., 2025), or for approximate Bayesian computation (ABC), model fitting (Hauenstein et al., 2019; Malchow et al., 2024). Recent work builds on this to create a more principled framework to assess trajectory-level metrics and the emergent properties of animal movement (Nicosia, 2026).

For landscape-centric predictions, there are approaches used in connectivity analyses focusing on large-scale movement patterns (McClure et al., 2016; Zeller et al., 2018). A common method compares predicted paths, such as least-cost paths or corridors, with observed dispersal trajectories, measuring their spatial overlap (Pullinger & Johnson, 2010; Poor et al., 2012; Abrahms et al., 2017). Another approach assesses whether observed locations fall in areas of high predicted connectivity, either directly or relative to random locations, thereby testing whether animals preferentially use predicted movement corridors (Finerty et al., 2023). Such tests can also be implemented within selection-model frameworks (Brennan et al., 2020; Hofmann et al., 2023). For instance, Hofmann et al. (2023) used path-selection functions to validate that dispersal routes of withheld individuals preferentially moved along areas of high predicted connectivity. For utilisation distributions, presence-only validation metrics such as the (continuous) Boyce index (Boyce et al., 2002; Hirzel et al., 2006), or space use metrics such as Bhattacharyya's Affinity (Fieberg & Kochanny, 2005) compare how well the UD surface predicts the (held-out) validation points (Sells et al., 2022, 2023; Forrest et al., 2025; Rogers et al., 2025).

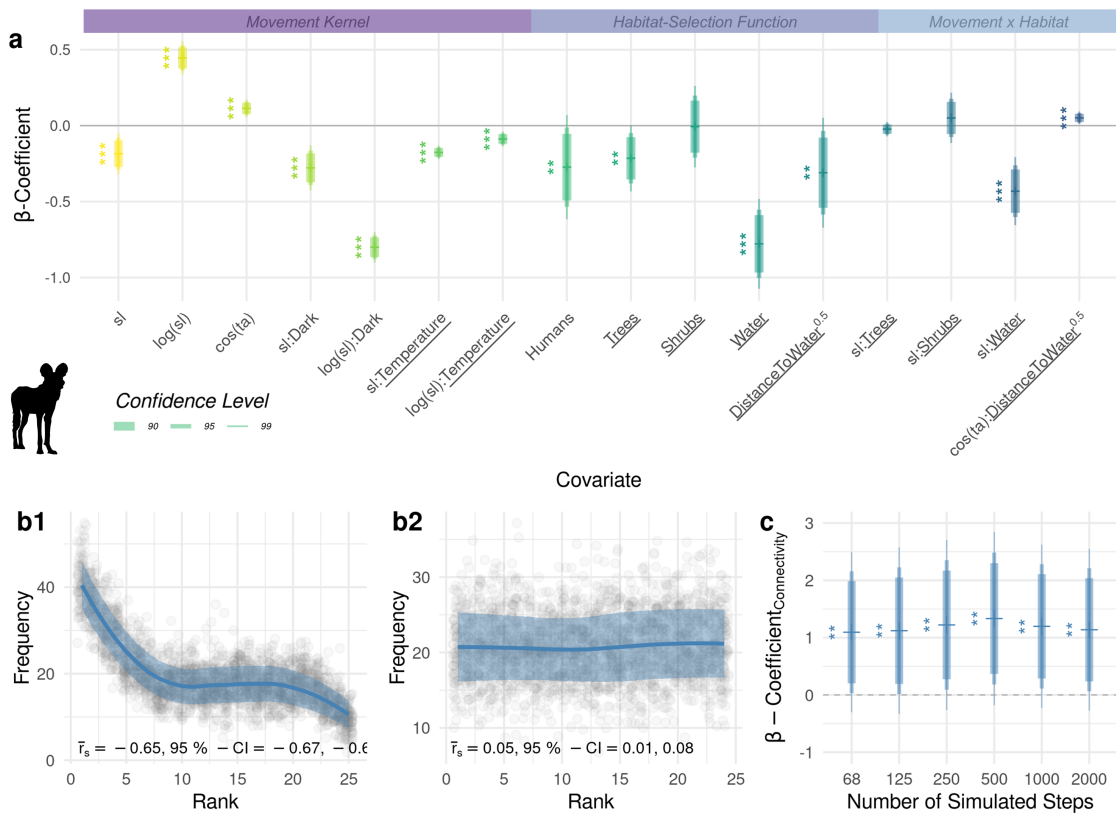


Figure 12: (a) Results from the integrated step-selection model for dispersing African wild dogs (see Supplementary Materials Section A). Estimated coefficients are grouped according to their relevance for the movement kernel (purple), habitat-selection function (violet), and interactions among the two (blue). (b) Validation results of the predictive performance of the SSF model using k-fold cross validation. (b1) Rank of the observed steps weighted by selection probabilities under the fitted model (Spearman correlation coefficient,  $\bar{r}_s = 0.65$ ), as opposed to (b2) under a null model ( $\bar{r}_s = 0.05$ ). (c) Selection coefficients from the path-selection analysis using the connectivity map as covariate, showing positive selection of dispersers for areas with high predicted connectivity. Figures adapted from Hofmann et al. (2023).

### 3.8 Out-of-domain predictions

As outlined in Section 3.1.1, out-of-domain predictions are intended to inform decision-making by exploring potential outcomes beyond the domain of the training data. They do so by predicting into novel space, time, or environmental configuration. Hence, out-of-domain predictions should be carefully scrutinised.

#### 3.8.1 Assessing the degree of environmental extrapolation

Several steps can be taken to assess the extent to which a movement model is extrapolating into novel environmental conditions, and to evaluate the potential impact of extrapolation on a given application. First, the environmental distance between conditions at training data locations (observed and random steps) and the target site can be measured and visualised. Simple plots of training data coverage across individual covariate ranges relative to the entire target site serve as a useful starting point (Figure 13b-d). Approaches to then quantify environmental distance from training to target conditions principally involve measuring a Euclidean or multivariate (e.g. Mahalanobis distance) distance from the centre or edge of training environmental conditions to the target, with the multivariate approach identifying novel combinations of variables. Thresholds to denote ‘analogous’ and ‘extrapolative’ conditions are then delineated with simple bounding boxes, rectilinear envelopes, or cross-validation schemes. The latter is particularly robust since it sets an interpretable threshold beyond which model evaluation is less reliable (see Meyer and Pebesma, 2021). Different methods from the SDM literature are available to apply these approaches (reviewed by Kass et al. (2025) including relevant R packages; Velazco et al., 2022), but we broadly recommend considering multivariate, continuous measures (e.g., Shape; Velazco et al., 2024) where possible, reserving bounding box approaches (e.g., MESS; Elith et al., 2010) for fast, simple evaluations.

Once environmental distances to the target site are measured, plotting these distances in space can highlight regions of higher extrapolation risk (e.g., Figure 13a, including an extrapolation threshold) which might be compared alongside maps of predictive outputs to understand model behaviour under extrapolation. Where specific sites (e.g., a protected area) are of interest, this environmental distance map can inform whether model predictions are reliable at that location (Pinilla-Buitrago et al., 2026). Model performance under extrapolation might also be examined by visualising model response curves and delineating the boundary of extrapolative conditions (Pinilla-Buitrago et al., 2026), or by plotting environmental distance against each covariate value to indicate which covariates contribute the most to potential model extrapolation (Figure 13b-d; Velazco et al., 2024). Finally, key model results such as predictive maps might be inspected with and without masking predictions in thresholded extrapolative conditions. This could indicate whether extrapolative predictions alter the main conclusions from an output.

After using these visualisation tools to evaluate the likely impact and drivers of environmental extrapolation, the final step is to decide how to address any identified extrapolation. The most conservative approach would be to mask extrapolative predictions out of any maps. However, predictions are often necessary despite uncertainty, so other approaches might be to give a visual indication of uncertainty in these regions (e.g., with shading), or to consider an approach that constrains extrapolative predictions (reviewed for SDMs by Pinilla-Buitrago et al., 2026).



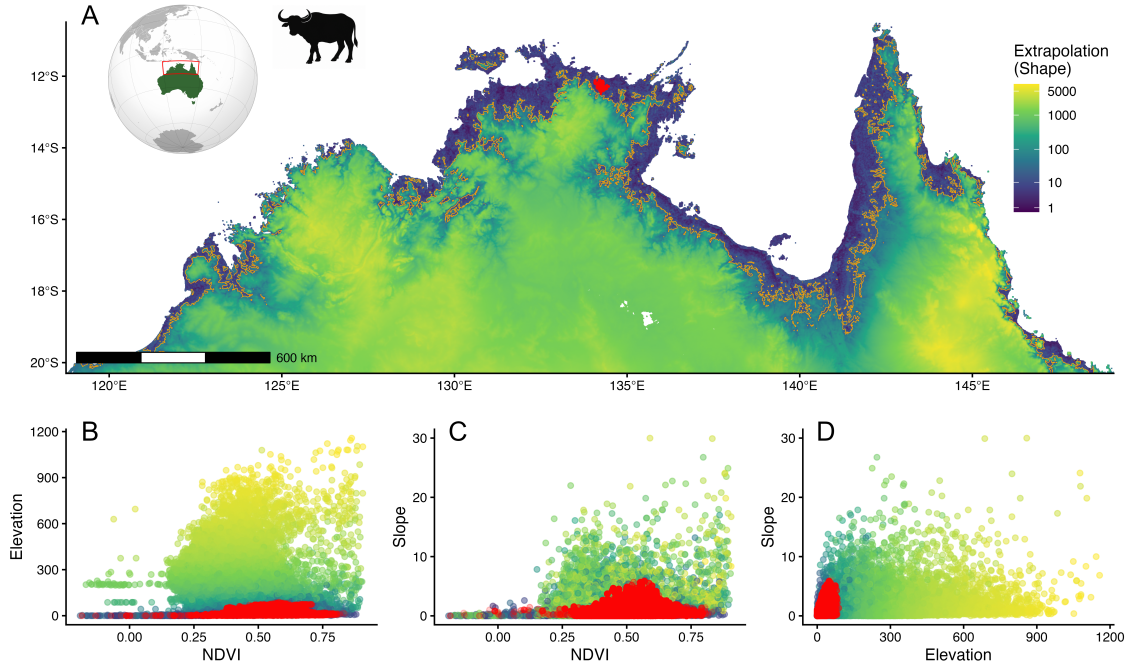


Figure 13: Assessing environmental extrapolation using the Shape method (Velazco et al., 2024) for tracking data from water buffalo (*Bubalus bubalis*) in the Djelk Indigenous Protected Area (Pike et al., 2024; Forrest et al., 2025; Pike et al., 2026), fitted to NDVI, elevation and slope. **Panel A** shows a map of Shape values across northern Australia, with an illustrative threshold (orange contour) set to the maximum observed Shape value in the training data (containing both used and randomly sampled steps), which was Shape = 21.1. Buffalo data locations are shown in red (to the north of the map). The darker regions are closer in environmental space (more analogous conditions to the training data), and the brighter, more yellow regions are more extrapolative. **Panels B, C and D** show the distribution of covariate values for northern Australia (with a subset of 0.1% of cells, coloured by their Shape values), and the training data (red points). Although the buffalo data cover most of the range of NDVI (x-axis in Panels B and C), they are from a floodplain area entirely below 100 metres in elevation (Panels B and D). Higher elevations are therefore considered more extrapolative, which can be seen in the map in **Panel A**. The colour scale is shown for all three plots with a ‘log1p’ transformation, which is the natural logarithm with 1 added to every value. The orthographic map of Australia in **Panel A** was downloaded from [commons.wikimedia.org/wiki/File:Australia\\_\(orthographic\\_projection\).svg](https://commons.wikimedia.org/wiki/File:Australia_(orthographic_projection).svg) / CC-BY-SA-3.0.

### 3.8.2 Generating landscape scenarios

Environmental change is likely to alter observed animal movement patterns (Hacker et al., 2026). To anticipate how animals may change their movement behaviour, one can generate scenarios of the expected change. Changes may be due to large-scale environmental events such as climate change, wildfire, or climatic and weather events such as drought or flooding (Hofmann, Behr, et al., 2024), or anthropogenic disturbances such as deforestation or habitat fragmentation, urban development, expansion of water bodies for hydroelectricity (Dorber et al., 2023), or the placement of mines (Cowan et al., 2025), power lines (Cappello et al., 2025; Pay et al., 2025), or wind farms (Estellés-Domingo & López-López, 2025). Given the assessment of animal movement and landscape connectivity is often lacking in development plans for large-scale disturbances (Bergès et al., 2020), out-of-domain predictions under potential scenarios could contribute much needed information before development begins. As long as the scenarios can be represented spatially (or interacted with spatial covariates), and the model has been fitted to covariates that represent the aspect of the environment that is changing, then it is straightforward to generate predictions by substituting in the scenario covariates. Regardless of the changes being made however, the degree of extrapolation



should be assessed, as predictions into novel conditions may not be reliable (Tsiftsis et al., 2024). When generating out-of-domain predictions, the period for which to generate predictions will need to be sourced. This may require forecasting dynamic covariates (e.g. temperature, precipitation, climate, etc) before we can make future predictions of animal movements.

### 3.8.3 Considerations for generating out-of-domain predictions

Although there are mechanistic components to spatial simulations, such as the movement kernel, the parameters in SSFs that relate the animal to the surrounding environment are correlative. This means that the simulations assume the behavioural responses to environmental covariates remain constant. For instance, in the models that we have described, there are typically no physiological processes, such as overheating or dehydration, or demographic processes such as reproduction and death. These limitations mean that these models may not be suitable for predicting quantities like the tolerable range of a population in terms of climatic extremes, as they are determined by physiological processes other than movement and correlative relationships to the surrounding environment. Mechanistic niche models that include physical and chemical constraints derived from first principles, such as NichMapR (Kearney & Porter, 2017), may be appropriate to consider. These models do not account for movement, but integrating these mechanistic parameters into movement models may be a beneficial area to explore.

## 3.9 Prediction outcomes and interpretation

The final step in our workflow focuses on interpreting prediction outputs and translating them into ecological understanding, policy-relevant insights, and management recommendations or implementation. Prediction outcomes should be interpreted in the context of the original research aim or management goal and linked directly to ecological decision-making. Globally, development planning in unsampled areas often lacks assessment of the likely effects on animal- and landscape-centric movement (Bergès et al., 2020). The exclusion of such information is precarious given that landscape modification can drive large scale negative impacts on animal movement (Doherty et al., 2021). Understanding these impacts will likely lead to better biodiversity outcomes (Tarabon et al., 2019), and predictive movement ecology offers a means for achieving this.

### 3.9.1 Animal-centric predictions

In-domain animal-centric metrics are valuable for validating predictions, as discussed in Section 3.7, and can be used to scale-up the amount of data in a given area (Mawer, Pauwels, et al., 2023; Mawer et al., 2025), particularly for identifying uncommon events such as road crossings (Zeller et al., 2021) and collisions with human infrastructure (Cappello et al., 2025). Out-of-domain animal-centric outputs are easily interpreted in an ecological sense, as the aggregated distributions can be compared to those in sampled areas. One example is from Cowan et al. (2025), where SSFs with a memory process were used to simulate northern quoll (*Dasyurus hallucatus*) movement under different mining landscape scenarios (current, dispersed, aggregated, non-mining). Animal-centric outputs were calculated for each scenario, including home range size, energetic costs, and habitat revisitations, which were then compared across scenarios. Results suggested mining scenarios had negative impacts on movement relative to the non-mining scenario, with variation among them.

Such approaches could be used to understand optimal design for future mines to limit movement impacts on northern quolls.

### 3.9.2 Landscape-centric predictions

In-domain landscape-centric predictions are highly valuable for informing conservation management by identifying important habitat, movement corridors, dispersal pathways, or areas of elevated mortality risk (e.g. roads) within the sampled landscape. Utilisation distributions can be used to inform spatio-temporal management practices, such as the management of threatened (Sells et al., 2022) or invasive animals (Forrest et al., 2025), and landscape betweenness can identify cells critical for connectivity, with evidence from African elephants (*Loxodonta africana*), giant Galapagos tortoises (*Chelonoidis niger*), mule deer (*Odocoileus hemionus*), and African wild dogs (*Lycaon pictus*; Bastille-Rousseau, Douglas-Hamilton, et al., 2018; Hofmann et al., 2023). Such findings may guide prioritisation of restoration activities, mitigation of infrastructure impacts, and species recovery actions. For example, Westaway et al. (2025) created landscape betweenness maps using movement trajectories simulated from SSFs, and identified the remnant native vegetation patches in a fragmented agricultural landscape that were most important for optimal movement of shingleback lizards (*Tiliqua rugosa*) through cleared paddocks.

Out-of-domain landscape-centric predictions can inform conservation management in unsampled areas, possibly under different hypothetical scenarios, such as in Figure 14. These findings may help guide landscape-scale design before major disturbances, or assist in conservation activity planning, such as for species reintroductions or restoration actions. For example, Whittington et al. (2022) simulated landscape-centric connectivity from SSFs of grizzly bears (*Ursus arctos horribilis*) and gray wolves (*Canis lupus*) under different landscape scenarios (existing urbanisation conditions, reference conditions, expected future conditions). They determined that current urbanisation reduced landscape connectivity by 85% and recommendations were made to protect the species from existing urbanisation threats, including reduction of the human footprint, spatial consolidation of recreational activity, and trail closures. Aiello et al. (2023) simulated movement trajectories from SSFs of desert bighorn sheep (*Ovis canadensis nelsoni*) to determine landscape-centric utilisation distributions under scenarios with and without highways. High use areas under highway-free scenarios suggested that the removal of highways would increase genetic connectivity and access to a broader range of habitats, and reduce roadkill events.

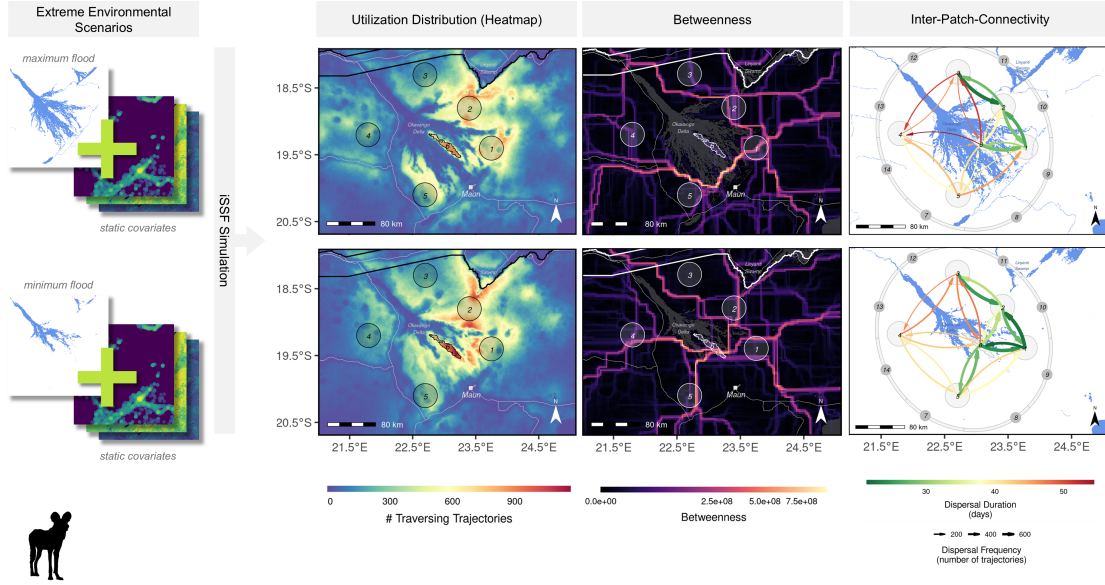


Figure 14: Landscape-centric prediction maps derived from dispersal simulations of African wild dogs using SSFs under climatic extremes (see Supplementary Materials Section A). Simulations were conducted under two scenarios, one assuming a maximum flooding extent of the Okavango Delta, one assuming a minimum flooding extent. Results from the simulation analysis further indicated that most major dispersal corridors were encompassed within KAZA’s boundaries, though some important routes fell outside its borders (also see Figure 11). These findings were communicated to the KAZA Secretariat to inform and improve corridor management within the conservation initiative. By highlighting shared priority areas across administrative or organisational boundaries, these predictions may also support coordination among NGOs, governmental bodies, and local management authorities. Figure adapted from Hofmann, Behr, et al. (2024).

## 4 Future prospects for predictive movement ecology

While there are many existing tools and applications for modelling and predicting animal movement, the field is developing rapidly. Technological advances such as high-frequency GPS (Thums et al., 2018; Nathan et al., 2022), low-cost trackers that utilise human infrastructure (Farine et al., 2024), and high-throughput reverse-GPS tracking systems such as ATLAS (Toledo et al., 2020) are providing more data, often at higher frequencies, than ever before. These large volumes of movement data are also being collated into open-access repositories such as Movebank (Kranstauber et al., 2011; Kays et al., 2022) and large-scale initiatives such as the COVID-19 Bio-Logging Initiative (Rutz et al., 2020; Rutz, 2022) and MegaMove (Sequeira et al., 2025), propelling movement ecology into the big data era (Nathan et al., 2022) and allowing for analyses across many species (Tucker et al., 2018, 2023; Oliver, Yanco, et al., 2026; Potts et al., 2026). The accuracy of prediction models depends on how realistically they can reflect the true process of animal movement, and there is still plenty of room for methodological and conceptual developments that can capture broad patterns of animal movement, as well as the subtleties and complexities of animal behaviour at fine-scales. Here, we highlight some conceptual and methodological considerations that we think are key to moving movement ecology forward as a predictive science.

## 4.1 Statistical and conceptual developments for improved predictions

An emerging development for generating animal movement predictions is to use machine and deep learning models, which can be considered as flexible ‘function approximators’ that build a representation of the animal movement process. Due to their large number of parameters, understanding and interpreting what the model has learned can be more challenging (but see Fronville et al., 2026), but they can improve predictive accuracy (Wijeyakulasuriya et al., 2020; Roy et al., 2022; Forrest et al., 2026; Patras et al., 2026) and scale to very large amounts of data (Kaplan et al., 2020; Cífka et al., 2023). Fitting models across multiple datasets is a common practice in deep learning, and may follow a ‘pre-training/fine-tuning’ approach, which can improve the model’s ability to generalise and extrapolate, given the wider range of conditions encountered in the training data (Zhuang et al., 2021; Forrest, 2026; Patras et al., 2026). In movement ecology, there is great potential for fitting models across many datasets, approaching a generalisable foundation model for animal movement (Forrest, 2026). For complicated processes such as memory and social interactions, deep learning tools can naturally incorporate histories of past locations (recurrent neural networks or transformers) and dyadic relationships to other individuals (graph neural networks), which can inform the next step in the trajectory (Roy et al., 2022; Cífka et al., 2023). These more sophisticated architectures should lead to more accurate predictions, and with some interrogation it is possible to investigate what the model has learned, potentially offering new insights into difficult-to-measure internal processes (Cífka et al., 2023; Fronville et al., 2026). There are also other deep learning approaches that predict entire trajectories at once, rather than requiring a Markovian step-by-step approach, and may be better at predicting the emergent structure of animal movement trajectories, possibly addressing the goal-orientation and multi-scale considerations below (Roy et al., 2022; Patras et al., 2026).

### 4.1.1 Perception and goal-orientation

Animals respond to environmental features and make movement decisions in their present time, but are likely to perceive and navigate towards objects that are some distance away (Fagan et al., 2017; Bastille-Rousseau, Murray, et al., 2018). They are also likely to have an internal, spatial representation of the landscape that they are familiar with, sometimes termed a ‘cognitive map’ (Bennett, 1996; Tsoar et al., 2011; Harten et al., 2020; Toledo et al., 2020). Both modes of navigation will lead to goal-orientation, where an animal is navigating towards a goal that is not immediately accessible. A limitation of most of the models that we presented is that proposed steps, and therefore the ‘perceptual’ radius, is determined by the time interval between sampled locations. This means that for most models, goals beyond the immediate step cannot be perceived and navigated towards (unless specified *a priori*), and that as the sampling frequency increases, the ‘available’ area and simulated animal’s perception will decrease. With only a limited ability to navigate to features beyond the next step, predictions will be less realistic and accurate, particularly for applications like the identification of migration corridors, where animals have a defined goal they are navigating towards. There have been valuable attempts to model far-away goals into step-selection models (Bastille-Rousseau, Murray, et al., 2018), and distance-to or angular covariates are commonly used, but a limitation is that it is very difficult to search across all possible goals for the one that is most likely of interest to the animal. Emerging deep learning methods that include a very sophisticated representation of prior context, such as Transformers (Cífka et al., 2023), may present a promising direction here, as well as Generative Adversarial Networks (GANs) and diffusion models (Roy et al., 2022; Patras et al., 2026), but these methods remain untested in terms

of goal-orientation towards unspecified goals.

#### **4.1.2 Multi-scale or nested movement models**

High-frequency tracking data presents opportunities to model the movement and habitat selection processes as a multi-scale or nested process, where broad-scale selection patterns can determine the overall trend of movement and allow for goal-orientation, but finer-scale movement-driven processes can fill in the gaps and follow movement corridors through the landscape. Multi-scale approaches have been developed for state-switching models (Leos-Barajas et al., 2017; Adam et al., 2019), habitat selection models (McGarigal et al., 2016; Zeller et al., 2017), and species distribution models (Guisan et al., 2025), but their implementation for step-selection models has remained limited. Having a nested structure of movement and habitat selection may also address the previous point regarding goal-orientation, where a high-level behaviour would identify a goal (possibly by selecting between alternatives), which could then be navigated towards at fine-scales.

#### **4.1.3 Incorporation of SSFs into agent-based modelling frameworks**

Although simulations from step-selection models are themselves a type of individual- or agent-based model (ABM), the field of agent-based modelling is much broader, covering ecology, evolution, psychology, and social sciences (Grimm et al., 2006; Railsback et al., 2006). Beyond the implementation of SSFs and their variants described in this review, ABM frameworks provide a robust scaffold that can naturally incorporate demographic parameters such as births, deaths, and different life-histories (Lustig et al., 2017; Malchow et al., 2024; Patterson et al., 2024), complex processes such as social interactions and interactions between different species, as well as learning and spatial memory (Bennett & Tang, 2006). For reviews of agent-based models in wildlife ecology and animal movement, including the processes that may be incorporated, see Tang and Bennett (2010) and McLane et al. (2011). There are likely to be opportunities to further integrate empirically derived movement and habitat processes, such as from SSFs, into the more robust and flexible computational frameworks of ABMs, allowing for additional demographic and behavioural processes (Hauenstein et al., 2019; Zhang et al., 2026).

## **5 Conclusions**

Animal movement is a fundamental ecological process which shapes populations, communities, and the structure of ecosystems. Predicting movement can therefore advance cognitive, behavioural and ecological theory, and generate predictions that can be used for a wide range of conservation management applications. In this review, we have provided concepts and guidance to promote movement ecology as a predictive science, with a focus on using general and flexible spatial simulations. A key strength of spatial simulations using step-selection is that it reproduces dynamics made at the scale of individual animals and individual decisions, offering a powerful bridge between behavioural mechanisms and emergent, landscape-scale movement patterns. This connection provides a valuable route from the fine-scale behavioural processes that can be directly observed, to more ecological- and management-relevant outcomes at broader spatial and temporal scales. We have outlined a number of considerations and limitations for predicting animal movement, provided a detailed case-study highlighting the decisions to make along the workflow, and illustrated how

the field may progress into the future. Despite the rapid technological, statistical and conceptual developments in recent years, there are many open questions and methodological developments needed, owing to the complex nature of animal movement.

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## Glossary

**animal-centric predictions** Predicted quantities that are calculated per individual trajectory, which are typically non-spatial. Examples include the distance travelled by a simulated trajectory, home range size, energetic expenditure, number of revisitations to certain habitat categories, or the number of times that roads are crossed or anthropogenic features such as wind turbines or powerlines are intersected.

**betweenness** Quantifies the importance of different elements of the matrix in facilitating connectivity between other patches or habitats within the landscape. It identifies key corridors or bottlenecks that serve as critical links for maintaining overall connectivity in the landscape. It is calculated as the number of times the simulated individuals enter each raster cell (which are typically aggregated to a coarser scale than the spatial covariates used in the simulations). Betweenness measures the importance of each cell within the landscape for maintaining functional connectivity.

**conductance** The degree to which the landscape allows movement or flow of organisms across it. It considers factors such as habitat structure, land use, and barriers that affect the ability of organisms to move through the landscape. This may be quantified via heatmaps (Hofmann et al., 2023; Hofmann, 2024).

**connectedness** The degree to which different patches or habitats within a landscape are functionally connected. It measures the ease and frequency with which organisms can move between different areas of the landscape. This may be quantified via Inter-Patch Connectivity Maps (Hofmann et al., 2023; Hofmann, 2024).

**environmental distance** The distance in **environmental space**, as opposed to the **geographic distance**, between two sets of covariates, such as where the data was collected and the space and time that is being predicted over. The environmental distance can be estimated using approaches such as the ‘Shape’ method (Velazco et al., 2024).

**geographic distance** The geographic dimension (as measured by spatial coordinates) of an area, as opposed to the **environmental distance**. Geographic areas may be very different, such as two different countries, but have similar environmental spaces, such as if they have a similar climate, topography, and vegetation.

**landscape connectivity** Landscape connectivity, as originally defined by Taylor et al. (1993), is the degree to which the landscape facilitates or impedes the movement of organisms among resource (or habitat) patches. The concept combines a description of the physical structure of the landscape with an organism’s behavioural response to that structure, and is commonly partitioned into two components (Tischendorf & Fahrig, 2000): **structural connectivity**, based purely on the spatial arrangement of landscape elements independent of any species’ movement behaviour (e.g., patch proximity, corridor presence), and **functional connectivity**, which incorporates how a given species actually perceives and responds to that structure during movement (e.g., resistance, permeability, or step-selection responses to habitat and configuration). Landscape connectivity may be quantified using measures such as **betweenness**, **connectedness**, and **conductance** (Hofmann, 2024).

**landscape-centric predictions** Predicted quantities that are spatial and calculated per pixel over the landscape being simulated over. Examples include the spatiotemporal distribution of animals (see [utilisation distribution \(UD\)](#)) and landscape connectivity measures such as [betweenness](#), [connectedness](#), and [conductance](#).

**relative selection strength (RSS)** Defined in Avgar et al. (2017), relative selection strength (RSS) is the ratio of the (relative) probability of selection between two locations — or, in a step-selection framework, between two candidate endpoints of steps sharing the same starting point — as estimated by a habitat- and/or step-selection function. Formally,  $RSS(x_2, x_1) = w(x_2)/w(x_1)$ , where  $w(x)$  is the fitted exponential selection function. Using linear habitat selection coefficients with estimated SSF coefficients  $\beta_i$ , this becomes  $RSS(x_2, x_1) = \exp\{\sum_{i=1}^p \beta_i(h_i(x_2) - h_i(x_1))\}$ , where  $h_i$  is the value of the  $i$ th covariate at each location, so that  $\sum_{i=1}^p \beta_i(h_i(x_2) - h_i(x_1))$  gives the log-RSS. In the case where the two locations differ in only one covariate  $h_i$  (all others held equal), this reduces to  $\beta_i \cdot \Delta h_i$ , where  $\Delta h_i = h_i(x_1) - h_i(x_2)$ . RSS thereby quantifies effect size by expressing how much more (or less) likely one location is to be selected than another, when holding all other covariates fixed.

**step-selection function (SSF)** A step-selection function (SSF) is a statistical model defines an animal selecting a ‘step’ from candidate possibilities in their surrounding environment at a future time step, which is often defined as the next telemetry location, with respect to their movement behaviour and habitat selection preferences (Fortin et al., 2005; Potts et al., 2014; Thurfjell et al., 2014; Avgar et al., 2016; Fieberg et al., 2021; Michelot et al., 2024).

**utilisation distribution (UD)** A probability density function describing the relative frequency of occurrence of an animal (or population of animals) across space (or space and time) (Van Winkle 1975). For a single animal, the UD reflects its space use over a specified period, and isopleths of the UD (e.g., the 50% or 95% contour) are commonly used to define its core area or home range. For a population, the UD instead denotes the expected relative distribution of individuals across space and time, i.e., where individuals in a population are expected to be found at a given time (i.e. a spatial heatmap).



# Supplementary Materials

## A Case study: African wild dogs in the KAZA

### A.1 Research aims

The African wild dog (*Lycaon pictus*) is a pack-living carnivore and one of Africa's most endangered species. The species' long-term survival depends on successful dispersal between remaining subpopulations, which becomes increasingly challenging in a human-dominated world. One of the species' few remaining strongholds lies in northern Botswana, where researchers of the Botswana Predator Conservation Program have monitored the local population for more than three decades. This region also forms part of the Kavango–Zambezi Transfrontier Conservation Area (KAZA), the world's largest trans-boundary conservation initiative ( $\sim 520,000 \text{ km}^2$ ) aimed at restoring connectivity between national parks. At its core lies the Okavango Delta, a dynamic and flood-pulse-driven floodplain within the otherwise dry Kalahari basin. This case study presents insights from a series of articles in which researchers aimed to understand connectivity patterns for African wild dogs within the KAZA landscape, particularly in relation to seasonal flooding and human influence (Hofmann et al., 2021, 2023, 2024). The goals were to determine the degree to which different areas were functionally connected, as well as to identify crucial movement corridors and their implications for human-wildlife conflict. Such knowledge contributes towards validating and improving the design of the KAZA in alignment with the needs of the species it intends to protect.

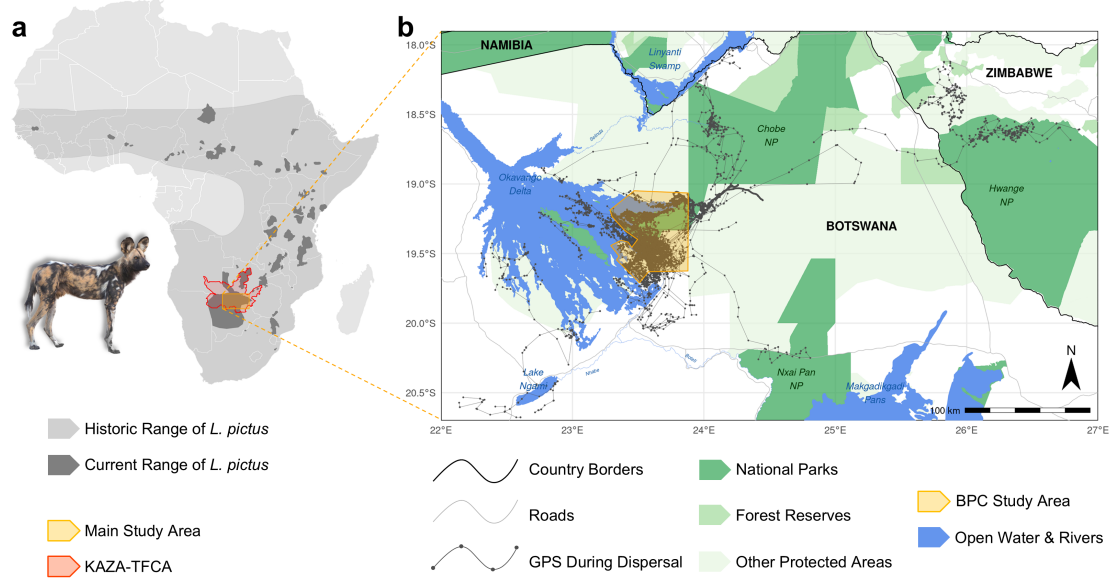


Figure A1: (a) Study area of the African wild dog case study in northern Botswana, representing a major stronghold for the species. The area forms part of the Kavango–Zambezi Transfrontier Conservation Area, which encompasses over  $520,000 \text{ km}^2$  and spans the countries of Angola, Namibia, Botswana, Zimbabwe, and Zambia. (b) Researchers from the Botswana Predator Conservation Program operate in the western part of the Okavango Delta and monitor the local population. Under this program, potential dispersers are equipped with GPS satellite collars and their dispersal trajectories are recorded, thus providing the foundation for simulating dispersal movements using step-selection functions.



## A.2 Movement data

Dispersal is the key demographic process linking subpopulations and maintaining connectivity (Baguette et al., 2013; Elliot et al., 2014; Keeley et al., 2017), hence the African wild dog project focused on collecting movement data on dispersing individuals using GPS satellite collars (Vectronics Aerospace). The ability to transmit data via satellite was crucial given the species' high mobility and potential to roam far beyond the researchers' study area (Figure A1b). To capture large-scale, trans-boundary movements while preserving collar battery life, locations were recorded at 4-hour intervals (i.e. six times per day). Collared individuals were regularly visited in the field to monitor individual well-being and pack composition. Dispersal events were identified either through direct field observations or by inspecting GPS trajectories for sustained movement outside an animal's established range (e.g. using net-squared displacement; Borger and Fryxell (2012)). The final dataset comprised dispersal trajectories from 33 individuals (17 males, 16 females), collected during different seasons. Only data during dispersal were assumed pertinent to connectivity and thus considered for further analyses ( $198 \pm 239$  locations/fixes per dispersing coalition).

## A.3 Environmental data and other covariates

For the African wild dog study, defining movement determinants and obtaining the necessary spatial data was challenging for several reasons. The study was conducted in a data-poor region, yet spatial layers needed to be consistent across international borders. To ensure uniform quality across countries, the authors mainly relied on global datasets, which were publicly accessible and could be efficiently processed thanks to platforms such as Google Earth Engine (Gorelick2017-ih). The spatial resolution of  $250 \times 250$  m was coarse, but appropriate considering the speed at which wild dogs move across the landscape and the extent at which corridors were inferred ( $\sim 1.4$  million  $\text{km}^2$ ). Another complication arose from the system's pronounced seasonal dynamics, which required updating certain spatial layers at regular intervals to capture temporal changes in the landscape. African wild dogs are ecological generalists, exhibiting a broad tolerance to environmental variation. Nevertheless, two critical dispersal barriers were evident: anthropogenic influence and water. Given their importance, the researchers developed (1) a custom human-influence index integrating settlements, roads, and land-use data, and (2) a dynamic mapping approach for the Okavango Delta, producing weekly updated flood maps from MODIS Terra satellite imagery. This also implied that observed GPS data needed to be temporally matched with those covariate layers that best represented environmental conditions at the time a GPS location was recorded. Further covariates included tree and shrub cover and non-spatial determinants, as measures of temperature and illumination from day- and moon-light.

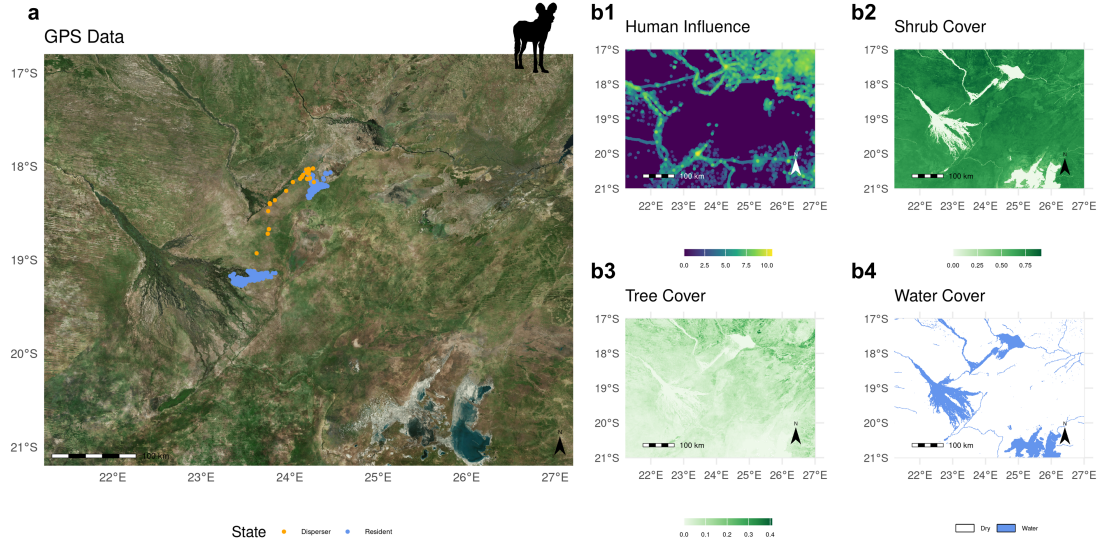


Figure A2: Visualization of spatial data used in the case study. **(a)** GPS data were collected on young African wild dogs (a track of one individual is shown here). Only data during dispersal (orange portion) were assumed pertinent to connectivity and thus considered for further analyses. **(b)** Observed dispersal movements were linked to the environment via a series of spatially mapped covariate layers, including data on human influence, shrub and tree cover, as well as water cover. Some layers were prepared as time-series layers to capture seasonal dynamics. The water cover layer (b4), for instance, was updated every week using remote sensed MODIS imagery to obtain accurate representations of the distribution of surface water in the ecosystem. Besides the depicted spatial layers, also non-spatial covariates, such as temperature and light availability, were used.

#### A.4 Data exploration

Data exploration served as a crucial step to verify data quality, uncover potential biases, and develop biological and data-informed expectations during the wild dog study. Movement data were screened for irregularities caused by missing GPS fixes and regularized (i.e. resampled) to comparable fix-rates (Figure A3a). Summary statistics describing turn angle and step length distributions were derived, and corresponding densities were visualized to characterize general movement behaviour (Figure A3b). Knowledge of turn angle and step length distributions helped to guide selection of appropriate parametric distributions to sample random steps for the step-selection analysis. GPS tracks were visualized in QGIS and overlaid with environmental covariate layers to reveal initial spatial relationships (Figure A3c). The initial screening allowed to identify first habitat selection patterns, such as clear avoidance of water bodies and human-dominated areas (Figure A3c), which later guided model formulation.

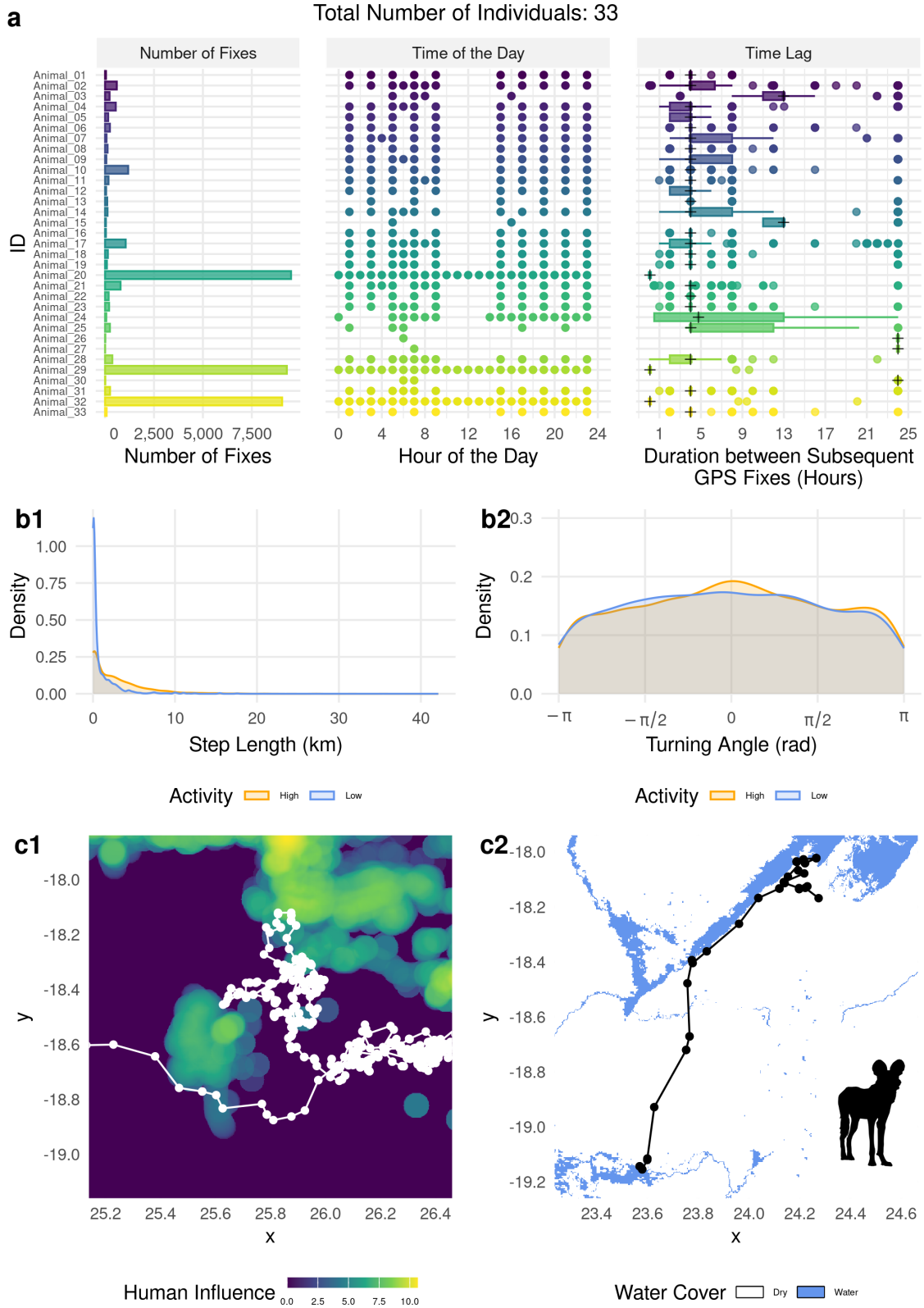


Figure A3: (a) GPS data from collared individuals were examined to determine the number of fixes per animal, time of day at which GPS fixes were obtained, and the duration between subsequent fixes. Using the time series of step durations, we determined a common fix-rate (4 hours) to which the data could be regularised/resampled. (b) Based on the regularized data, movement metrics, such as step lengths (b1) and turn angles (b2) were derived, providing initial insights into the movement characteristics of dispersing wild dogs. (c) Overlaying observed dispersal paths with environmental covariates facilitated an intuition for preferred and avoided covariates, e.g. avoidance of human settlements (c1, dispersal path in white) and water (c2, dispersal path in black).

## A.5 Building a movement model

The structure of the SSF model for the African wild dog case study was informed by prior knowledge of the species' ecology and on exploratory findings. Notably, the movement model comprised three components; a movement kernel describing movement patterns, a habitat-selection function capturing preferred and avoided habitats, and interaction terms that described how movement is affected by environmental conditions. For instance, an interaction between water and step-length was included to allow movements to differ depending on whether individual were in areas covered by water in areas that remained dry. To facilitate model convergence and bring covariate values to similar scales, continuous covariates were standardized to a mean of zero and standard deviation of one prior to model fitting. Step-descriptors (sl,  $\log(\text{sl})$ , and  $\cos(\text{ta})$ ), however, entered the models without standardization and only step lengths were converted to kilometres to prevent numerical instability. To account for individual variation, the authors employed the mixed-effects conditional logistic regression framework for SSFs proposed by Muff et al. (2020), which allowed incorporating random slopes for individuals. The most parsimonious model was then identified using forward model selection (the most parsimonious model may instead have been chosen using withheld data to ensure we were not biasing our estimates of predictive ability).

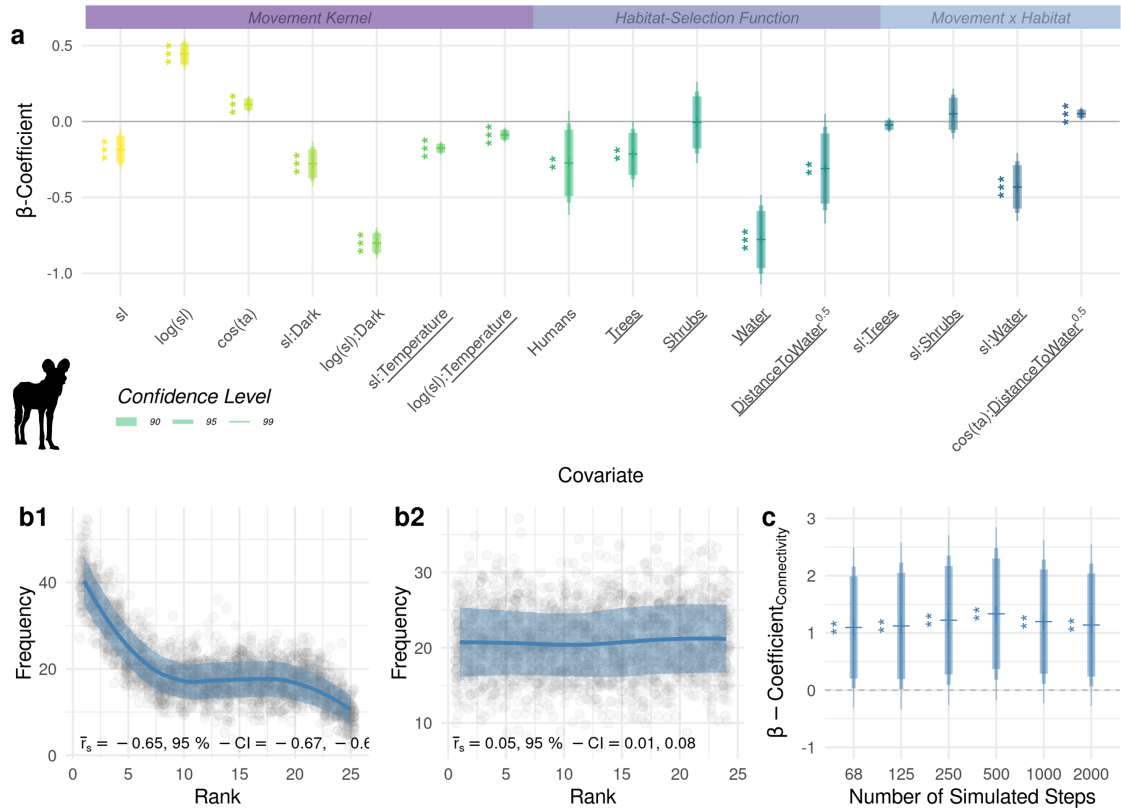


Figure A4: (a) Results from the integrated step-selection model for dispersing African wild dogs. Estimated coefficients are grouped according to their relevance for the movement kernel (purple), habitat-selection function (violet), and interactions among the two (blue). (b) Validation results of the predictive performance of the SSF model using k-fold cross validation. (b1) Rank of the observed steps weighted by selection probabilities under the fitted model (Spearman correlation coefficient,  $\bar{r}_s = 0.65$ ), as opposed to (b2) under a null model ( $\bar{r}_s = 0.05$ ). (c) Selection coefficients from the path-selection analysis using the connectivity map as covariate, showing positive selection of dispersers for areas with high predicted connectivity. Figures adapted from Hofmann et al. (2023).

## A.6 Simulations and predictive outputs

The fitted SSF model served as a mechanistic movement model from which dispersal trajectories were simulated to assess landscape connectivity across the KAZA. African wild dogs mainly reside inside national parks, and so 50,000 starting points were sampled randomly within protected areas. For lack of better information, the density of wild dogs was assumed to be similar across these areas. 30,000 starting locations were also chosen from the buffer area directly outside of the prediction to represent possible immigration. Simulations followed the logic of step-selection functions, where a set of 25 random steps were proposed from a starting location, the fitted model applied to predict step probabilities, and a step was sampled probabilistically based on these probabilities. A trajectory was simulated from each starting location, resulting in 80,000 trajectories that were simulated for 2,000 steps, which was approximately the maximum observed dispersal duration. Behaviour at map borders was handled by adding a randomised buffer zone (Koen et al., 2010). Three landscape-level connectivity metrics were derived: utilisation distributions (a.k.a. heatmaps), betweenness centrality maps (indicating areas that link other regions in the landscape), and inter-patch connectivity (highlighting the presence and frequency of connections between distinct protected areas) Figure A5. In-domain predictions were made for a single ‘average’ environmental scenario (Hofmann et al., 2023).

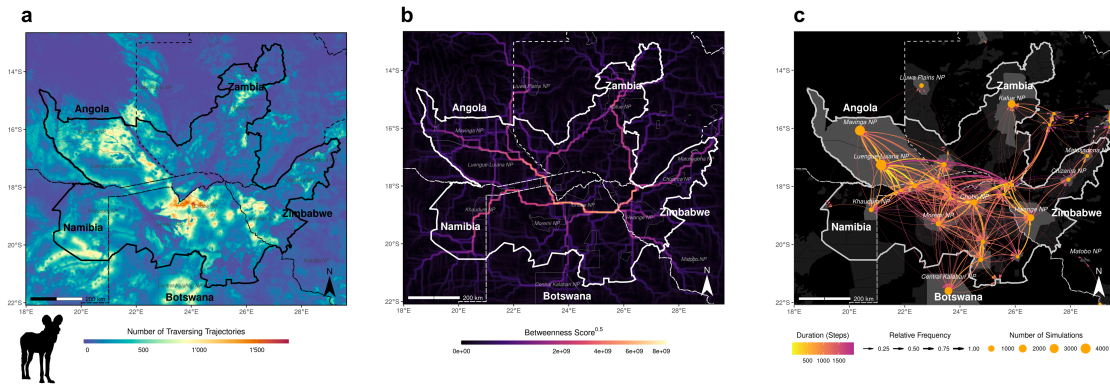


Figure A5: Connectivity maps derived from dispersal simulations across the entire extent of the Kavango-Zambezi Transfrontier Conservation Area (border indicated by the thick solid line). (a) A utilisation distribution (heatmap), (b) a corridor map, and (c) a map of inter-patch connectivity. Figure adapted from Hofmann et al. (2023).

## A.7 Validation

Model validation in the case study was performed both at the step- and path-level. Validation at the step-level was achieved by verifying that the fitted SSF model systematically assigned higher scores to selected steps over random steps. This was done via k-fold cross validation, where the SSF model was repeatedly fitted to a training dataset and then applied to predict step-scores to the remaining (observed and random) steps (Fortin et al., 2009). Spearman’s rank correlation coefficient then served to indicate whether there was a significantly higher frequency of chosen steps at high ranks. At the path-level, the authors employed path-selection functions on withheld dispersal data not used in model fitting, including predicted connectivity layer as sole covariate. This allowed testing whether dispersers indeed selected areas of high predicted connectivity. Both validation approaches demonstrated significant prediction power both at the step- and landscape-level (Figure A4b and A4c).



## A.8 Out-of-domain predictions

While initial predictions were made for a single ‘average’ environmental scenario (Hofmann et al., 2023), the authors later explored patterns of connectivity under extreme flooding scenarios of the Okavango Delta (Hofmann et al., 2024), as well as under a seasonally dynamic environment (in review). These scenarios were derived from a 20-year time series of satellite-based data of the Okavango Delta’s flood (2000–2019), from which 700 weekly flood maps were generated. Two composite landscape scenarios representing minimum and maximum flood conditions were constructed by averaging the 100 driest and 100 wettest flood maps, respectively. All other habitat layers remained static across scenarios. In a further extension, out-of-domain predictions were made under seasonally dynamic conditions in which landscape covariates varied through time and interacted directly with simulated movement trajectories. Spatial covariates describing landscape, climatic, anthropogenic, and light conditions were represented as time series spanning 2011–2022 and were additionally aggregated into static “average” conditions and into a representative seasonal cycle. The latter preserved within-year seasonality while removing inter-annual variation and were used to drive simulations in which environmental conditions changed in step with movement. This framework enabled simulation of movement and evaluation of connectivity not only under static or extreme scenarios, but also under temporally evolving landscapes where environmental state and movement processes were explicitly coupled.

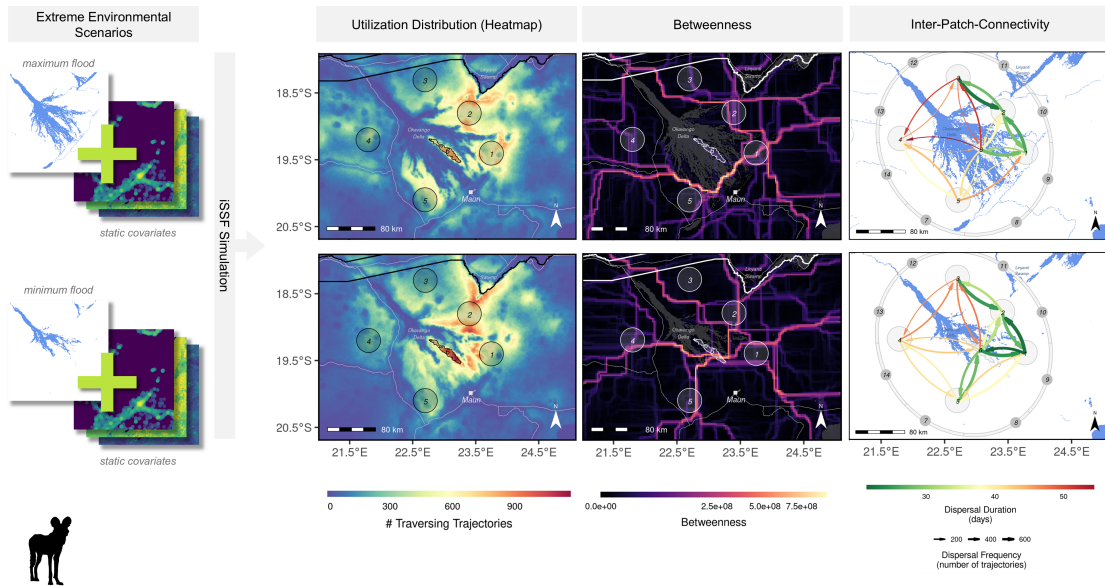


Figure A6: Connectivity maps derived from dispersal simulations of African wild dogs using SSFs. Simulations were conducted under two scenarios, once assuming a maximum flooding extent of the Okavango Delta, once assuming a minimum flooding extent. Simulated trajectories were used to compute a utilisation distribution (heatmap), betweenness map (indicating corridors), and a map of inter-patch connectivity (link-frequency and dispersal duration). Figure adapted from Hofmann et al. (2024)

## A.9 Prediction outcomes and interpretation

Model coefficients from the SSF model shed light on patterns of habitat selection and movement behaviour for African wild dogs (Figure A4). Notably, estimates of habitat selection parameters confirmed the initial notion of strong avoidance of human dominated areas and water. Results from



the simulation analysis further indicated that most major dispersal corridors were encompassed within KAZA's boundaries, though some important routes fell outside its borders [A5](#). These findings were communicated to the KAZA Secretariat to inform and improve corridor management within the conservation initiative. By highlighting shared priority areas across administrative or organisational boundaries, these predictions may also support coordination among NGOs, governmental bodies, and local management authorities. By using simulations that mechanistically captured movement behaviour and habitat selection during dispersal, the models achieved a much higher degree of realism than alternative connectivity models, and benefitted from a richer suite of connectivity metrics that could be computed on the basis of simulated trajectories. Despite the usefulness of these simulations, the authors also identified an important limitation: while the study captured environmental constraints, they failed to encapsulate social factors such as conspecific density or competitor presence. To address this, the researchers initiated a complementary camera-trap study to determine carnivore and prey distribution, which can be integrated as biotic interactions into future predictive models.

## B Additional materials

### B.1 Ecological interpretability of spatial covariates

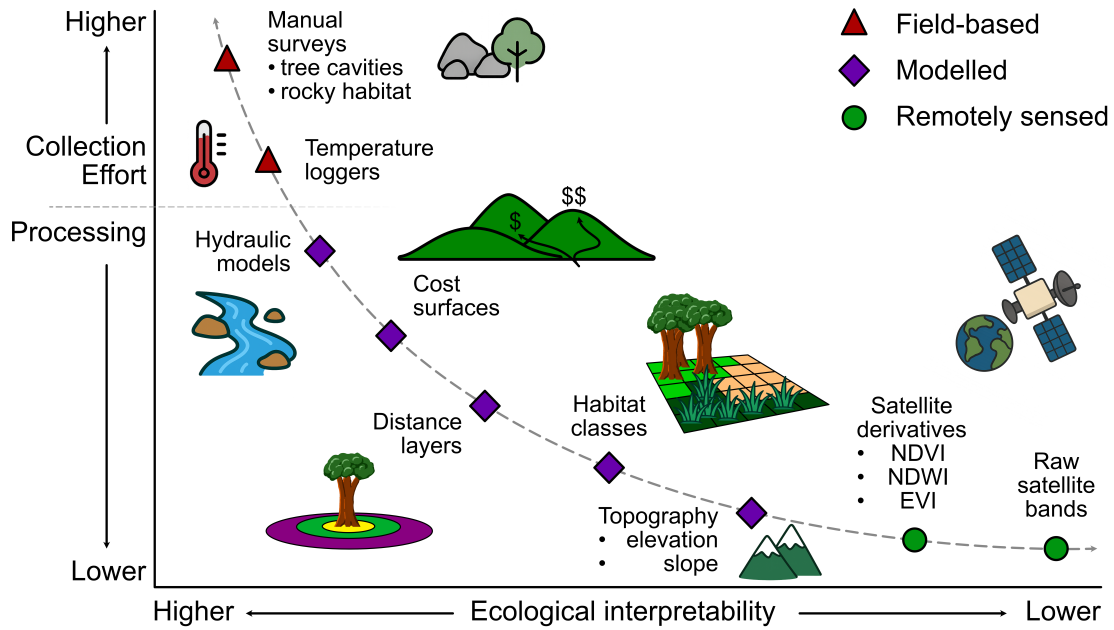


Figure A7: Conceptual overview of different types of spatial covariates, and an approximate relationship between their ecological interpretability and the amount of processing and/or modelling required to access the layers. Increased processing and modelling may reduce information content, such as the transformation from raw satellite bands to a derivative such as NDVI, but this processing can make the layers more ecologically interpretable. An additional consideration is the resolution and coverage in both space and time; satellite layers are available at relatively high spatial resolution (i.e. 10 m x 10 m) across the planet every few days, whereas cost surfaces and manual surveys for tree cavities or rocky habitat may be specific to a single area and time period, limiting the range of predictions.

## B.2 Hypothetical landscape scenarios

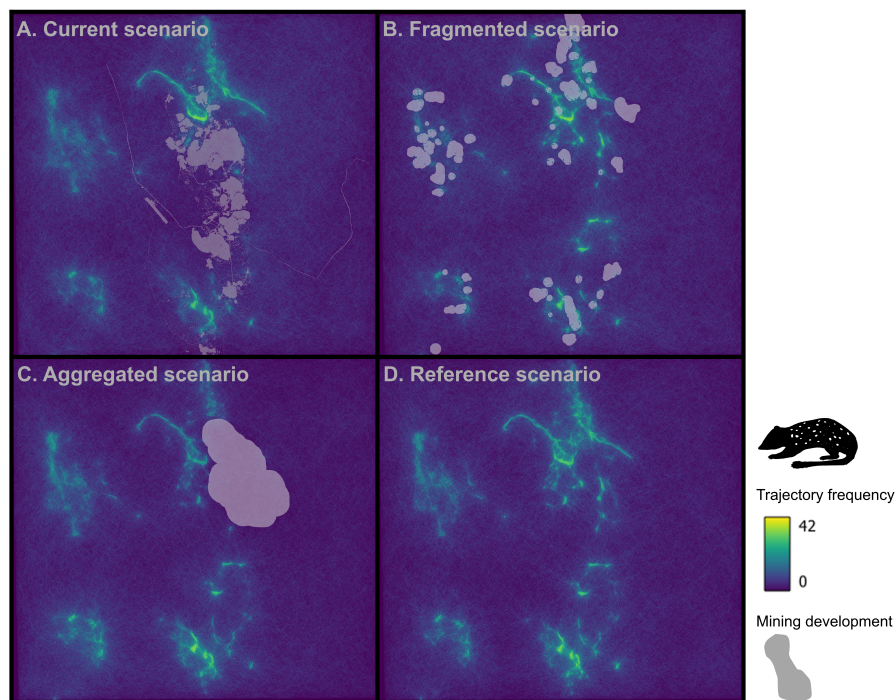


Figure A8: Utilisation distributions of northern quolls (*Dasyurus hallucatus*) under different mining landscape scenarios (current, dispersed, aggregated, non-mining), adapted from Cowan et al. (2025). The colour scale shows the traversal frequency of the simulated trajectories, and the grey shapes show the mining footprints. UD were created from 50 simulated trajectories ( $n = 438,000$  steps) for each scenario. The northern quoll icon was created by Gabriela Palomo-Munoz, and downloaded from PhyloPic under the <https://creativecommons.org/licenses/by-nc/3.0/> license.

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