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## What are we modelling and why?

1. Animal movement is often consistent across time, even though such movement types may be non-optimal in some situations;
2. The evolution of movement is challenging to study in real-world systems: spatially explicit agent-based models (ABM) are a solution;
3. Mechanistic models of intermediate complexity allow many agents in fluctuating landscapes to choose their movement at each timestep;
4. Agent replication with modification enables the study of the evolution of movement types in different regimes of spatio-temporal change.

## Fluctuating landscapes

### Spatial predictability

We use an infinite, continuous space landscape with varying range of **spatial autocorrelation** implemented as static Perlin noise[1].

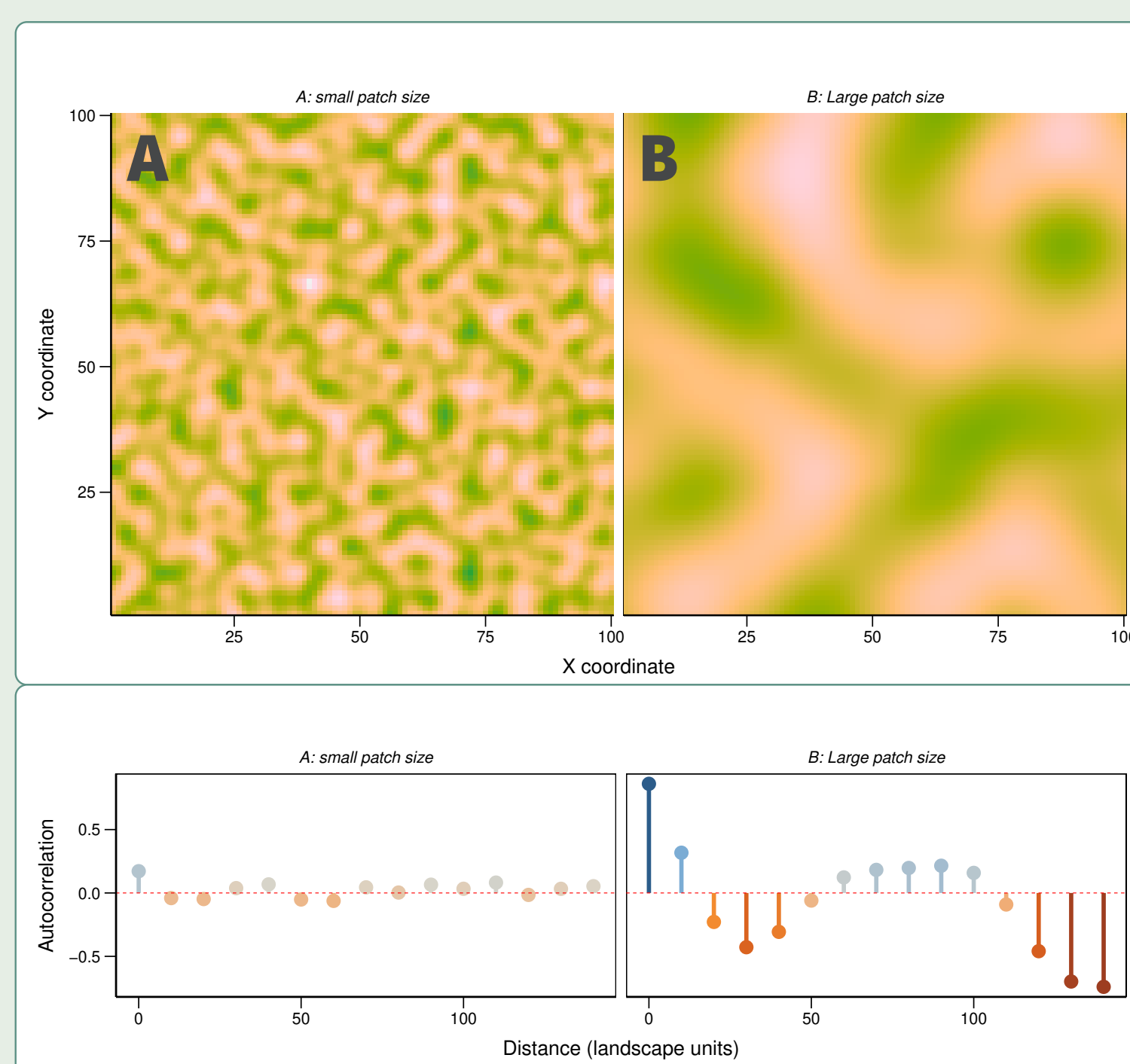


Fig. 1. Spatial autocorrelation of two landscapes generated as Perlin noise. **Landscape A** has a maximum vector field value of 20, while **landscape B** has a max vector field value of 5.

The patchy landscape A has a lower spatial autocorrelation range than B, and is less predictable in space.

### Temporal predictability

Temporal change in each simulation run is implemented as dynamic Perlin noise with a fixed frequency.

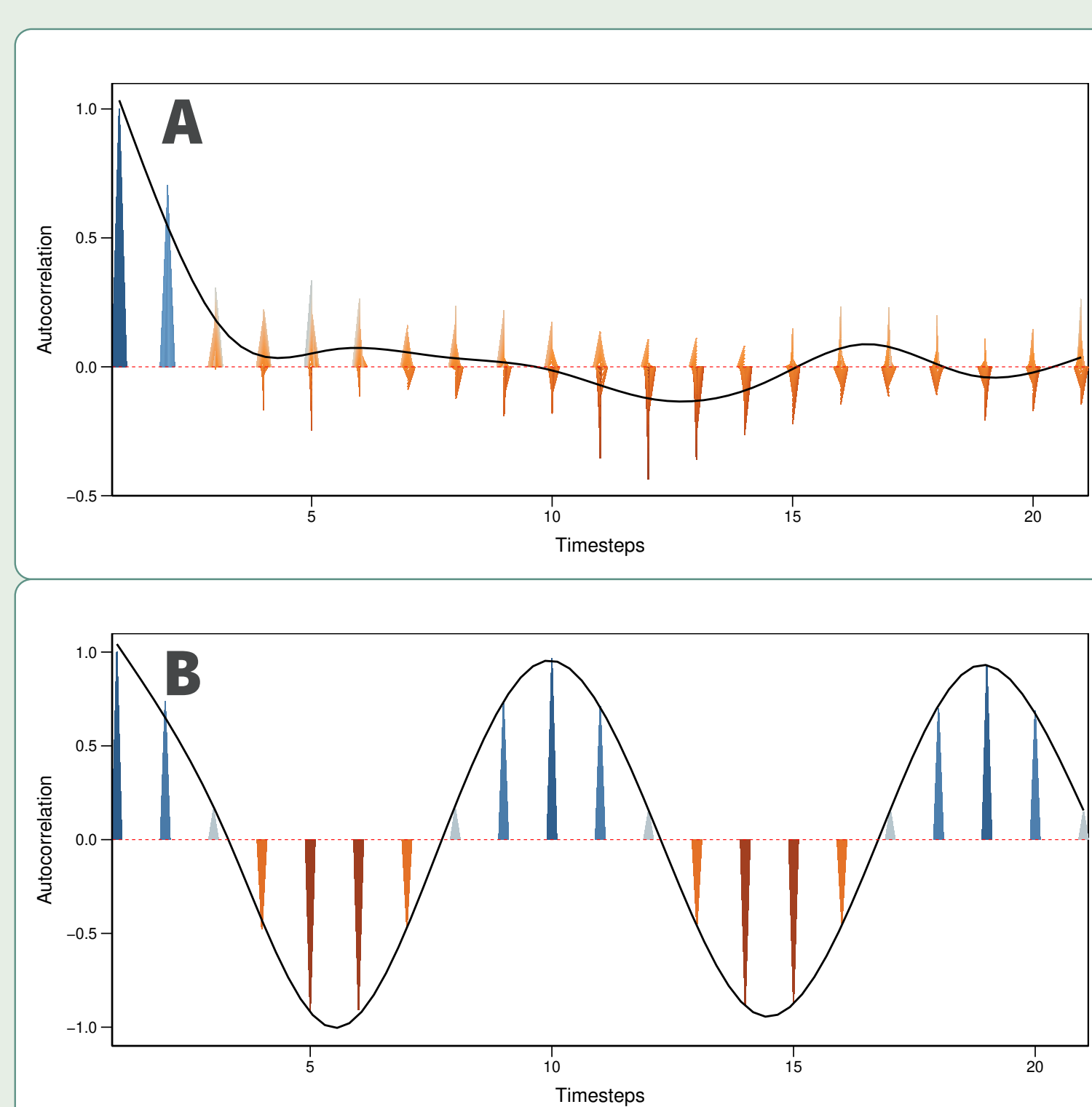


Fig. 2. Two regimes of temporal change: In A, the landscape lacks periodicity, while in B, the resource value at each point is strongly predictable over time. The periodicity of B can be varied over simulations.

## Moving agents

### Agent decisions

1. Agents use a recursive Artificial Neural Network (ANN) to process the value of **local resources** and choose their next **step-size** and **movement angle**;
2. Agents have an **inherited sampling frequency**, at which they sense the value of local resources.

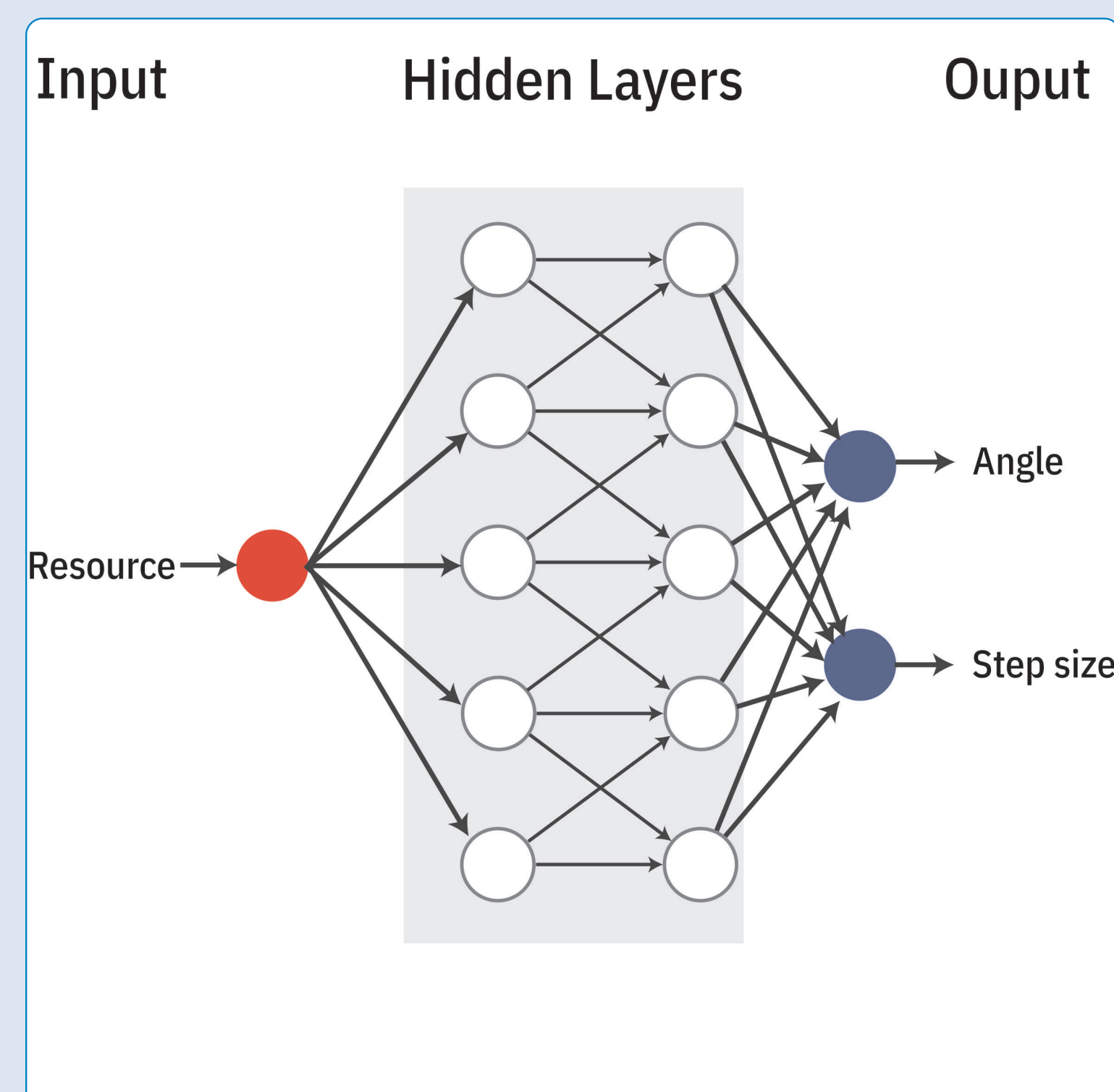


Fig. 3. The ANN takes local resources as input; this is processed through 2 hidden layers of 5 nodes each, and is used to decide a step size and movement angle.

### Process scheduling

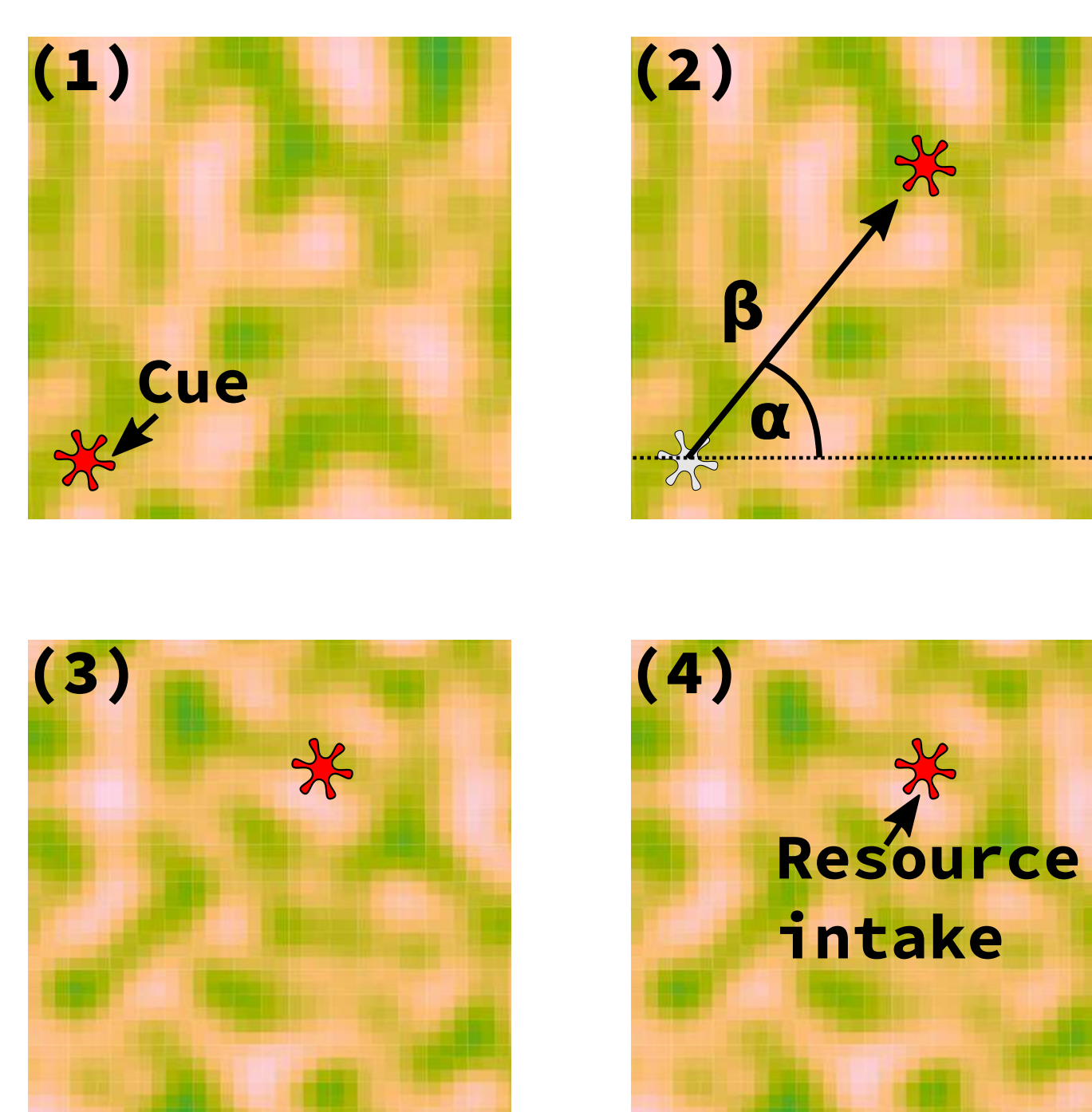


Fig. 4. (1) In timestep t, agents sample local resources, (2) move with an angle  $\alpha$  and step length  $\beta$ , (3) the landscape updates in timestep t+1, and (4) agents gather resources at their new position.

The process repeats over 100 time steps.



Courtesy Benjamin Gnep, 2018.

Fig. 5. Waders such as red knots can only sample buried resources at their own position on intertidal mudflats, and inspire our model.

## Evolutionary outcomes

### Network – phenotype mapping

Similar movement strategies may be the result of very different artificial neural network structure.

### Mode of adaptation

The evolved norm of reaction (step size ~ resource cue) will be determined by the predictability of the landscape, and the timescale of landscape change relative to agent lifetime[2].

### Movement polymorphism

Polymorphisms in movement strategies with equivalent fitness, or 'movement types' are expected to evolve in simulations with:

1. Low level of environmental predictability;
2. Intermediate, multi-generational timescale of environmental change.

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**References** [1] Perlin K. 1985. An Image Synthesizer. In: Proceedings of the 12th Annual Conference on Computer Graphics and Interactive Techniques. New York, NY, USA: ACM.

[2] Botero CA, Weissing FJ, Wright J, and Rubenstein DR. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. PNAS 112: 184–9.