Environmental Heterogeneity in Continuous-Space Continuous-Time Models

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Outline of the talk

1. Animal movement in heterogeneous space
2. Evolution of dispersal in heterogeneous space
Where is the butterfly heading?
Underlying mechanisms

Mathematical modelling.
Aim: to understand causal relationships at the general level

Ecological phenomenon

Statistical modelling.
Aim: to find out factors shaping empirical data

Approaches in ecological modelling
Empirical approaches for studying butterfly movements

Harmonic radar

Mark-recapture

mechanisms

Flight speed, directional persistence, behaviour at edges, ...

phenomenon

Movements in a mosaic of meadows, cultivated fields, and forests

Ovaskainen et al. 2009 (PNAS)

Ovaskainen et al. 2008 (American Naturalist)
What is the movement rate of a butterfly?

Mark-recapture data depends on

i) the properties of the species
ii) the structure of the landscape
iii) the design of the study
Combining the "mathematical" and "statistical" approaches

State-space models, Hidden Markov models, process based models...

Biological process of interest = process model, "mathematical modelling"

Hidden truth and process dynamics, \( x_t = g(x_{t-1}) \)

Observations and measurement model, \( y_t = h(x_t) \)

The way data are collected = observation model, "statistical modelling"
Simple model for butterfly movement: random walk + habitat selection

Time evolution of the probability density \( \nu(x,t) \) for the individual's location:

\[
\frac{\partial \nu}{\partial t} = Lv, \quad Lf(x) = \sum_{i,j} \partial_{ij} [a_{ij}(x)f(x)] + \sum_i \partial_i [b_i(x)f(x)] - c(x)f(x).
\]
Edges can be narrow compared to the dimensions of the landscape elements
Linear landscape elements 1/3: edge-mediated behaviour

1-dimensional approximation of the 2-dimensional model

Matching condition: discontinuous probability density, continuous flux

Relative difference $k$ is called the habitat selection parameter

Linear landscape elements 2/3: corridors

Matching condition: a non-zero probability that the individual is exactly in line representing the corridor

Ovaskainen & Crone (2010)
Linear landscape elements 3/3: barriers

2-dimensional model

1-dimensional approximation

Matching condition: discontinuity in probability density averages out with a time delay

Ovaskainen & Crone (2010)
Simple diffusion
Simple diffusion
Diffusion with corridors
Diffusion with corridors
Diffusion with barriers
Building biological assumptions in diffusion models: hypothetical movements in a mountainous landscape

Preference depends on altitude

Diffusion depends on altitude

Preference for forest over rocks

Colour: habitat preference (the darker the better)

Ellipse: diffusion

Arrow: advection

Roads as corridors

Anisotropy depends on slope

Advection downhill

Ovaskainen & Crone (2010)
Model predictions

- Preference depends on altitude
- Diffusion depends on altitude
- Preference for forest over rocks

Colour: probability density (the darker the higher)

Circle: initial position

Line: sample path

- Ovaskainen & Crone (2010)
Fitting models to data

Ovaskainen 2004 (Ecology), Ovaskainen et al. 2008 (Ecology), Ovaskainen et al. 2008 (American Naturalist)

Model with 7 parameters:
• habitat-specific diffusion coefficients (3 parameters)
• habitat selection (2 parameters, 1 normalized to one)
• mortality (1 parameter)
• capture probability (1 parameter)

Mikko Kuussaari      Miska Luoto      Iiiro Ikonen
Computing the likelihood with the finite element method
The time-evolution of probability density

Observation at time $t=5$

Initial location
Observation model:
Also not finding the individual is data

The capture probability $p$ is the probability of observing an individual given that it actually is at the site.

\[
x(1-p) \quad \frac{y}{1-px}
\]

Ovaskainen (Ecology 2004)
Biological inference from parameter estimates

Females move faster than males outside the breeding habitat
Example of model prediction

What is the probability that the butterfly ever visits this meadow?

Theorem. The hitting probability satisfies

$$L^* p(x) = 0$$

with boundary condition $B^{C_1}$.

Ovaskainen & Cornell 2003
(Journal of Applied Probability)
Model validation

Landscape A

Landscape B

Prediction

Model parameterized with data from Landscape A, prediction for Landscape B

Empirical data on Landscape B
Regional environmental centre opened a movement corridor in autumn 2002

Effect of a movement corridor

Fraction of butterflies

Moved between populations
Moved to the corridor area

Northern butterfly population

Southern butterfly population

2002
2003
What kind of a movement corridor would work?

Movement probability $p_1$

Movement probability $p_2$

Corridor helps ($p_2 > p_1$)

Corridor harms ($p_2 < p_1$)

Colour: effect of the corridor ($p_2/p_1$)
Outline of the talk

1. Animal movement in heterogeneous space

2. Evolution of dispersal in heterogeneous space
Landscape structure controlled by patch density, size, quality and turnover

- Patches $p$ appear at random locations at rate $\theta \sigma$ (per unit area)
- Patches disappear at rate $\sigma$ (per patch)
- Landscape quality $\omega = \Psi_p * p$
- The kernel controls patch size (length scale) and patch quality (integral)
Evolutionary model of dispersal

- Parameters at low density: fecundity $f$, establishment $e$, death $d$.
- Density-dependence affects death rate. Countour lines: local density of individuals
- Landscape quality affects fecundity

\[ f = f_0 \omega \]

Mean-field model: logistic population growth:

\[ \frac{dN}{dt} = rN(1 - N / K) \]
The model is a marked point process...

...or a Markov evolution in the space of finite configurations...

...and you can write it down as a spatial moment equation
Model analysis by moment closures or perturbation expansions

Approaching mean-field limit with length scale parameter $L$

\[ K(x) = \frac{k(x/L)}{L^d} \]

Expansion of density:

\[ \bar{n}(t) = n_0(t) + \frac{n_1(t)}{L^d} + \frac{n_2(t)}{L^{2d}} + \ldots \]

The expansion is asymptotically exact, but some moment closures may work better for small $L$. 

- Order $0$: 
  - Symmetric $(4-1-1)$ power-2 moment closure
- Order $1$: 
  - Asymmetric $(4-1-1)$ power-2 moment closure
- Order $2$:

![Graph showing the comparison of different moment closures](graph.png)
Evolutionary model of dispersal

Parameters at low density: fecundity $f$, establishment $e$, death $d$.

Density-dependence affects death rate. Contour lines: local density of individuals.

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$$f = f_0 \omega$$

Mean-field model: logistic population growth:

$$\frac{dN}{dt} = rN(1 - N/K)$$
Two ways of modeling evolution

Evolutionary Stable Strategy (ESS)

Assume a monomorphic population, see if a mutant can invade (adaptive dynamics, separation of ecological and evolutionary time-scales)

Evolutionary Stable Frequency Distribution (ESFD)

Assume a polymorphic population persisting in a balance between mutation and selection (coupled ecological and evolutionary dynamics)

North, Cornell and Ovaskainen, Evolution (2011)
North et al., Evolution (2010)
Two ways of modeling evolution

**ESS**
Eigenvalue perturbation expansion, pairwise invasibility plots

**ESFD**
Density perturbation expansion
Life-history & landscape structure influencing dispersal evolution

**STATIC LANDSCAPES, TOTAL AMOUNT OF HABITAT CONSTANT**

**DYNAMIC LANDSCAPES, TOTAL AMOUNT OF HABITAT CONSTANT**

![Graphs and images illustrating the impact of habitat structure on dispersal evolution.](image)

- **ESFD dispersal index**
  - high patch quality
  - low patch quality
  - small patches
  - large patches

- **STATIC LANDSCAPES UNDERGOING HABITAT LOSS**
  - **DYNAMIC LANDSCAPES UNDERGOING HABITAT LOSS**
Sometimes the coupling between ecological and evolutionary dynamics makes a qualitative difference.
Summary

- State-space models include a process model and an observation model, allowing one to bring biological knowledge into statistical inference, and estimate parameters that are not observed directly.

- Diffusion-advection models provide a flexible framework for incorporating environmental heterogeneity into movement models.

- Marked point processes can be used to study ecological and evolutionary dynamics in heterogeneous space. The model assumptions are formulated at the level of individuals, and emerging population level patterns can be studied using simulations or various approximations.
References (2008-)


