Environmental Heterogeneity in Continuous-Space Continuous-Time Models

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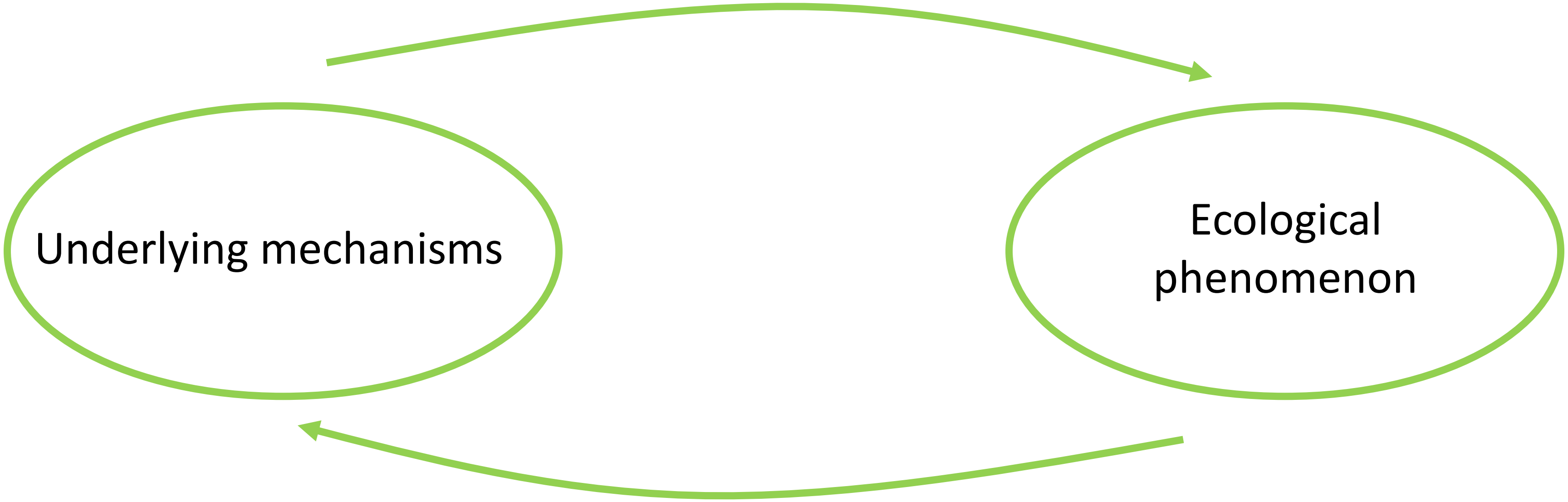
Outline of the talk

1. Animal movement in heterogeneous space
2. Evolution of dispersal in heterogeneous space

Where is the butterfly heading?

Approaches in ecological modelling



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

Underlying mechanisms

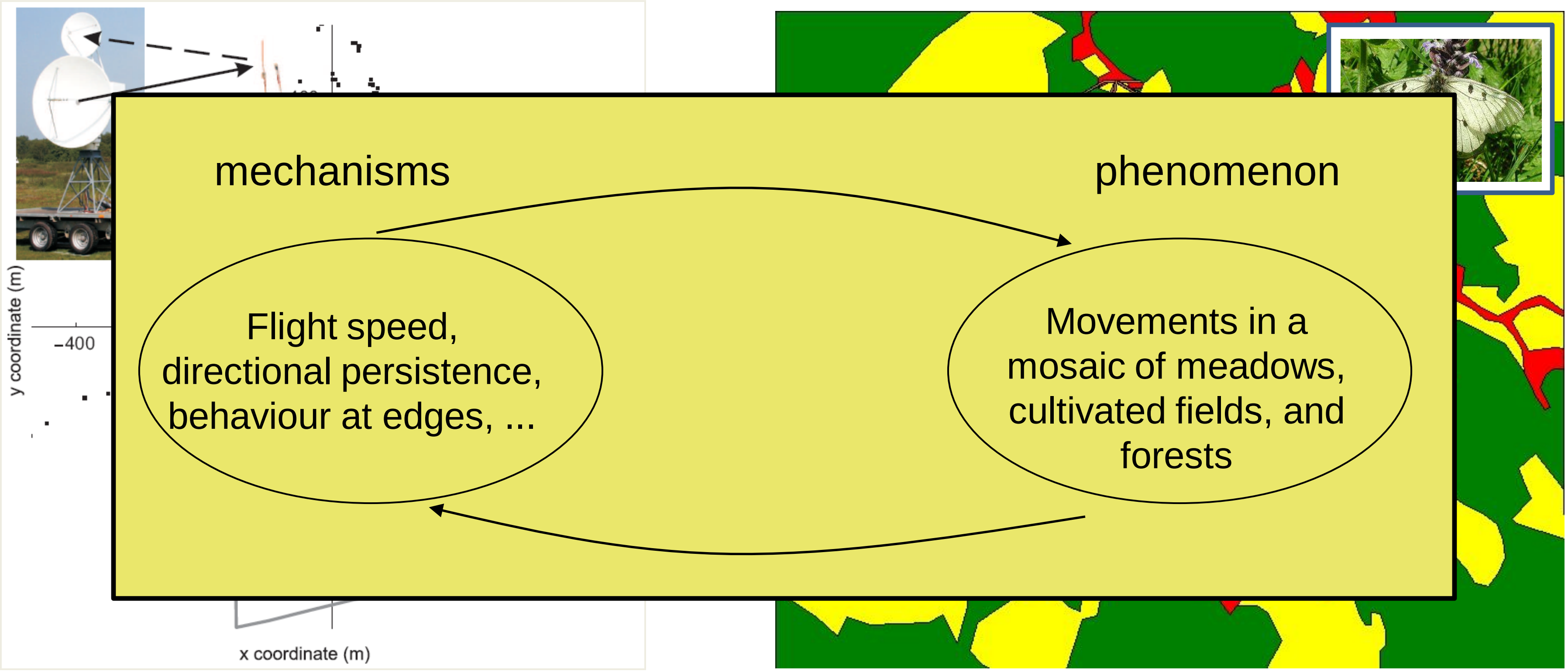
Ecological phenomenon

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

Empirical approaches for studying butterfly movements

Harmonic radar

Mark-recapture



mechanisms

phenomenon

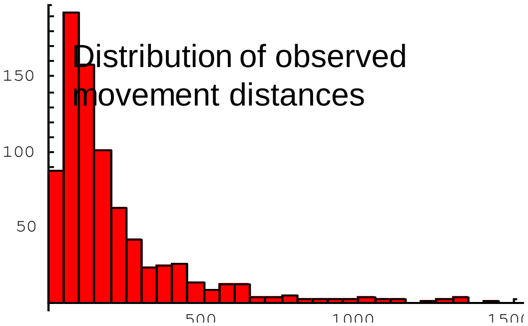
Flight speed, directional persistence, behaviour at edges, ...

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

Ovaskainen et al. 2009 (PNAS)

Ovaskainen et al. 2008 (American Naturalist)

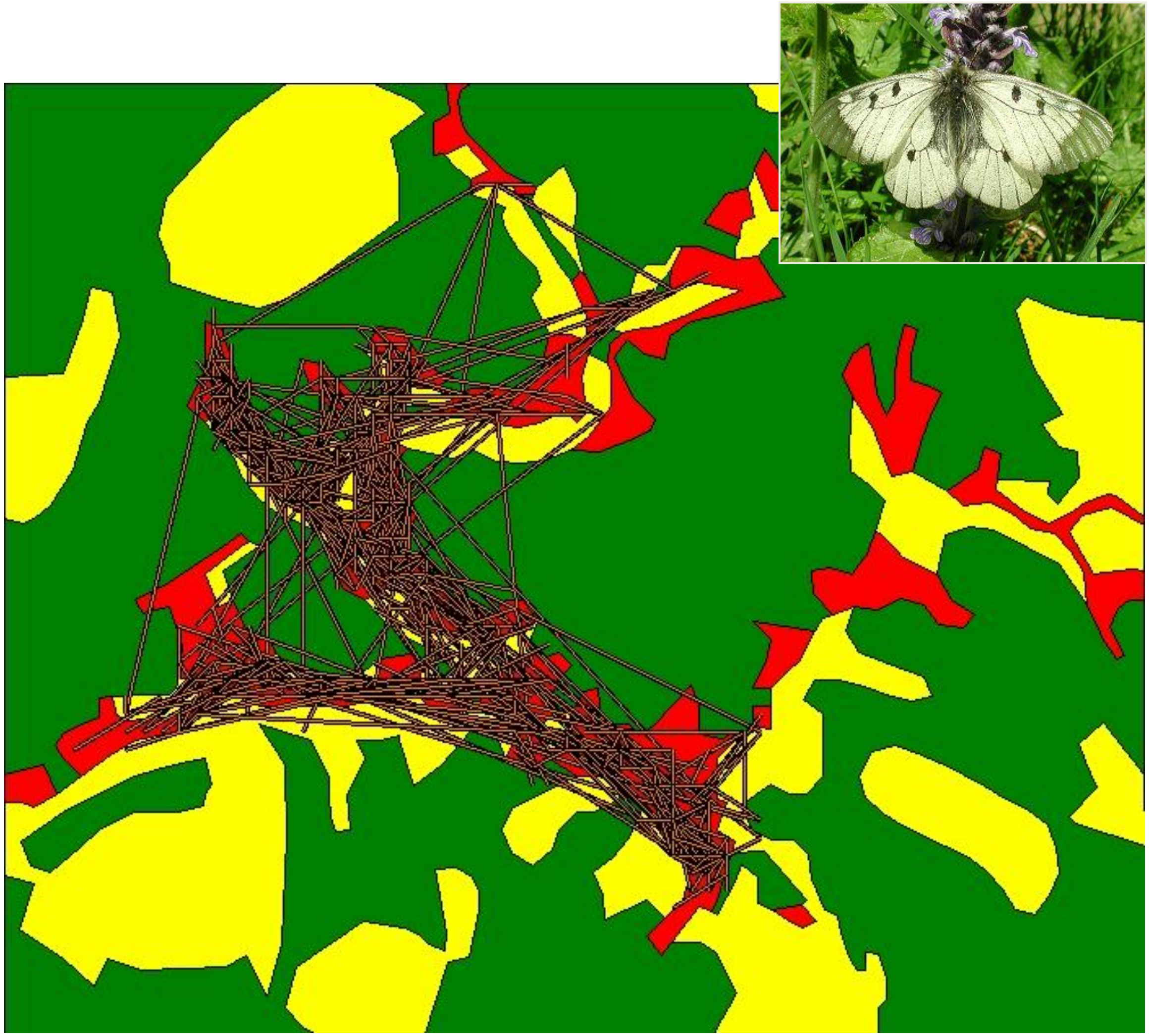
What is the movement rate of a butterfy?



Distribution of observed movement distances

Mark-recapture data depends on

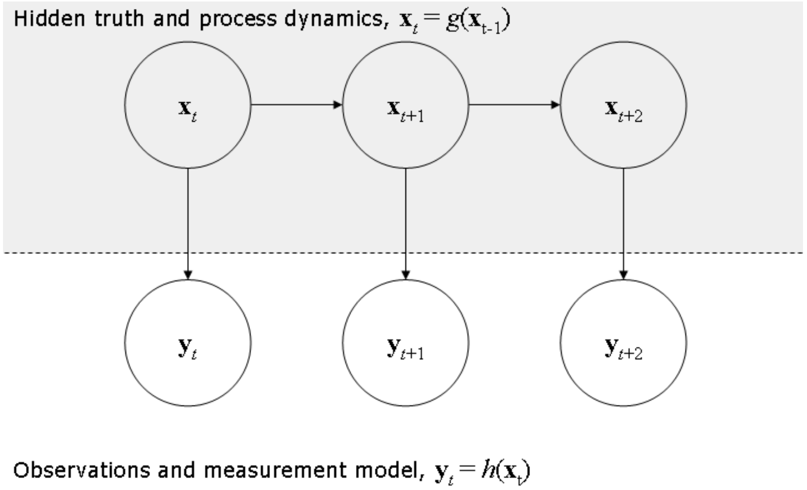
i) the properties of the species
ii) the structure of the landscape
iii) the design of the study



Combining the "mathematical" and "statistical" approaches

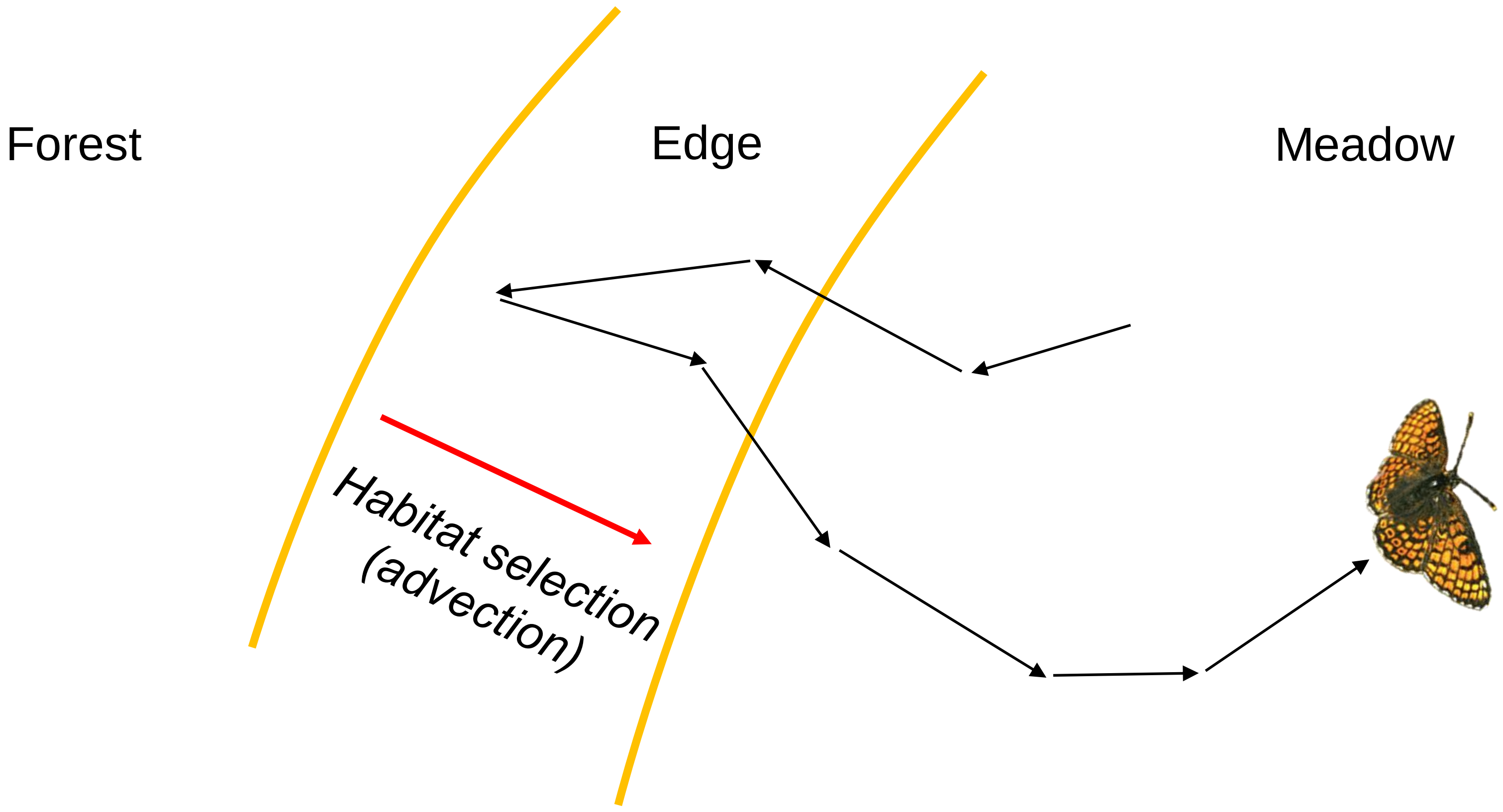
State-space models, Hidden Markov models, process based models...

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



The way data are collected = observation model, "statistical modelling"

Simple model for butterfly movement: random walk + habitat selection



Forest

Edge

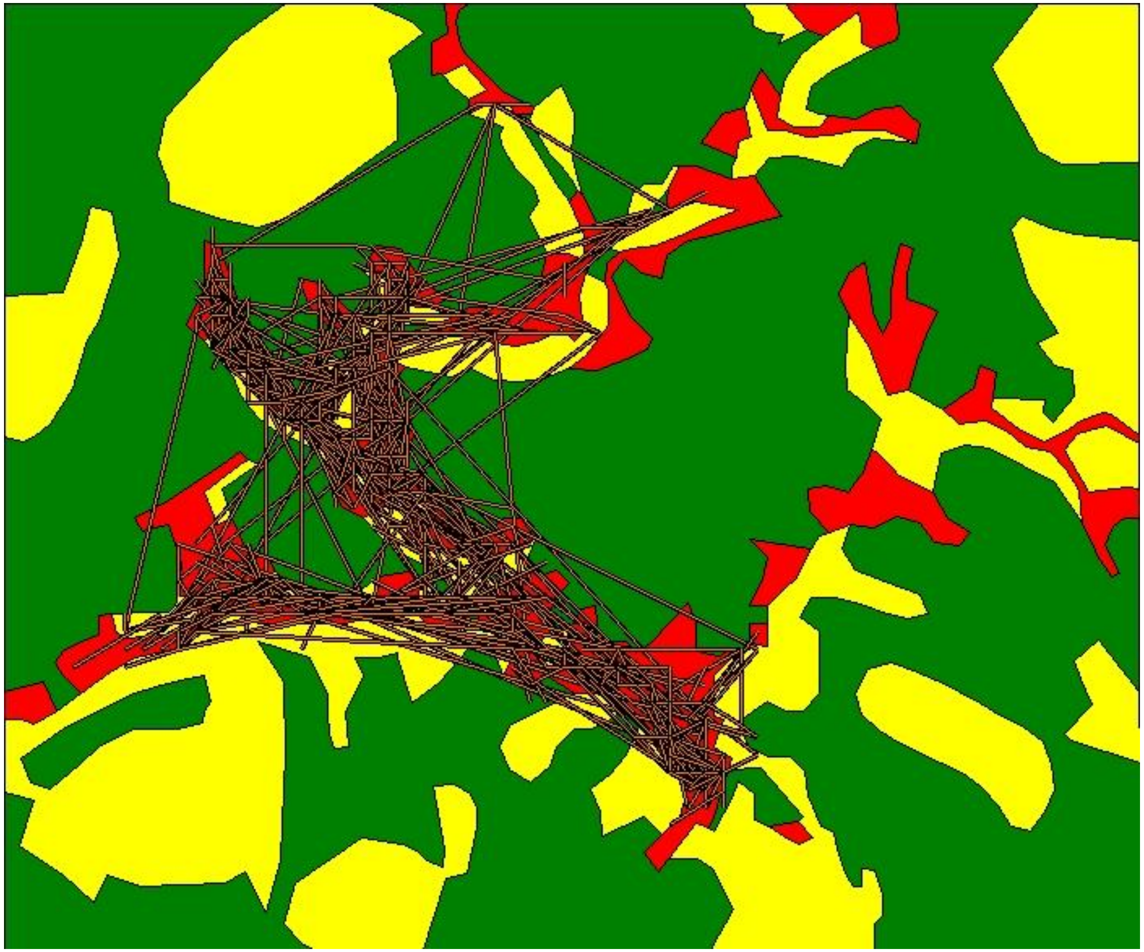
Meadow

Habitat selection (advection)

Time evolution of the probability density $v(\mathbf{x},t)$ for the individual's location:

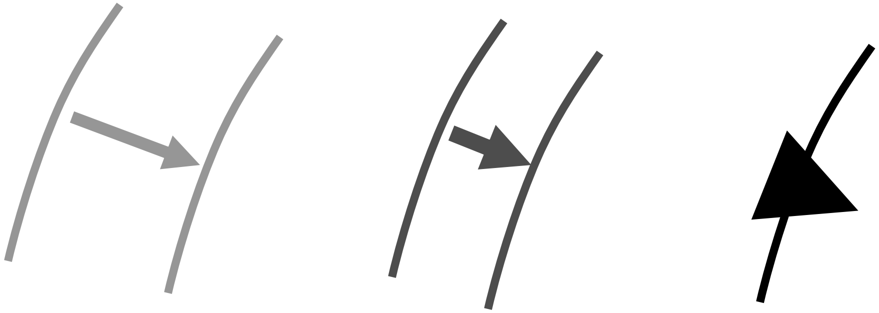
$$\frac{\partial v}{\partial t} = Lv, \qquad Lf(\mathbf{x}) = \sum_{i,j} \partial_{ij}[a_{ij}(\mathbf{x}) f(\mathbf{x})] + \sum_i \partial_i [b_i(\mathbf{x}) f(\mathbf{x})] - c(\mathbf{x}) f(\mathbf{x}).$$

Edges can be narrow compared to the dimensions of the landscape elements



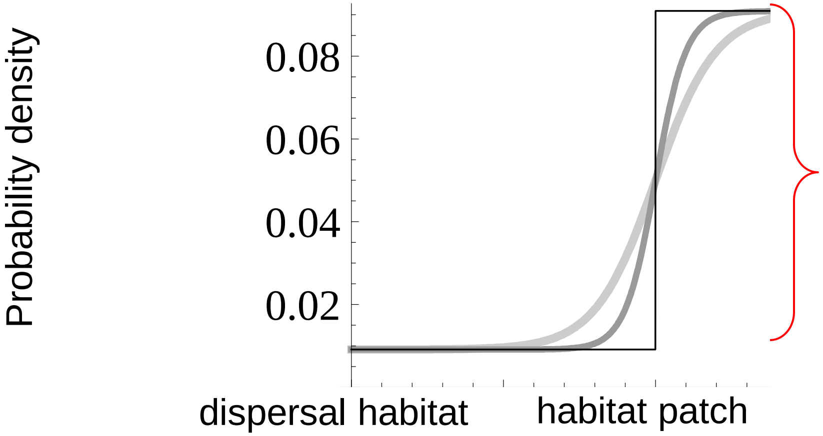
Linear landscape elements 1/3: edge-mediated behaviour

1-dimensional approximation of the 2-dimensional model



Matching condition:
discontinuous probability
density, continuous flux

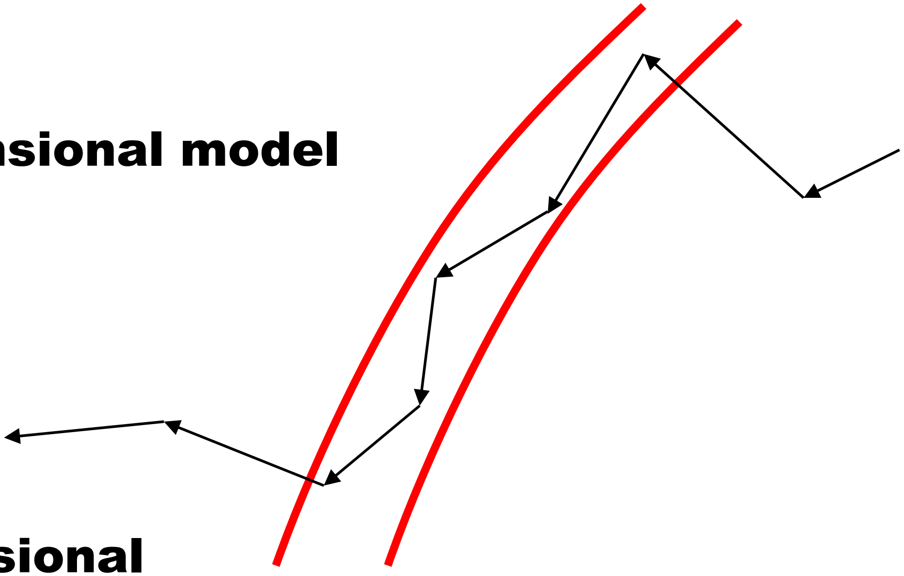
(Ovaskainen & Cornell, Journal of Applied Probability 2003)

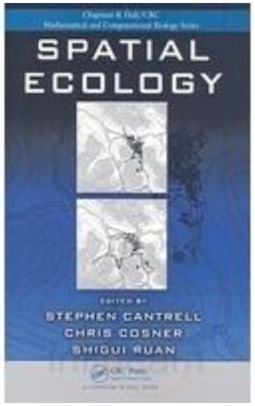


Relative difference *k* is called the habitat selection parameter

Linear landscape elements 2/3: corridors

2-dimensional model

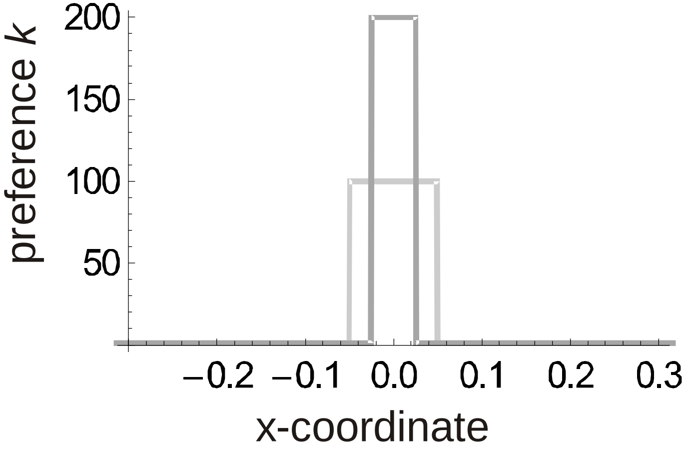


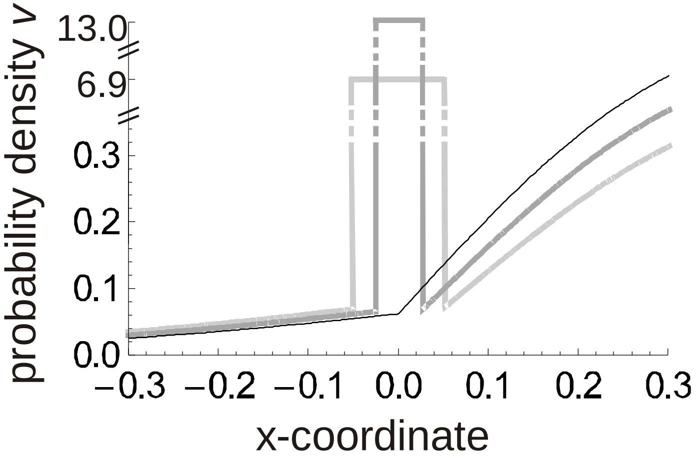


Ovaskainen & Crone (2010)

1-dimensional approximation

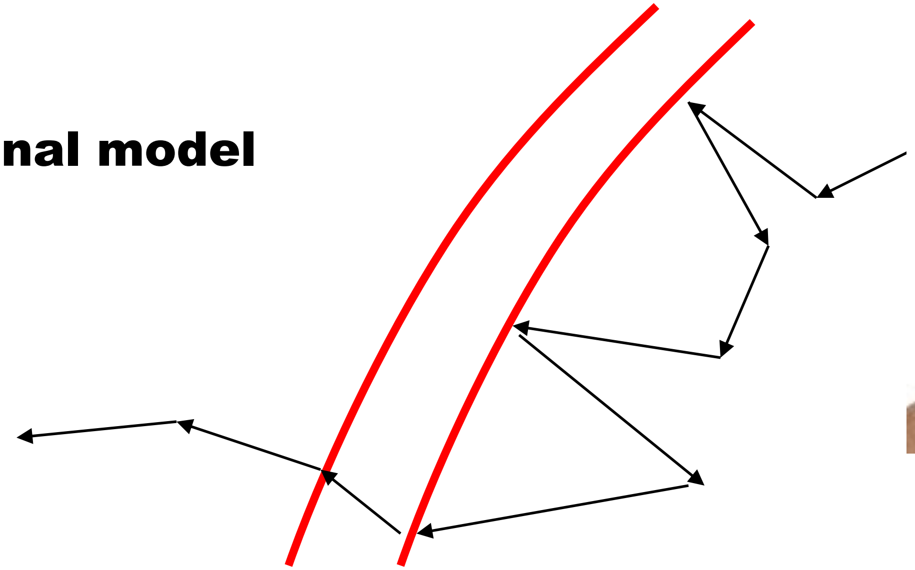
Matching condition: a non-zero probability that the individual is exactly in line representing the corridor

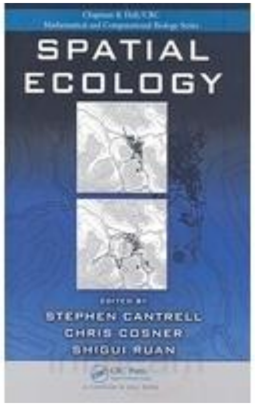




Linear landscape elements 3/3: barriers

2-dimensional model

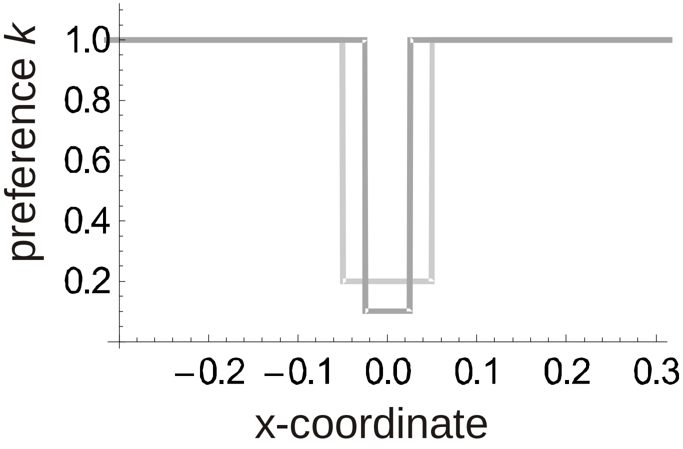


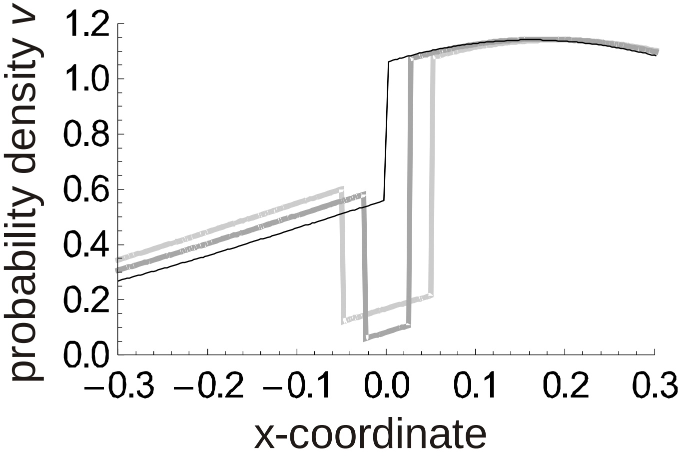


Ovaskainen & Crone (2010)

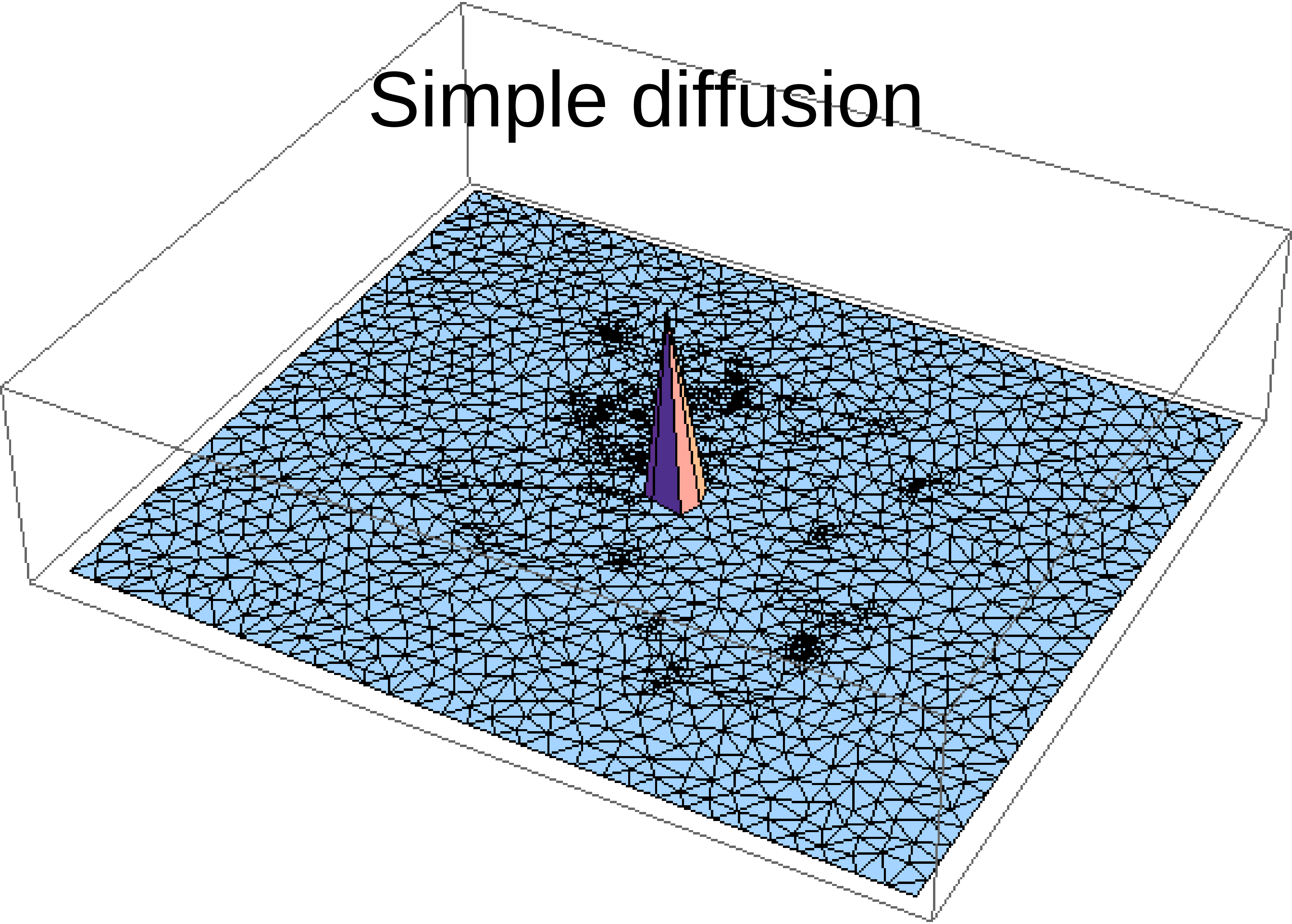
1-dimensional approximation

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

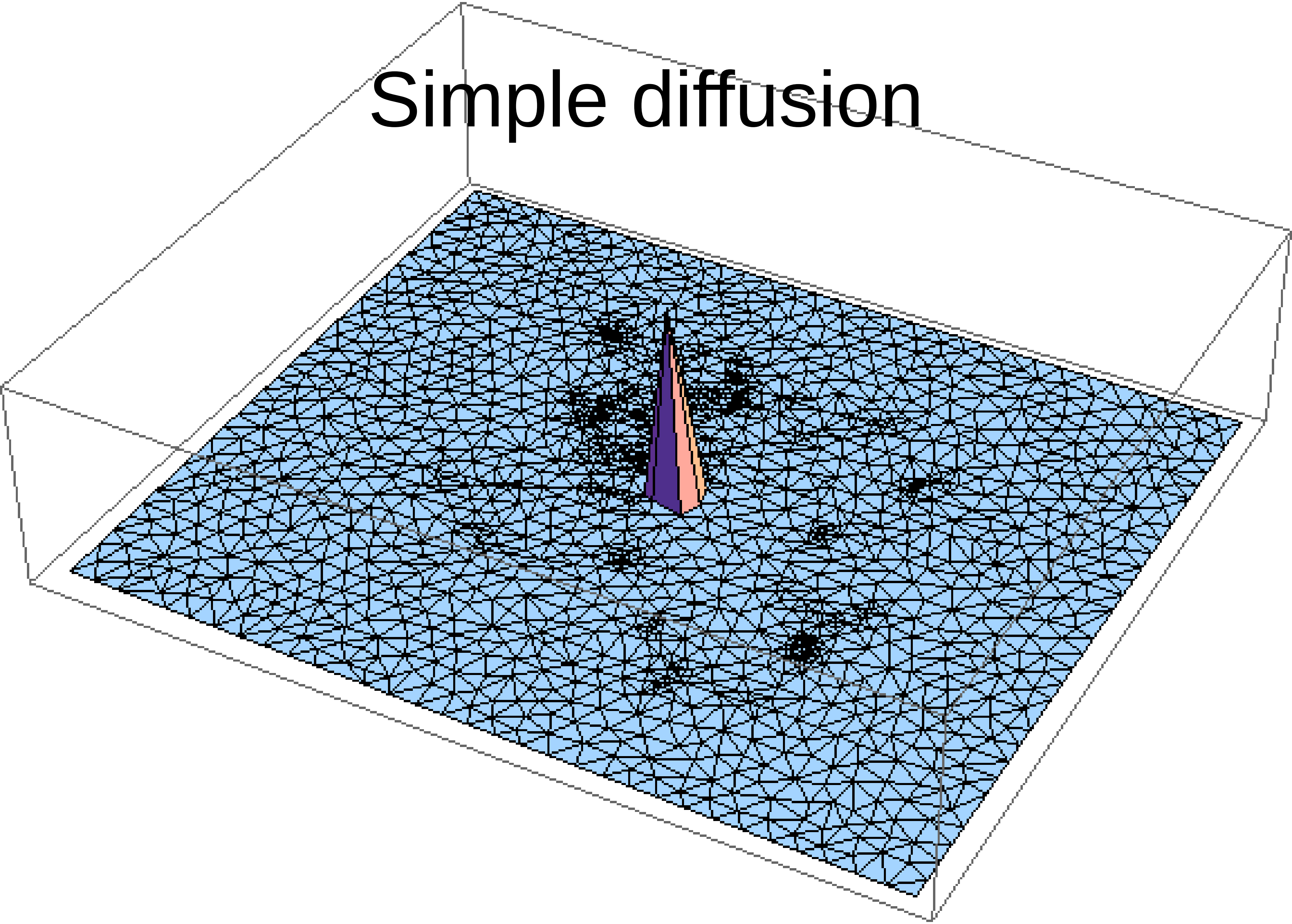




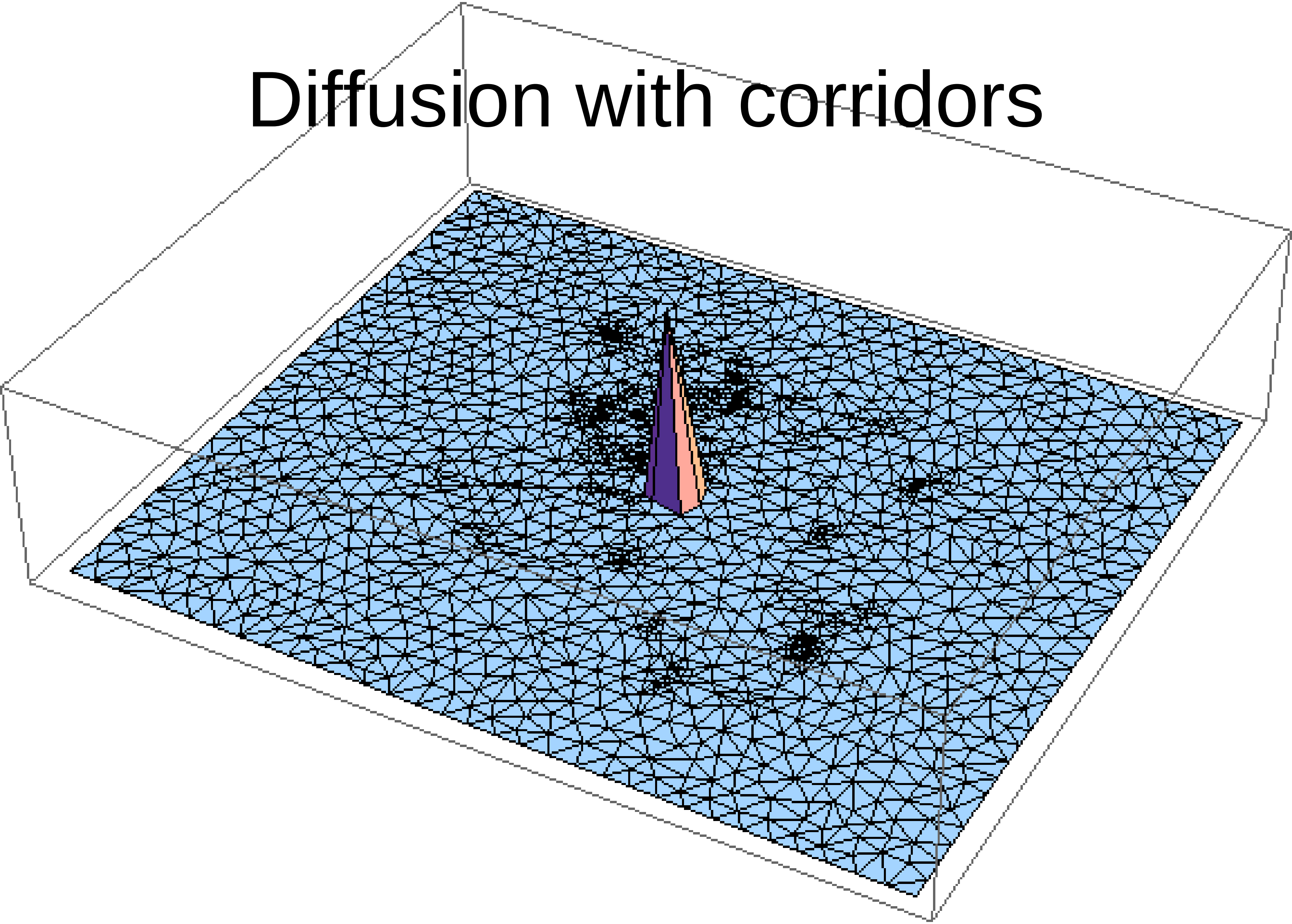
Simple diffusion



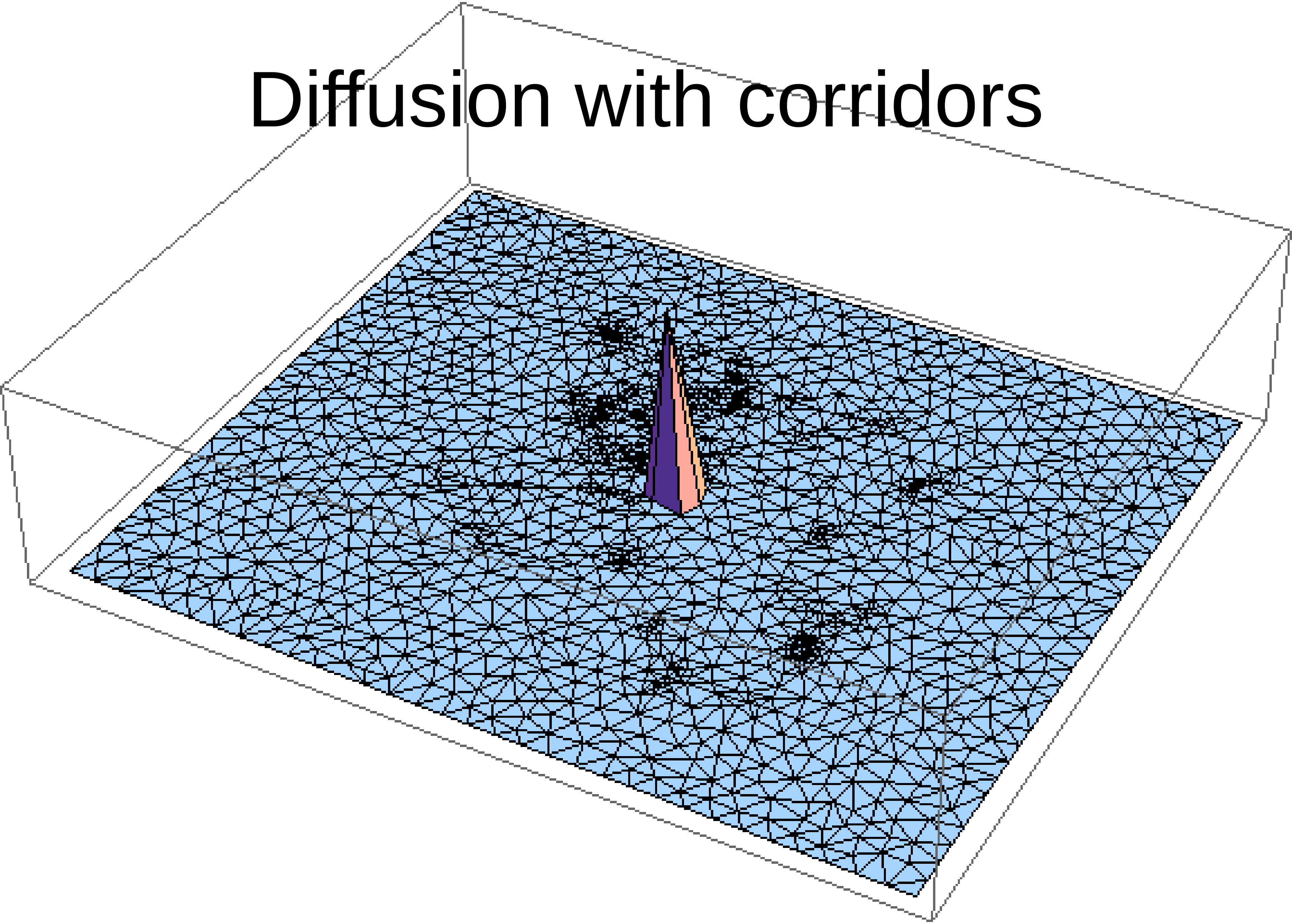
Simple diffusion



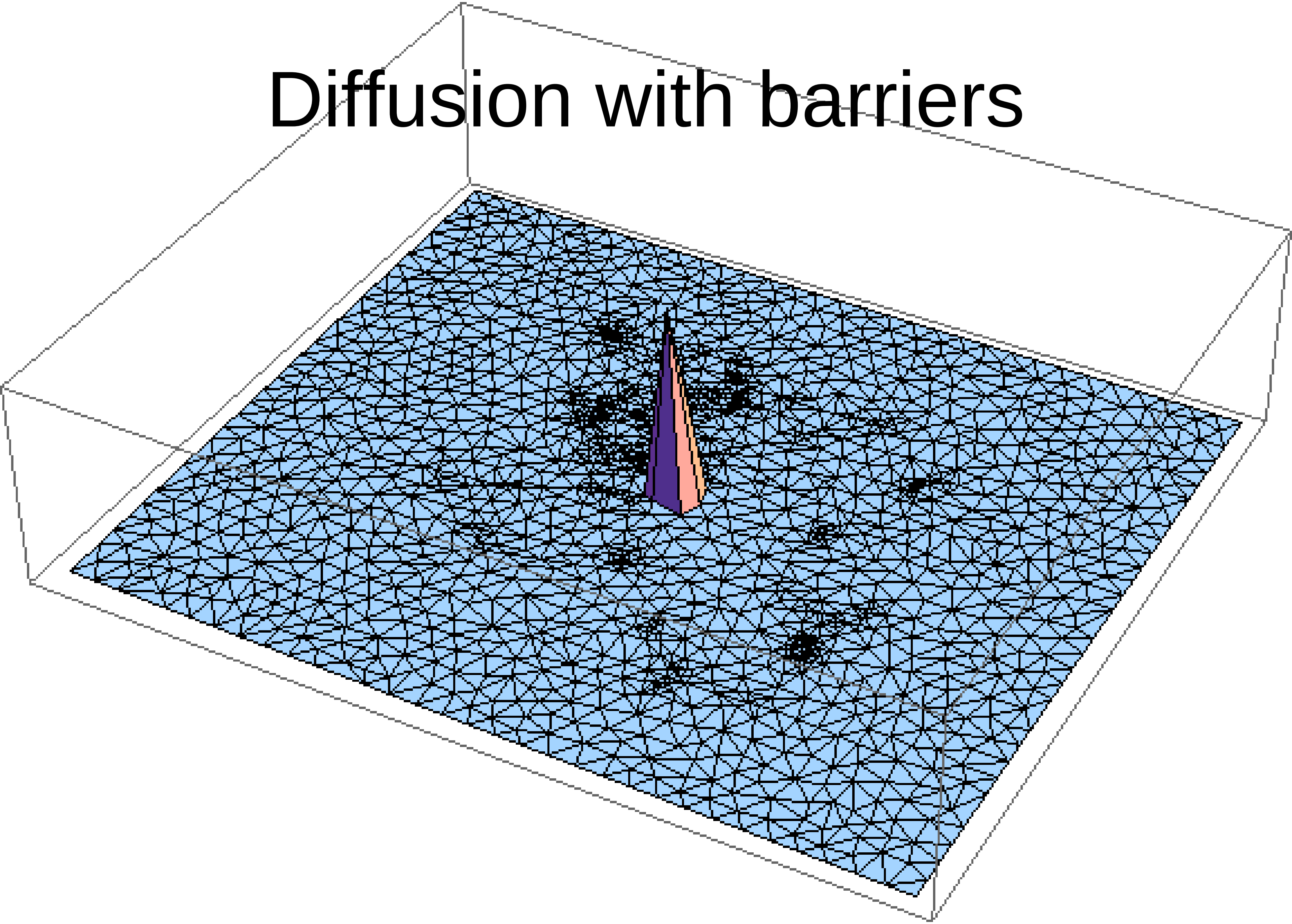
Diffusion with corridors



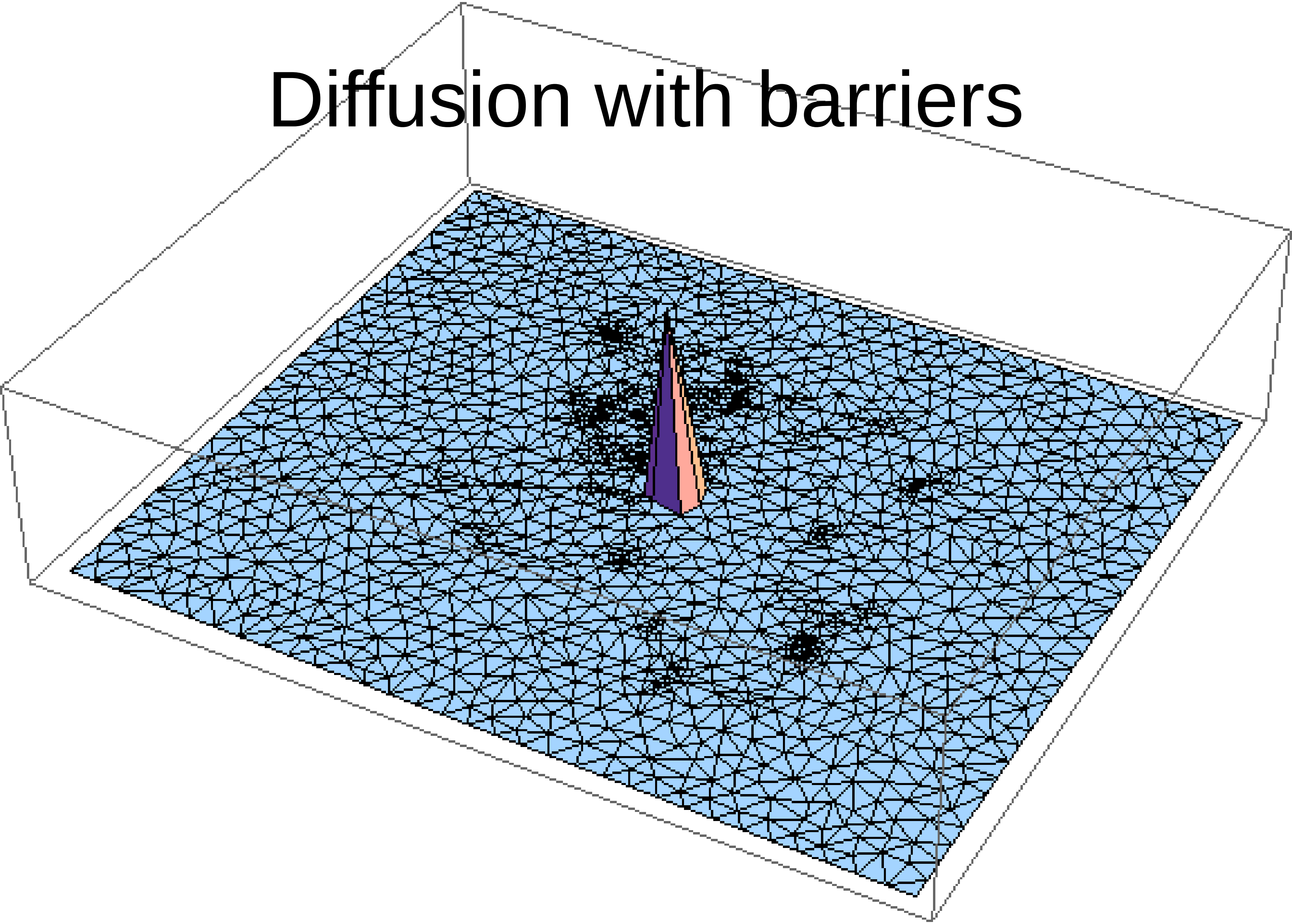
Diffusion with corridors



Diffusion with barriers



Diffusion with barriers



Building biological assumptions in diffusion models: hypothetical movements in a mountainous landscape

Colour: habitat preference (the darker the better)

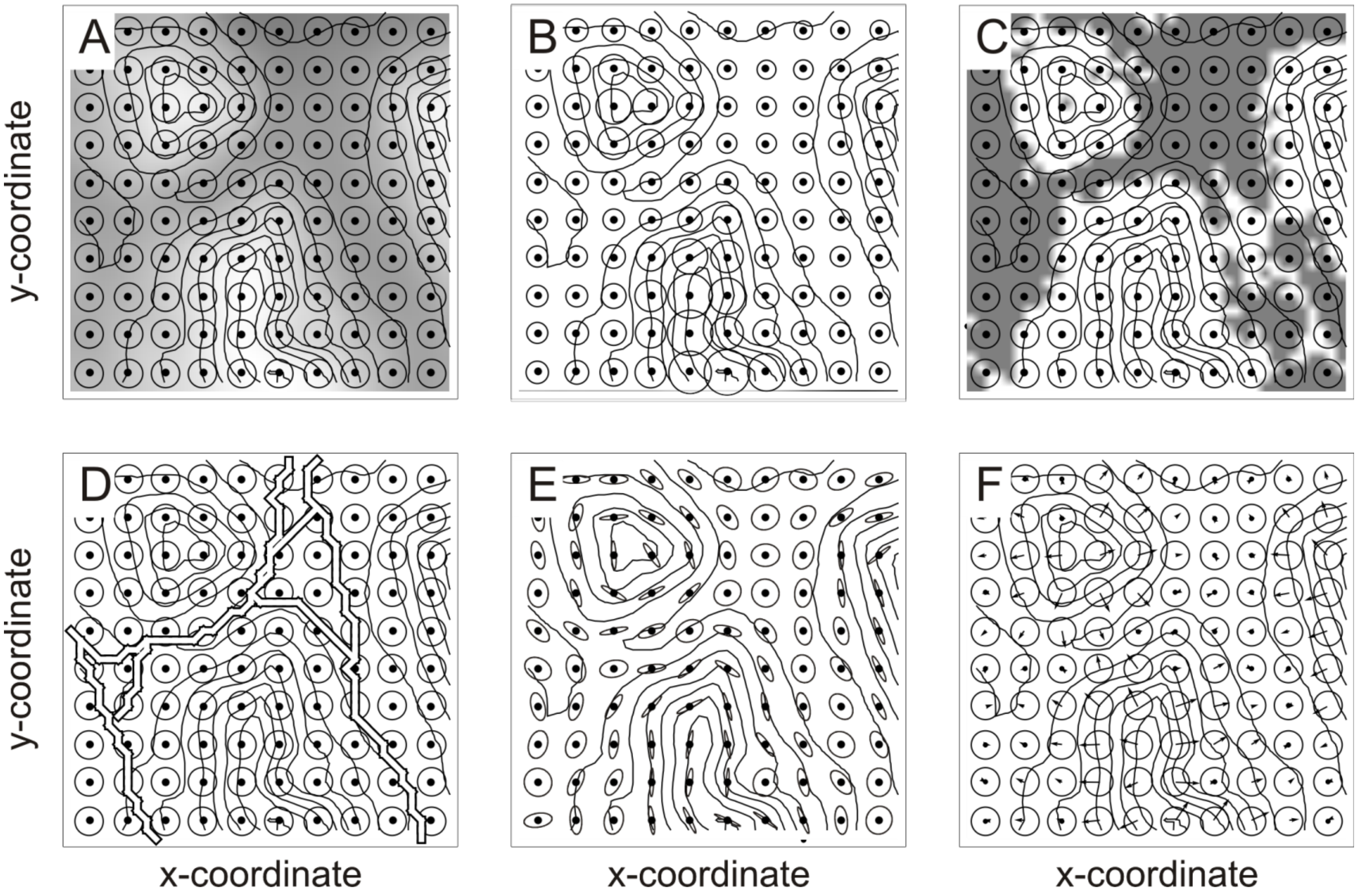
Ellipse: diffusion

Arrow: advection

Preference depends on altitude

Diffusion depends on altitude

Preference for forest over rocks



Roads as corridors

Anisotropy depends on slope

Advection downhill

Ovaskainen & Crone (2010)

Model predictions

Colour: probability density (the darker the higher)

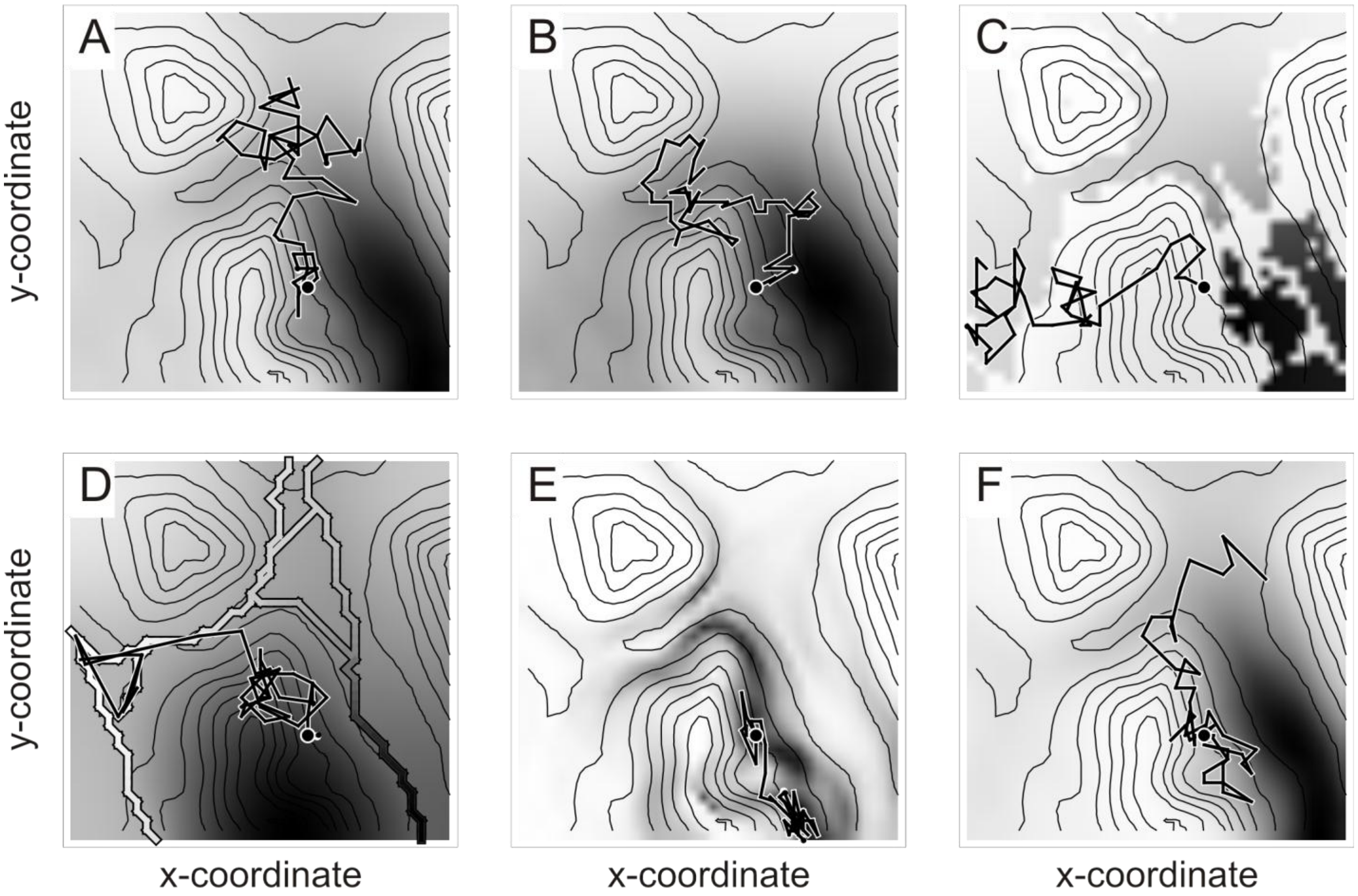
Circle: initial position

Line: sample path

Preference depends on altitude

Diffusion depends on altitude

Preference for forest over rocks



Roads as corridors

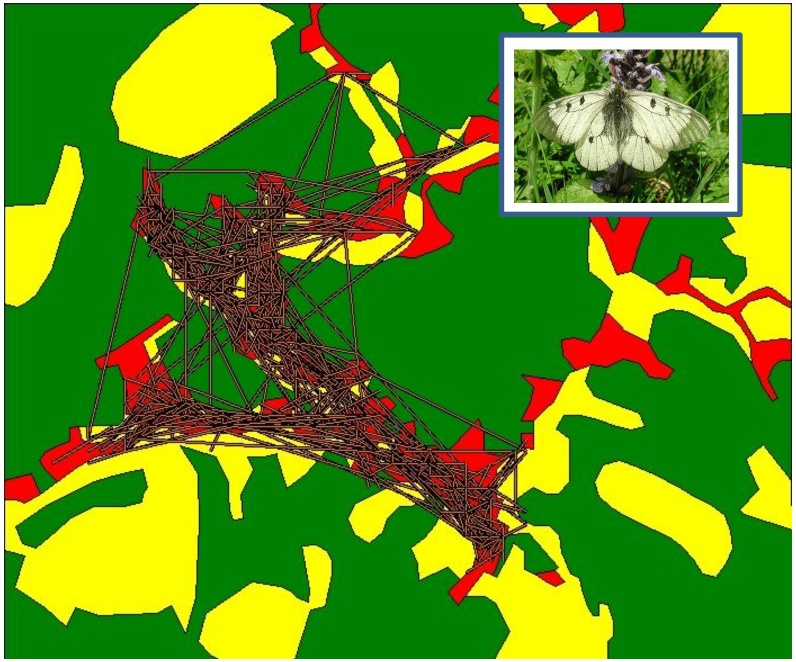
Anisotropy depends on slope

Advection downhill

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:

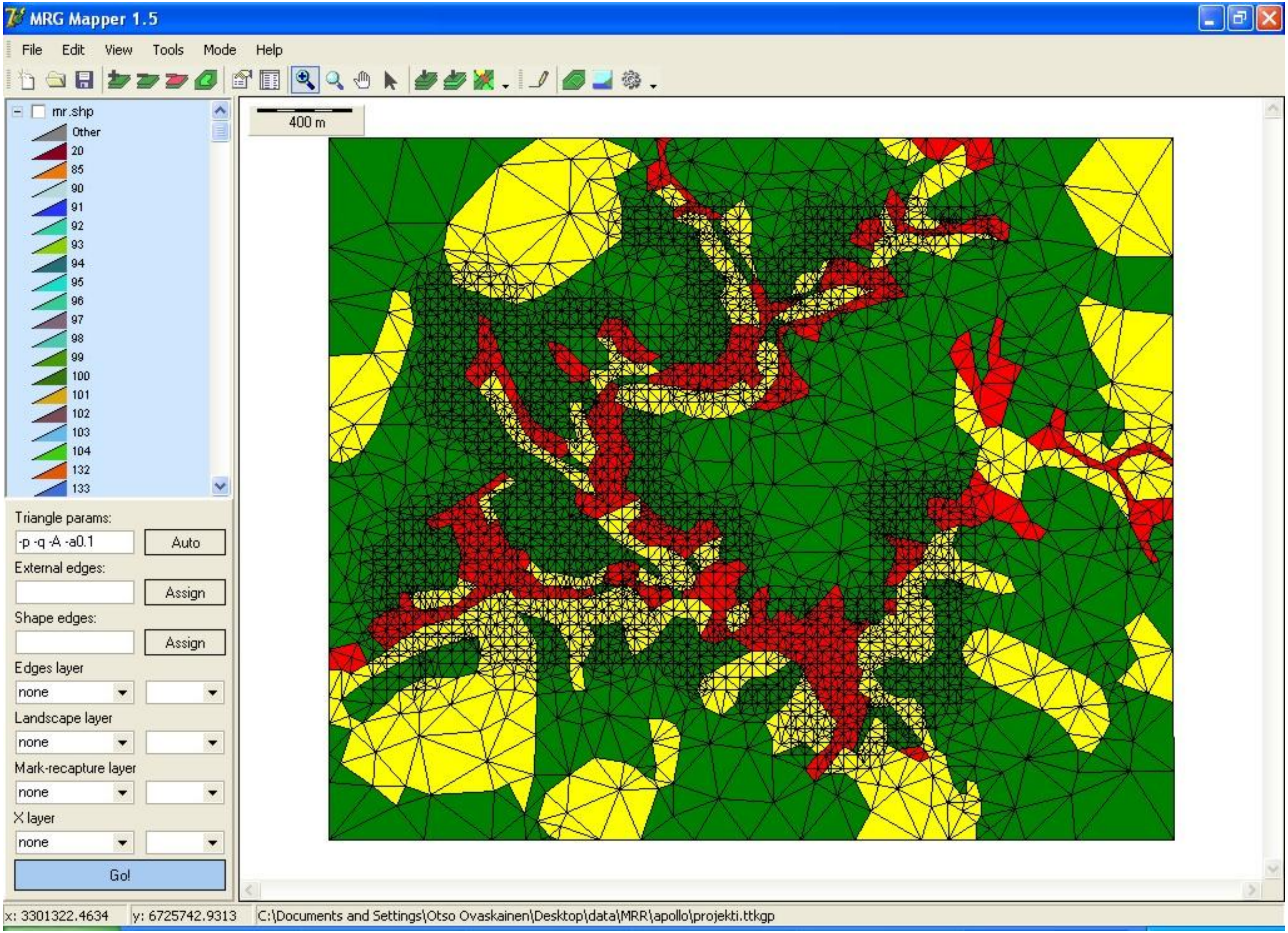
- habitat-specific diffusion coefficients (3 parameters)
- habitat selection (2 parameters, 1 normalized to one)
- mortality (1 parameter)
- capture probability (1 parameter)

Mikko Kuussaari

Miska Luoto

Iiro Ikonen

Computing the likelihood with the finite element method



Triangle params: -p -q -A -a0.1

External edges:

Shape edges:

Edges layer: none

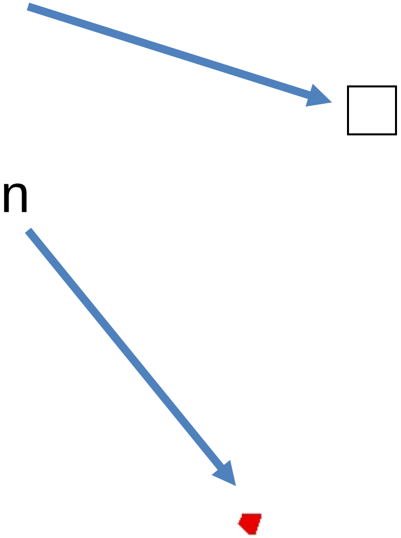
Landscape layer: none

Mark-recapture layer: none

X layer: none

x: 3301322.4634 y: 6725742.9313 C:\Documents and Settings\Otso Ovaskainen\Desktop\data\MRR\apollo\projekti.ttkgp

The time-evolution of probability density

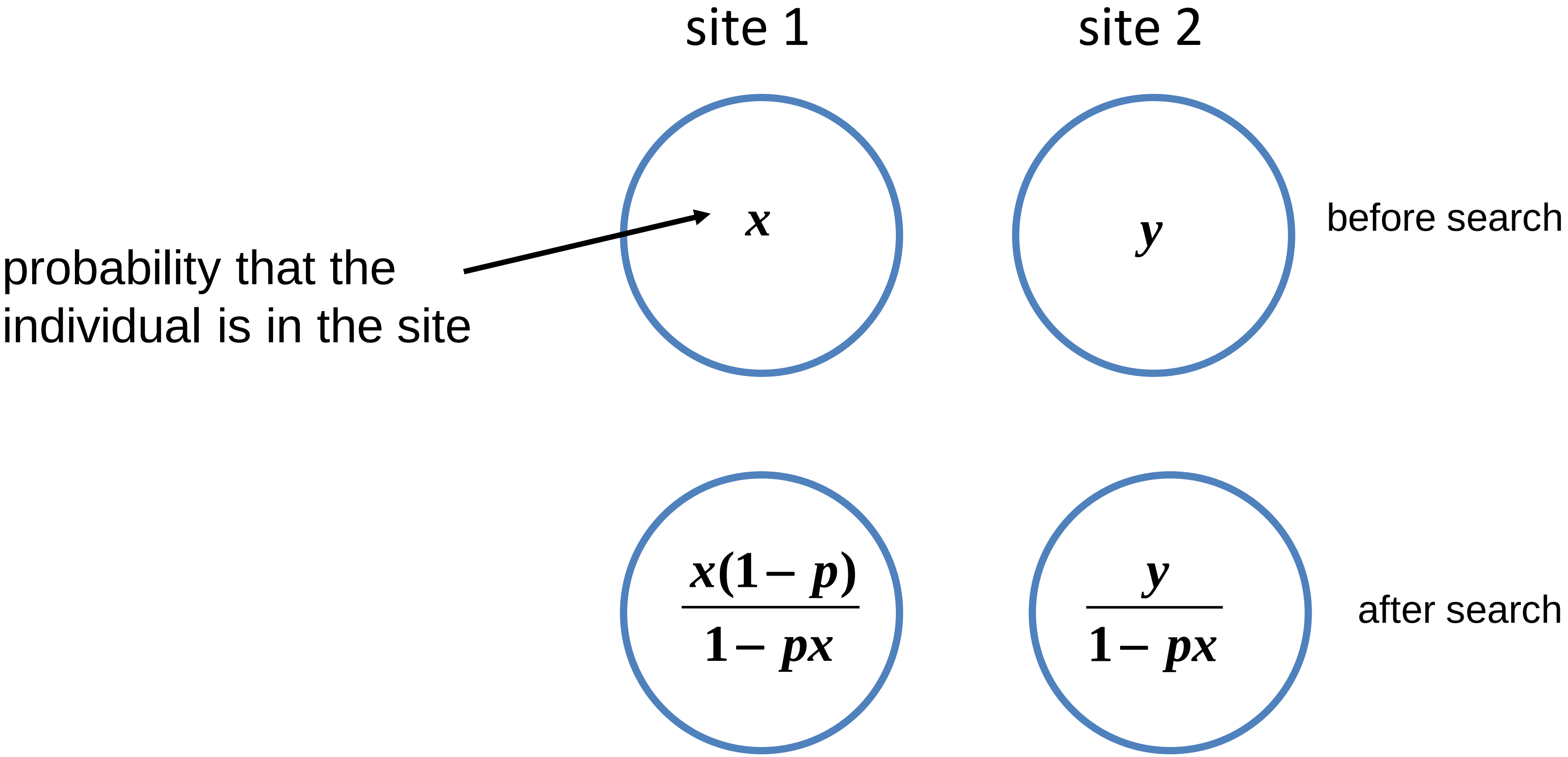


Observation
at time t=5

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



site 1

site 2

x

y

before search

probability that the individual is in the site

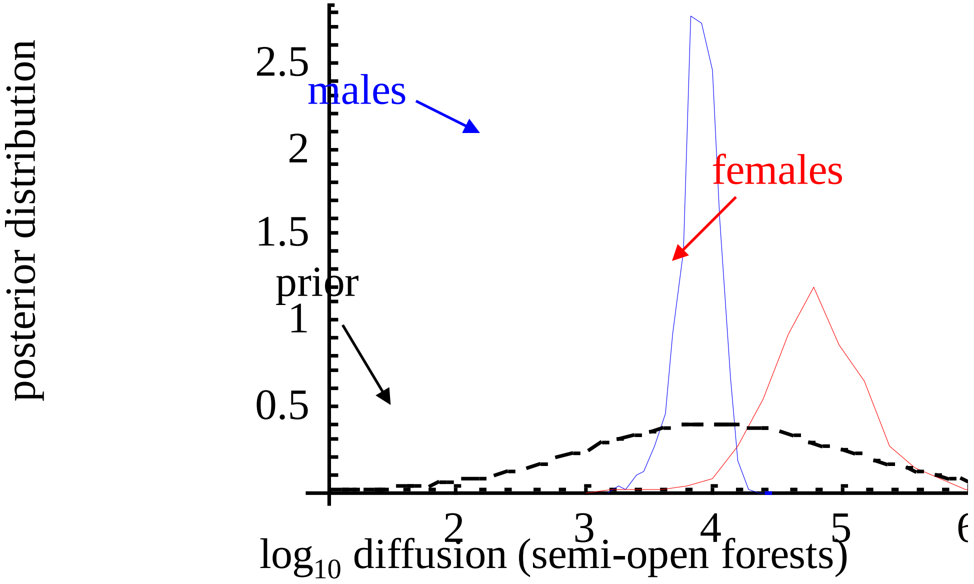
$$\frac{x(1-p)}{1-px}$$

$$\frac{y}{1-px}$$

after search

Ovaskainen (Ecology 2004)

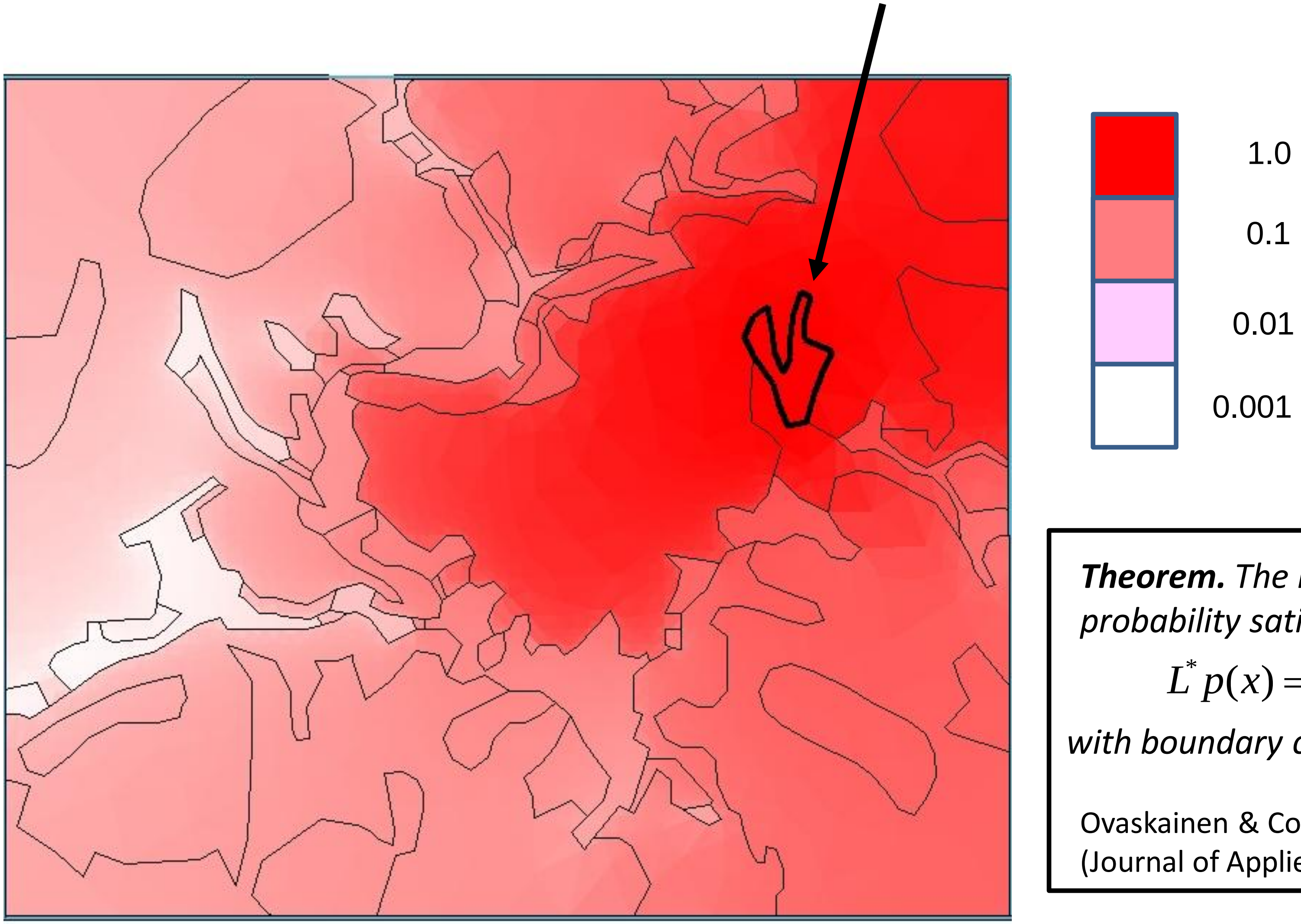
Biological inference from parameter estimates



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*

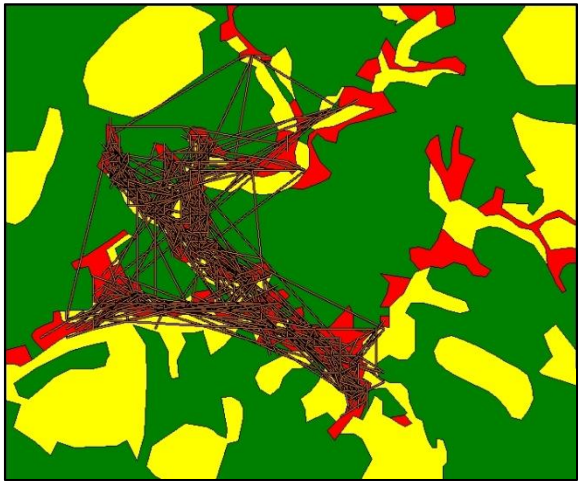
$$L^* p(x) = 0$$

with boundary condition $B^{C_{1*}}$

Ovaskainen & Cornell 2003
(Journal of Applied Probability)

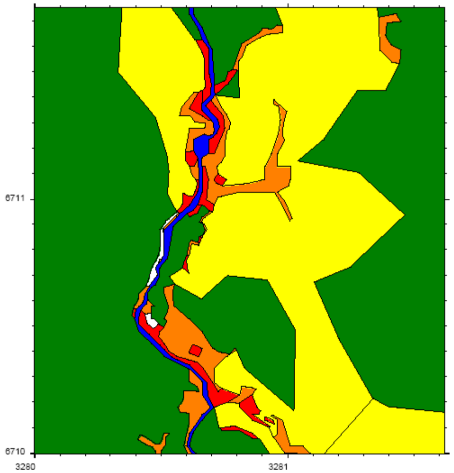
Model validation

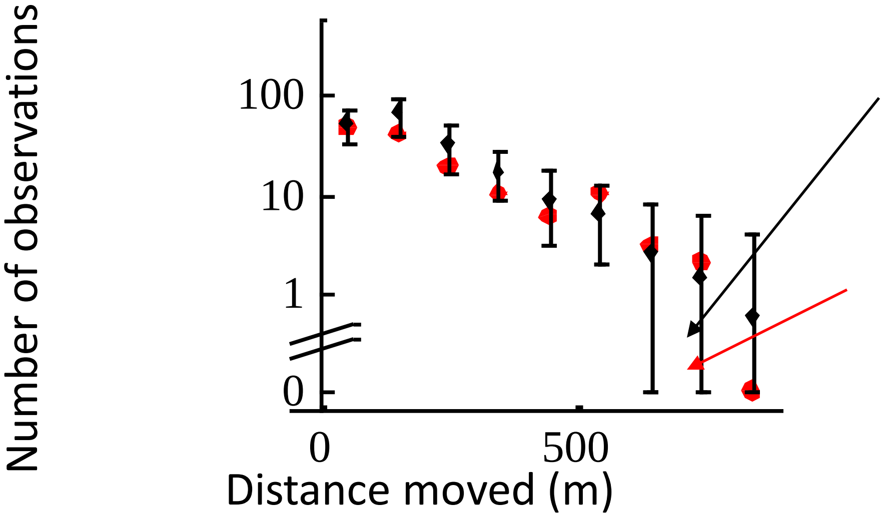
Landscape A



prediction

Landscape B



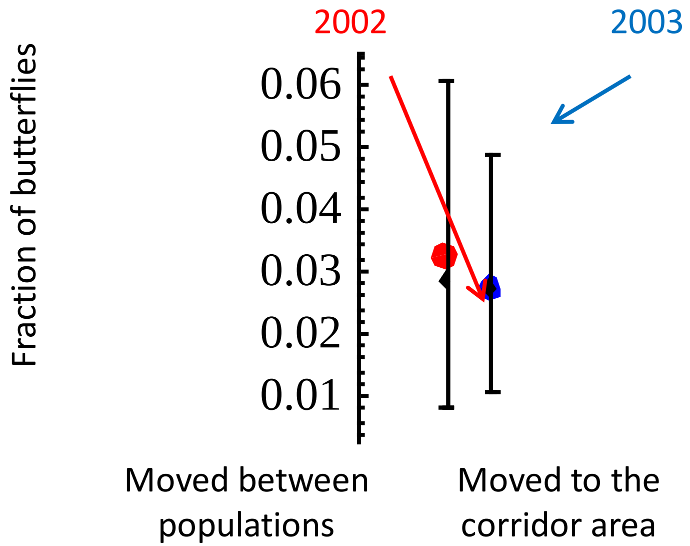


Model parameterized with data from Landscape A, prediction for Landscape B

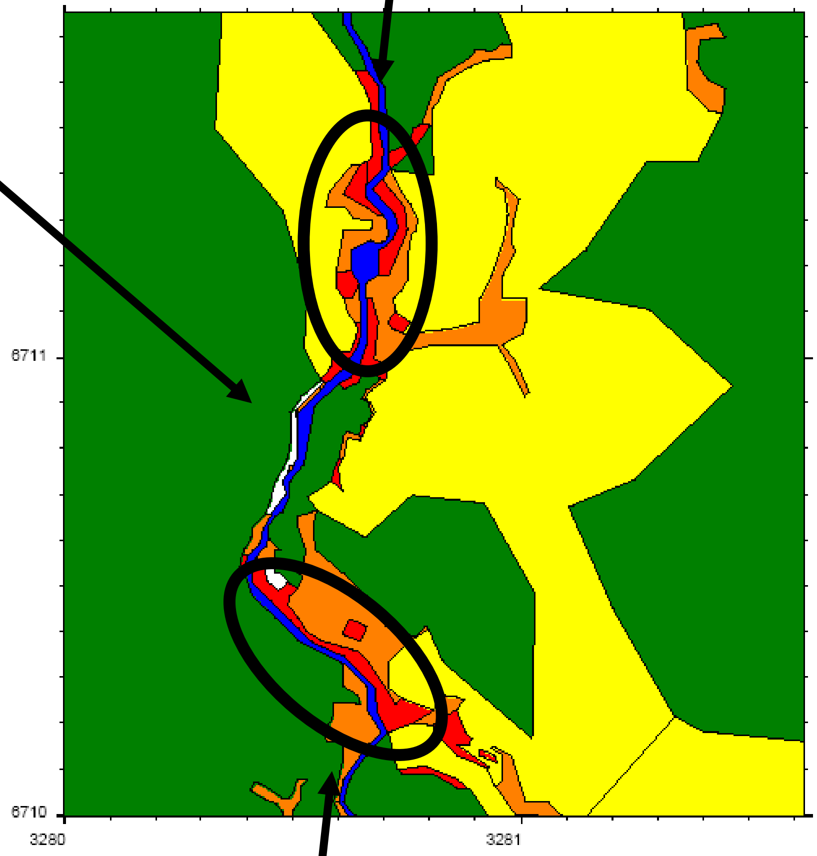
Empirical data on Landscape B

Effect of a movement corridor

Regional environmental centre opened a movement corridor in autumn 2002



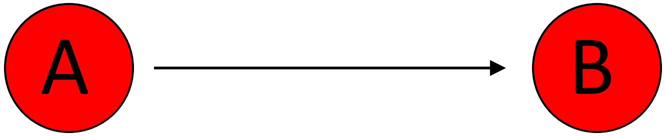
Northern butterfly population



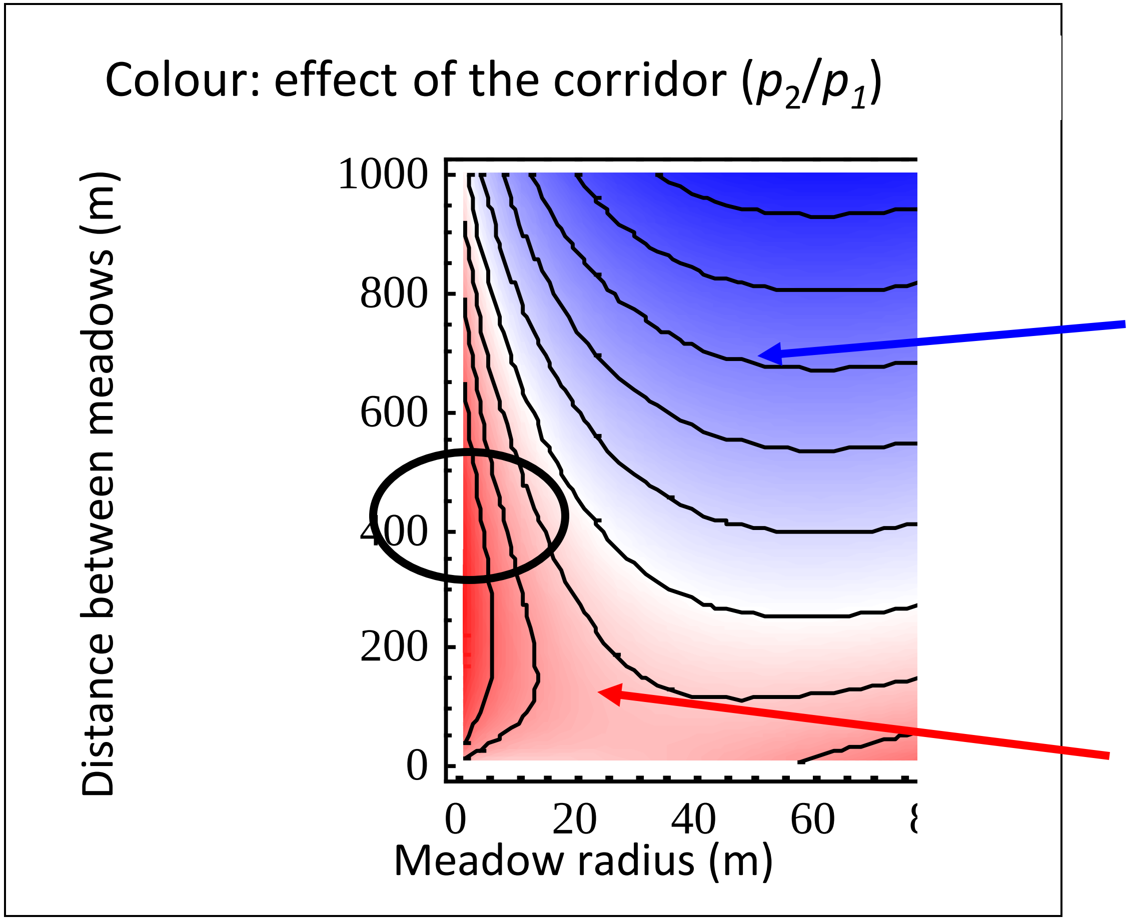
Southern butterfly population

What kind of a movement corridor would work?

Movement probability p_1



Movement probability p_2



Colour: effect of the corridor (p_2/p_1)

Corridor harms ($p_2<p_1$)

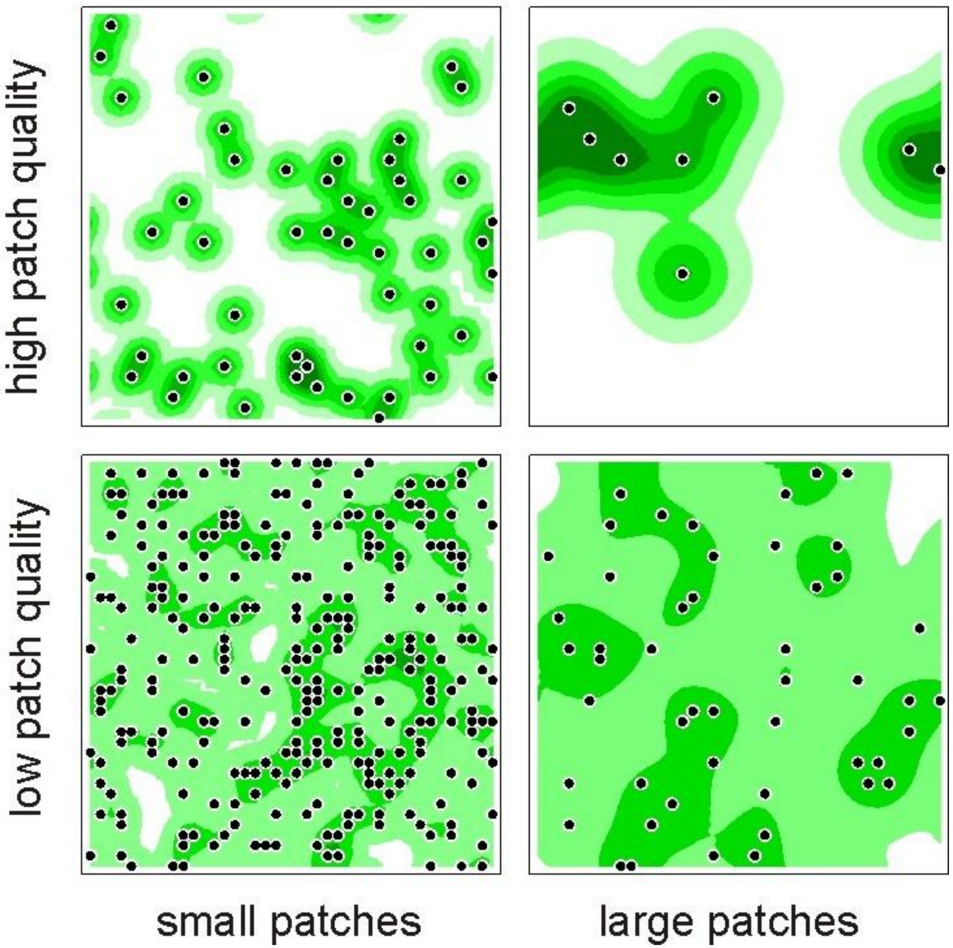
Corridor helps ($p_2>p_1$)

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

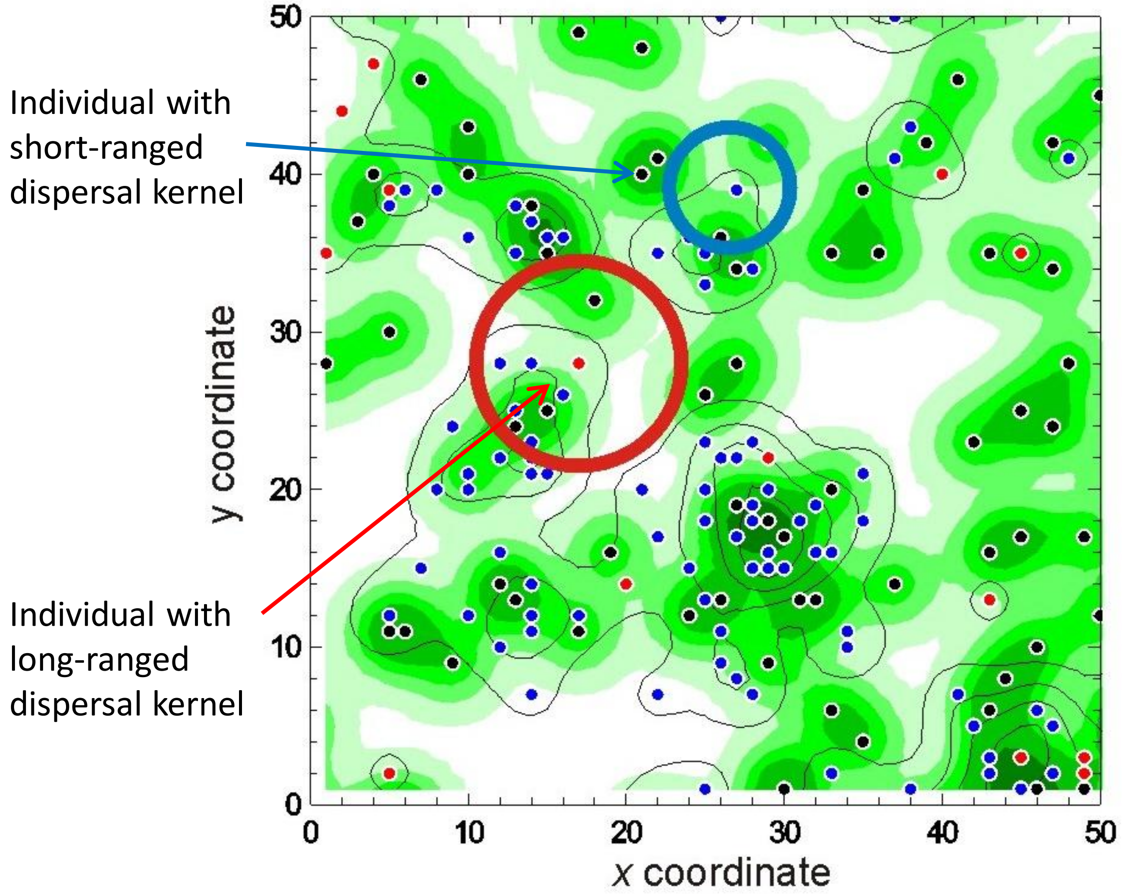


- Patches *p* appear at random locations at rate $\theta\sigma$ (per unit area)
- Patches disappear at rate σ (per patch)
- Landscape quality

$$\omega = \Psi_P * p$$

- The kernel controls patch size (length scale) and patch quality (integral)

Evolutionary model of dispersal



Individual with short-ranged dispersal kernel

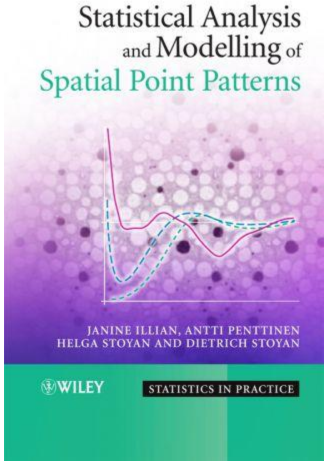
Individual with long-ranged dispersal kernel

- 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: $\frac{dN}{dt} = rN(1 - N/K)$

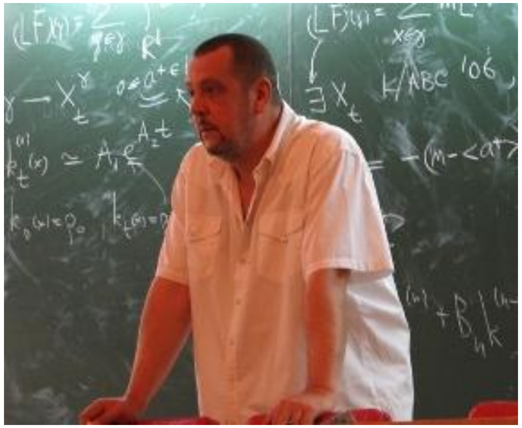
The model is a marked point process...


Statistical Analysis
and Modelling of
Spatial Point Patterns

JANINE ILLIAN, ANTTI PENTTINEN
HELGA STOYAN AND DIETRICH STOYAN

WILEY

STATISTICS IN PRACTICE



Prof. Yuri Kondratiev

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

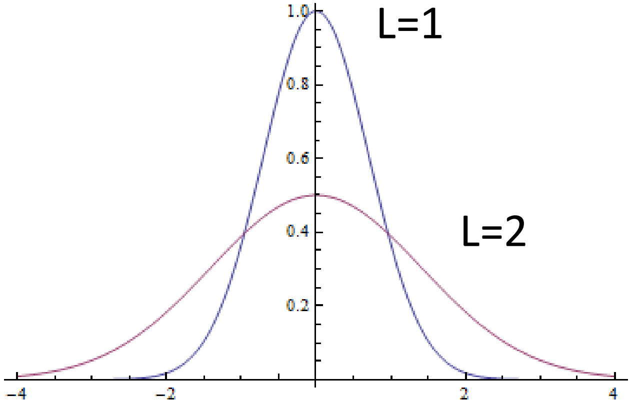
...and you can write it down as a spatial
moment equation

Prof. Ben Bolker

Model analysis by moment closures or perturbation expansions

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

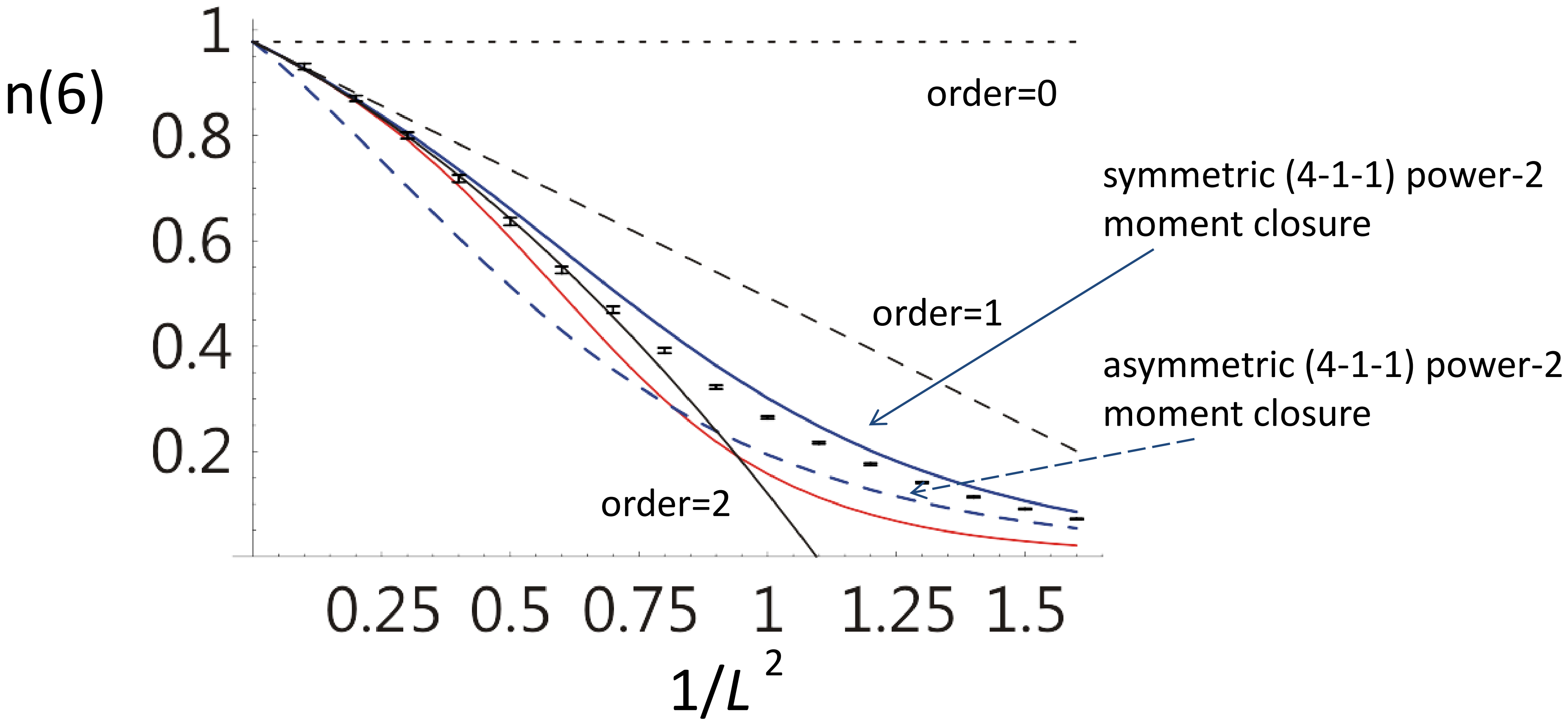
$$K(x) = \frac{k(x/L)}{L^d}$$



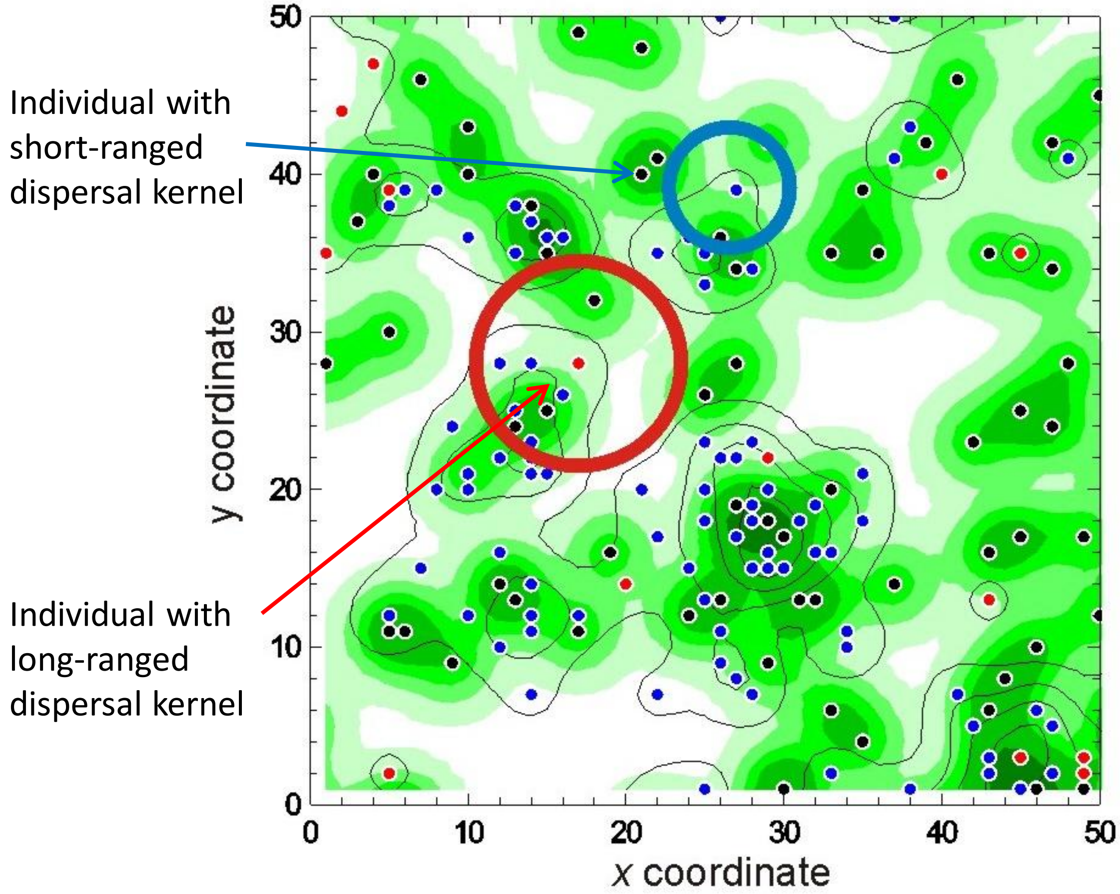
Expansion of density: $\overline{n(t)} = n_0(t) + \frac{n_1(t)}{L^d} + \frac{n_2(t)}{L^{2d}} + \ldots$

Ovaskainen & Cornell, PNAS (2006)

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



Evolutionary model of dispersal



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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)

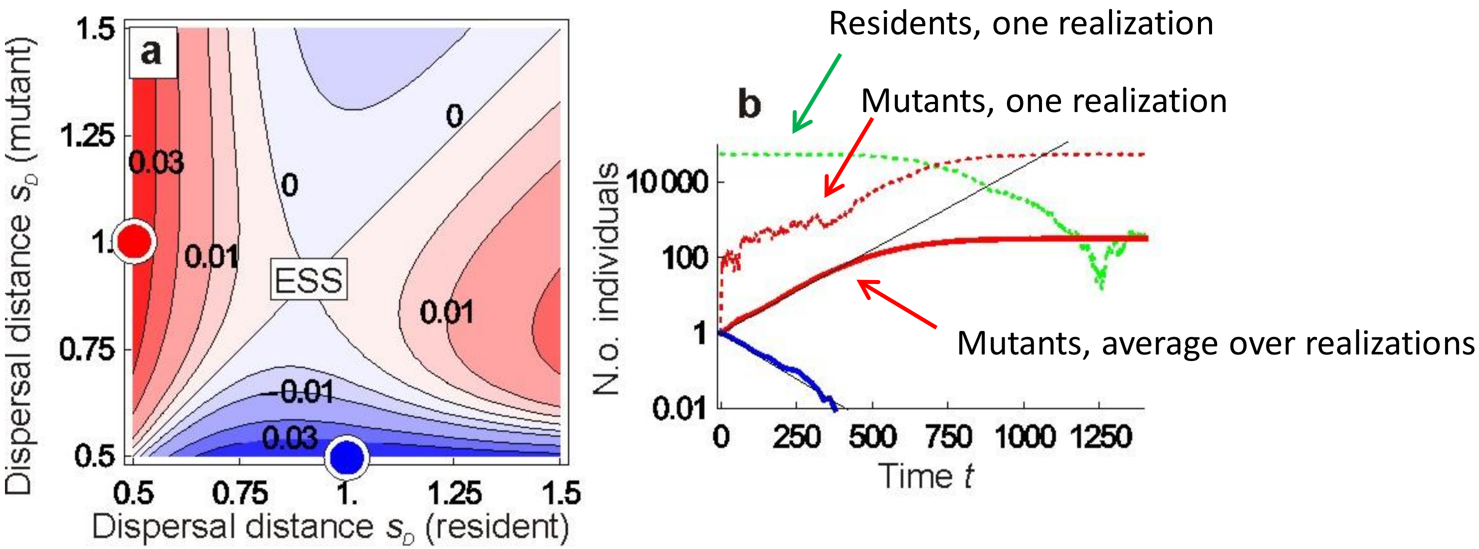
North, Cornell and Ovaskainen, Evolution (2011)

North et al., Evolution (2010)

Two ways of modeling evolution

ESS

Eigenvalue perturbation expansion, pairwise invasibility plots



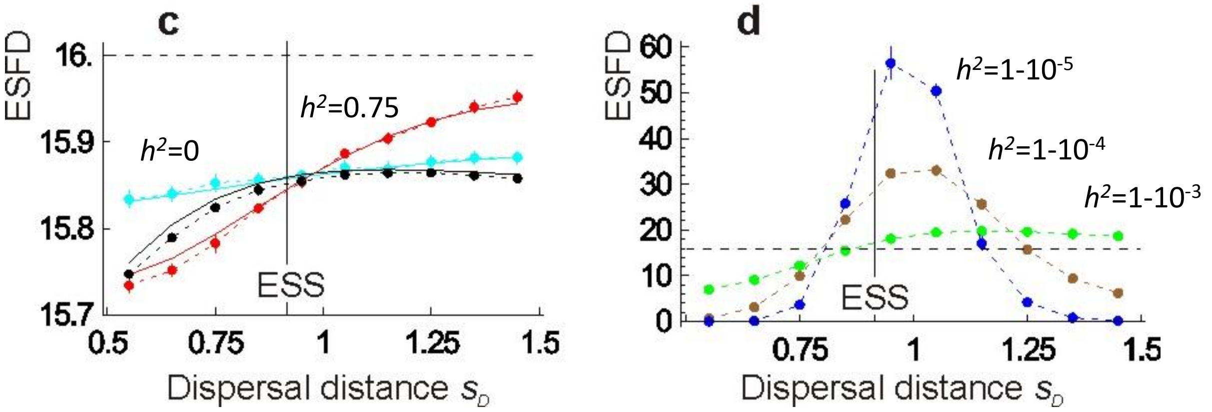
Residents, one realization

Mutants, one realization

Mutants, average over realizations

ESFD

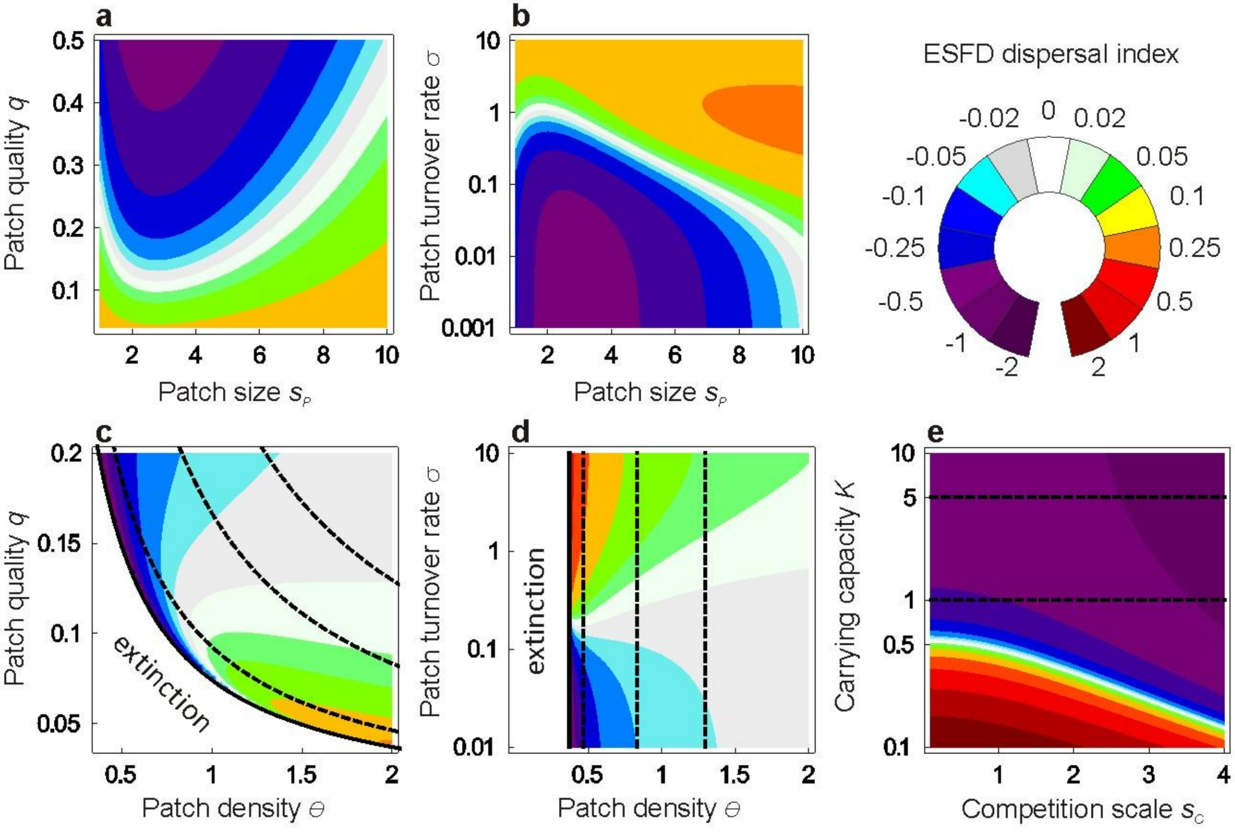
Density perturbation expansion



Life-history & landscape structure influencing dispersal evolution

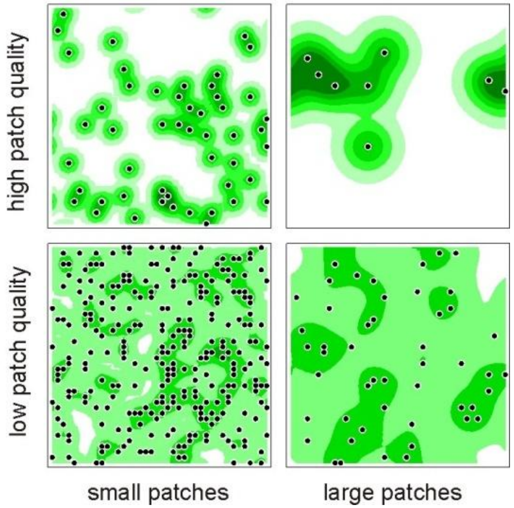
STATIC LANDSCAPES, TOTAL AMOUNT OF HABITAT CONSTANT

DYNAMIC LANDSCAPES, TOTAL AMOUNT OF HABITAT CONSTANT

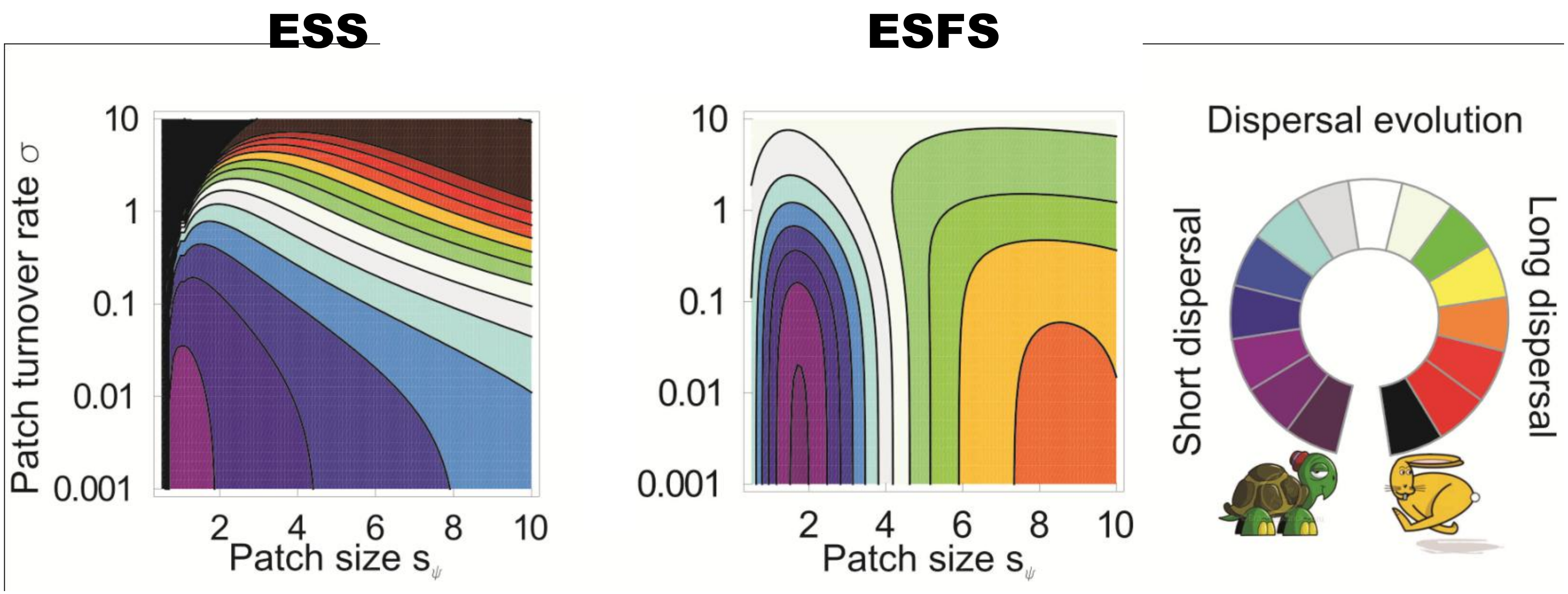


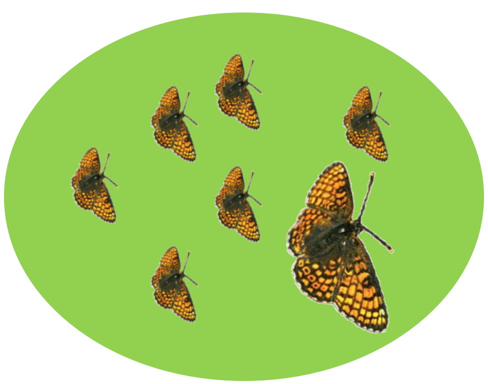
STATIC LANDSCAPES UNDERGOING HABITAT LOSS

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-)

1. Ovaskainen, O. Smith, A. D., Osborne, J. L., Reynolds, R. D., Carreck, N. L., Martin, A. P., Niitepõld, K. and Hanski, I. 2008. Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. *PNAS* **105**, 19090-19095.
2. Cornell, S. J. and Ovaskainen, O. 2008. Exact asymptotic analysis for metapopulation dynamics on correlated dynamic landscapes. *Theoretical Population Biology*, **74**, 209-225.
3. Ovaskainen, O., Luoto, M., Ikonen, I., Rekola, H., Meyke, E. and Kuussaari, M. 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist* **171,** 610-619.
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