Investigating feedbacks between behavioural strategies and landscape characteristics: An Introduction

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1 Introduction

This wiki/document is a primer on how to approach this project. The online wiki: **https://github.com/pratikunterwegs/klepto_spatial/wiki** has the same information as the pdf.

2 Contact

2.1 Who

There are two supervisors, Pratik and Christoph, but this project was born of Pratik's old and failing mind. Contact Pratik for immediate issues with R, Python, git/Github, and/or Peregrine, but get in touch with either/both of us for conceptual issues.

2.2 How

You can contact us by email for now, until we set up a Slack or similar. If you have a preference let us know.

Name	Email
Pratik	p.r.gupte@rug.nl
Christoph	c.f.g.netz@rug.nl

2.3 When and why

In general, feel free to contact us when you think it's necessary. We'll get a system set up for contact hours etc. in discussion with you. Below, you can see when we're busy with other meetings.

Name	Usually unavailable
Pratik	Mondays 11:00 – 12:00
—	Wednesdays 10:30 – 12:00
—	Fridays 10:00 – 12:00
—	All days 18:00 – 20:00
Christoph	Wednesdays 10:30 – 12:00

NB: These are difficult times, and we get that. Feel free to contact us if you have an external issue that may impact your participation in the course. You needn't give details, but let us know.

3 Project Description

Just in case you'd forgotten what you signed up for.

The availability of resources determines the movement and behaviour of individuals on resource landscapes. Simultaneously, individuals deplete resources and thus change the resource landscape they inhabit. The feedback between individuals and resources can have important eco-evolutionary implications, as individuals adapt their behavioural strategies to the resource landscape. This change can itself modify the resource landscape such that it favours a very different behavioural strategy.

Such eco-evolutionary dynamics are difficult to investigate, particularly if there are qualitatively different types of behaviour among individuals. In the Kleptomove simulation model, we have considered two such behaviours: searching for food, or stealing food from other individuals who have already found a food item ('kleptoparasitism'). The model implements the evolution of the two strategies and the implications for the resource landscape. Though kleptoparasitism always evolves and establishes itself as a common strategy, visual inspection of the simulation results suggests that this only occurs at specifc locations in the resource landscape.

This project will study the correlation between each strategy and the spatial characteristics of the resource landscape, and examine the consequences of the evolution of kleptoparasitism on the resource landscape. The student will use Kleptomove output to identify global 'tipping points' in the behavioural strategy, quantify local indicators of spatial association in the landscape at distinct time-points before, during, and following the establishment of kleptoparasitism in the population, and quantify the global change in LISA classes.

4 Workflow

Work should ideally follow this sequence over the next few weeks. Get in touch to discuss changes and so on.

1. Get organised
    - Set up communication channels
2. Reading literature: Consult the *Literature* page from the sidebar.
    - Install Zotero
    - Access the online library
    - Go through the papers
3. Learning tools
    - R, RStudio, and RProjects
    - Python and PyCharm
    - git and Github
4. Getting data
    - Access data from iRODS
5. Outline methods for your project
    - Identify which tools you need
    - Intensive learning session if needed
6. Mid-project presentation (8th June)
    - Convert section (5) into a presentation
7. Final presentation and poster (22nd June)
    - Prepare poster sections text and figures
    - Prepare presentation

5 Literature

It's important to know what you're dealing with, and reading previous findings is a good place to begin. Take a week to read the important literature, **below in bold**. Read the optional literature on the subject that interests you.

A literature collection is being assembled in a Zotero group library: **https://www.zotero.org/groups/2499059/course-2020-comm-ecol**. You'll need to register on Zotero and request access. Contact us if this gets confusing.

Zotero **link: https://www.zotero.org/** is a reference management program for the storage and citation of academic papers. Download Zotero, the connector for your browser, and optionally the plugin for your word processor. Create an account and sync the group library for access to the references and pdfs.

How to approach the literature list

1. Begin by reading papers that give a broad overview of the fields of spatial ecology **(Levin 1992)** and the links between the movement of individuals and large-scale processes such as community assembly **(Jeltsch et al. 2013; Schlägel et al. 2020)**.

   Optional: Consider a specific example from a simulation study of how individual movement behaviour can lead to large scale patterns in the spread of rabies (Jeltsch et al. 1997).

2. Move on to reading about the evolution of individual behavioural strategies (Wolf and Weissing 2010), and the consequences of variation in strategies for ecology and evolution **(Wolf and Weissing 2012)**. Finally, read about the North American bluebird system in **Duckworth and Badyaev (2007)** as an illustration of these concepts

3. The data you'll analyse comes from *Kleptomove*, a spatially explicit individual based simulation model (IBM) inspired by competition among foraging waders *Charadrii*. Read **Case and Gilpin (1974)** to see how interference competition can structure communities

   Read how IBMs are used to study large scale patterns **(Grimm et al. 2005)**.

   Return to this document to read more about *Kleptomove* in the section below. Optionally, read Vahl et al. (2005) and Vahl et al. (2007) to read about interference competition in waders.

   For an overview of how IBMs were developed take a look at Huston, DeAngelis, and Post (1988), and to see where they are today, see DeAngelis and Mooij (2005) and DeAngelis and Diaz (2019).

Advanced reading

4. In *Kleptomove* the strategy of stealing food from other individuals, or kleptoparasitism, abruptly takes over the population until a large proportion of individuals attempt to steal from others.

   Such abrupt shifts in a system are called *critical transitions* **(Scheffer et al. 2001)**, and the state of a system at which these shifts occur is called a *tipping point* (van Nes et al. 2016).

   Critical transitions occur in many different systems: from landscapes (Hirota et al. 2011) to animal groups (Tunstrøm et al. 2013). Read these papers about critical transitions to understand more.

5. You'll be doing spatial autocorrelation analysis at two scales: global, i.e., referring to the full extent of the Kleptomove landscape, and local, i.e., relating to smaller areas within the landscape. Read about how local spatial autocorrelation is used to detect 'hotspots' in ecological data in **Nelson and Boots (2008)**.

   Read about global spatial autocorrelation (Sokal and Oden 1978a, 1978b), and then local spatial autocorrelation (Sokal, Oden, and Thomson 1998a, 1998b). Read (Anselin 1995) to look at a specific measure of local spatial autocorrelation called *Moran I local*.

5.1 Literature list

[**1**] Anselin, Luc. 1995. "Local Indicators of Spatial Association—LISA." *Geographical Analysis* 27 (2): 93–115. https://doi.org/10.1111/j.1538-4632.1995.tb00338.x.

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[**13**] Nes, Egbert H. van, Babak M. S. Arani, Arie Staal, Bregje van der Bolt, Bernardo M. Flores, Sebastian Bathiany, and Marten Scheffer. 2016. "What Do You Mean, 'Tipping Point'?" *Trends in Ecology & Evolution* 31 (12): 902–4. https://doi.org/10.1016/j.tree.2016.09.011.

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6 About Kleptomove

6.1 Basic structure

The Kleptomove simulation was developed for a master's project in the Modelling Adaptive Response Mechanisms (MARM) group. It is a development of the predator-prey co-evolution simulation described in (Netz 2017).

Kleptomove is an individual based model and simulates the co-evolution of movement and behavioural strategies. A population of agents 'lives' and moves on a resource landscape grid. Each grid cell contains food items which agents feed on to gain energy. The resource landscape is structured, i.e., it has more food items in the centre and fewer at the edges. Agents must 'handle' food items for a fixed number of timesteps (or turns) before they can consume it. Food items regenerate on the landscape over time.

6.2 Kleptomove versions

There are two versions of Kleptomove, one in which agents only forage for food items, and another in which agents have a choice of whether to forage or steal from others ('kleptoparasitism'). Agents which steal from another take over its handling, i.e., if the previous owner of the food had handled it for half the required time, the kleptoparasite only has to handle it for the remaining half before gaining the energy.

There are 1,000 non-overlapping generations of agents, with 100 timesteps each. Agents replicate theselves each generation to produce 'offspring', and the number of offspring is related to how much energy they have collected from food items over their 'lifetime'. The genetic mechanism (actually an artificial neural network) controlling the behaviour and movement choice mutates with a fixed probablity of 0.1% at each replication.

Agents' choice of strategy is evolved, i.e., while all agents *can* steal, not all agents are pre-disposed to do so. Some agents never steal, some steal when there is a high chance of success, and some always try to steal. Stealing as a strategy is initially uncommon in the population, with few agents attempting to steal. This state may continue for tens, if not hundreds of generations. However, in some simulation runs, after a few hundred generations, stealing establishes itself as a viable and common strategy.

It is not entirely clear why kleptoparasitism establishes itself when it does in a simulation run. The low probability of mutations that favour stealing, and the low probability of encountering suitable targets in the sparsely distributed population (which has a density of 0.03 – 0.06 individuals per grid cell) likely explains the observed pattern that kleptoparasitism evolves faster when population densities are higher.

6.3 Feedback between landscape and behaviour

The establishment of the kleptoparasitic strategy in the population leads to signficant landscape changes. Initially, the landscape structure (more food in the centre, less at the edges) is broken up by agents depleting the central areas of food items. As agents move around the landscape towards areas with remaining food items, the landscape becomes patchy, and agents become locally concentrated at 'resource hotspots'.

This local concentration creates the conditions for kleptoparasitism to become an effective strategy, since it increases the encounter rate between kleptoparasites and their targets. When kleptoparasites become common, they tend to be attracted towards areas where there are many foragers, from whom they can steal. Since kleptoparasites themselves do not forage from the landscape, they reduce the total number of foraging agents, allowing the landscape to regenerate its original structure.