Using Simple Models to Explain Ecosystem Patterns

Simple (mathematical) models are useful learning tools. Given a set of observations, we use models to explain emergent patterns in the data. In this sense, models are hypotheses in the form of equations. If a model can reproduce patterns in the data, the hypothesis might not be wrong. However, if the model cannot explain the observations, the hypothesis is rejected, and we go back to the drawing board. Either way, we learn!

In this post, I illustrate the power of simple models in the context of river ecosystems. I begin by identifying a pattern. Then, I borrow a hypothesis from the literature to explain the pattern. Finally, I mathematically formalize the hypothesis and test it by seeing if the model can recreate the pattern.

It is necessary to provide some background on stream ecology and Antarctic rivers. I apologize if the background is too dense. I’ve embedded links along the way that direct to you to sources where you can learn more.

# Background

## Nitrogen cycling

Nitrogen (N) is a fundamental building block of ecosystems. It is an essential nutrient for life on earth, along with carbon and phosphorous. Understanding N fate and transport provides insight into how ecosystems operate. Nutrient spiraling theory provides a framework for understanding how N moves through river ecosystems. The spiral begins with downstream transport of an inorganic N species dissolved in flowing waters. Organisms in need of inorganic N assimilate it into their organic matter. Eventually, organic matter decomposition by microbes mineralizes inorganic N back into the water column. The spiral is complete.

Nitrogen cycling is extremely well studied. Uptake and assimilation of inorganic N is one of the best-understood parts of N cycles. This is partially because inorganic N is a pollutant, so assimilation (retention) can be beneficial. However, the fate of assimilated N remains poorly resolved, hampering our ability to close ecosystem N budgets.

## The McMurdo Dry Valleys, Antarctica

As it turns out, rivers in the McMurdo Dry Valleys of Antarctica are excellent end-member systems for studying the fate and transport of assimilated N. A few key points you need to know about Antarctic rivers:

* The McMurdo Dry Valleys are one of the coldest and driest places on earth. In this region it is too cold to rain and most snowfall sublimates before melting.
* Glacial melt is the primary source of flow in Antarctic rivers. Rivers are hydrologically disconnected from adjacent hillslopes.
* Algae are some of the only primary producers found in the region. Rivers are an ideal habitat for algae, which form in mats on the riverbed. There are three types of algae mats. Orange and green mats live in the water column. Black mats live along channel edges.
* Black mats are nitrogen fixers (i.e. they can assimilate N2 gas from the atmosphere).
* Nitrogen in the stream comes from glacier melt or in-stream N fixation (by black mats). Very little N comes from adjacent hillslopes. This is unusual. In most places on earth, streams get a lot of N (and water) from adjacent hillslopes.
* High flows scour algal mats from the streambed. This is a key mechanism controlling particulate organic matter (POM) concentration.
* Hyporheic zone interactions are extensive. Surface water is constantly mixing with shallow groundwater along the course of the stream.

## Nitrogen isotopes.

Nitrogen isotopes help to track N moving through river ecosystems. Isotopes are atoms with differing numbers of neutrons. Nitrogen has two stable isotopes; 14N and 15N. 15N is the ratio 15N:14N. As N moves through different components of the nutrient spiral, the value of 15N increases and decreases. This makes 15N a useful tracer for tracking the fate and transport of N.

The nitrogen isotope-scape of Antarctic rivers is constrained by two end-members. On one hand, black mats are N fixers, so they have 15N signature near the atmospheric standard (15N 0 per-mil). On the other hand, atmospheric deposition is the primary source of N in glacier ice. Therefore, glacier ice is characteristically depleted in 15N (from -9.5 to -26.2 per-mil).

# Data

Tyler Kohler, my friend and colleague, collected samples of algae along several Antarctic Rivers. He measured the 15N signature of algae organic matter and constructed a data set of the spatial variation. He graciously provided me with these data. Read his peer reviewed paper to learn more about the data.

Here, I am working with data from a river named *Relict Channel*. It flows intermittently between October and February and is freeze dried for the remainder of the year. Algal mats are abundant along the channel bottom. Eight sites were sampled along a 3-km longitudinal transect. The upstream-most site is located 1.5 km from the glacier.

[LOAD AND EXPLORE THE DATA]

# Pattern

One pattern observed in the data is an upstream to downstream enrichment of orange mat 15N. The pattern is asymptotic. The furthest upstream samples are depleted in 15N and resemble glacial water. Moving downstream, samples become enriched in 15N, and approach the signature of atmospheric N (15N 0 per-mil).

[PLOT THE PATTERN]

# Hypothesis

Tyler and his co-authors put forward a hypothesis to explain the asymptotic enrichment of 15N. The hypothesis may be frames as a series of events:

First high flows scour black mats at the channel margin. Then mat-derived POM is transported downstream and stored in the hyporheic zone. Hyporheic microbes mineralize black mat POM and produce inorganic N. Finally, exchange flows flush inorganic N from the hyporheic zone into the open channel. As a result, inorganic N mineralized from black mats becomes a progressively larger source of available N with distance downstream.

[INSERT KOHLER SCHEMATIC]

# Model

## Mathematical form

Can this hypothesis explain the asymptotic enrichment pattern? I formalized the hypothesis with a mathematical model. The model simulates downstream changes in glacier- and black-mat derived inorganic N concentrations. It is a system of two ordinary differential equations. The Equation 1 represents the spatial rate of change in glacier-derived inorganic N. Equation 2 represents the spatial rate of change in black mat-derived inorganic N.

(1)

(2)

Where is the concentration of glacier-derived inorganic N, is the concentration of black mat-derived inorganic N, is the inorganic N uptake rate of orange mats, is the flux of inorganic N from the hyporheic zone to the stream, and is channel distance (m).

[Build out further to get to 15N

[DEVELOP MODEL WITH CODE: boundary & initial conditions, domain, function]

# Insights

## Model Behavior

* Explore model behavior by tweaking parameters
* Plot N concentration and 15N signature profiles as lines. Many lines for many parameter combos. Label lines with parameter values.

## Calibration

* Rig the model up to an optimization routine with an objective function (RMSE)
* Fit model to the data

## Sensitivity

# Discussion

* The model can fit the data, what does this suggest?
* What other evidence exists to support this hypothesis?
* What else can we do to test the hypothesis. For example, is there evidence that inorganic N concentration increases as the model predicts?
* Have we observed black mats in the hyporheic zone? Is there nough microbial respiration to going on to justify the optimal value of the phi parmater?
* How do simulated uptake rates compare to those published by Gooseff and McKnight from tracer studies?

# Conclusion

* The model fits the data. Our hypothesis cannot be rejected.