Biodiversity dynamics in stream communities

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Goal

To investigate the evolutionary dynamics of traits concerning adaptation to the local environment and to analyze how environmental factors affect the biodiversity of aquatic insects in streams and rivers.

Background and motivation

Stream and river ecosystems are especially vulnerable to various types of natural and anthropogenic disturbances, which threaten their capacity to provide important ecosystem services, like food and clean water. Water quality affects aquatic insects (or, slightly more generally, benthic macroinvertebrates) particularly strongly: these play a functional role in aquatic food webs (Song et al. 2007), and have therefore been widely used as indicators of ecosystem health (Hellawell 1986; Rosenberg and Resh 1993). Understanding how their biodiversity dynamics depend on environmental factors is thus a question of pivotal importance for the management of aquatic ecosystems.

Streams and rivers have characteristic longitudinal profiles of latitude and environmental factors (e.g., temperature, oxygen, pH, substrate size), which are typically steeper in the uplands, where the streams originate, and have a more gradual slope in the lowlands near a river's terminus. River segments may vary in length, from one kilometer to tens of kilometers, and this is the spatial scale of major floodplains and channel features. Homogeneous units recognized within a segment are called reaches. In practice, reaches are often defined as a repeating sequence of channel units, such as riffle–pool–run sequences (Frissell et al. 1986). A reach can be 100 m or less in length in a small stream, and several kilometers in a large river.

Aquatic insects are adapted to stream ecosystems morphologically and in terms of their life-history traits. They typically have a life cycle consisting of four phases (egg, larva, pupa, and adult), which they spend in two different environments: in the water (egg, larva, and pupa) and outside the water (adult). Sexual reproduction is the norm, but parthenogenesis also occurs. The larval phase is relatively long (on the order of years), while the phase as a flying adult outside of the water is relatively short (on the order of weeks); adults often do not engage in much more activity than finding a mate and laying eggs before they die. As a consequence of physical and biological processes, the particle size of organic material that enters the water upstream (mostly leaf litter) during its transport downstream becomes progressively smaller (Vannote et al. 1980). Being typical generalists, aquatic insects can be classified into only a handful of functional feeding groups such as shredders, collectors, scrapers, and predators, according to their role in the processing of this organic matter, by considering a number of factors: the origin and size of the food items infested, the general location from which the food is taken (from the substrate or from the water column), the mechanisms of food acquisition (enabled by morphological and/or behavioral adaptations), as well as the trophic level. Accordingly, the traits reflecting the adaptation of benthic organisms to local environmental conditions mostly allow inferring their feeding strategy.

Aquatic habitats can be characterized passably by a surprisingly low number of important environmental factors (Cummins 1964), including current velocity, substrate size, food availability, and physical and chemical properties (e.g., oxygen content, temperature, and pH). Current velocity is the defining feature of streams and rivers. Temperature affects all life processes. The substrate is important to aquatic insects as the surface on which they dwell. Dissolved oxygen and pH are especially influenced by anthropogenic and non-anthropogenic pollution.

The dynamics of benthic macroinvertebrate communities are empirically studied by analyzing species–abundance distributions (SAD; e.g., Magurran 2004). SADs are usually visualized as rank–abundance diagrams which graph, on a logarithmic vertical scale, the relative abundances of species ranked horizontally in order of descending abundance. Community responses to changes in environmental factors, such as caused those by pollution, impose characteristic signatures on the observed SADs (Qu et al. 2008).

In this project, I will model and analyze the biodiversity dynamics of benthic macroinvertebrate communities and their responses to pollution using an individual-based eco-evolutionary model that considers essential life events such as birth, death, random movement, downstream movement, and upstream flight, and includes the effects of both competition within the community and local adaptation to, or tolerance for, extrinsic environmental factors.

Research questions

I will model macroinvertebrate biodiversity by considering realistic spatial variation in local conditions along streams and rivers, and compare the SADs obtained from the model to empirical SADs reported from Korean streams and rivers (Qu et al. 2008; Tang et al. 2010). Specifically, I will address the following questions:

- How do basic environmental factors and functional feeding groups enhance the biodiversity of macroinvertebrates in the modeled stream ecosystems?
- How well can a relatively simple eco-evolutionary model reproduce empirical biodiversity patterns observed in Korean streams and rivers?
- How does pollution affect the biodiversity of stream communities in the model?
- How well can the model reproduce biodiversity patterns of polluted Korean streams and rivers?

Methods and work plan

Model overview

I construct an individual-based eco-evolutionary model that considers essential life events of macroinvertebrates – such as random movement, downstream movement, upstream flight, birth, and death – as they occur in continuous time and space along a one-dimensional stream. Only larvae are explicitly modeled. An individual has several traits that describe its tolerance to local environmental conditions, as well as its movement behavior. I consider a stream or river of 10 to 100 km length from headwaters to mouth. Consequently, individuals that move out of this range downstream are lost, while individuals that attempt to move out of this range upstream remain in the headwaters region. The various events occur with a frequency that is determined by the ratio of their maximal rate to the sum of all maximal event rates. Given the

event type, a focal individual is selected with uniform probability; the event is then realized with a probability given by the ratio of the individual event rate to the maximal rate for that event type. Waiting times between possible events are sampled from an exponential distribution with the sum of all maximal event rates as the expected value (Allen and Dytham 2009).

Death

Individuals i die with a death rate d_i that is proportional to the competition they experience, and inversely proportional to the local carrying capacity and their tolerance for the local environmental conditions,

$$ d_i \propto \frac{\sum_{j \neq i} N_{\sigma_x}(x_i - x_j)}{K(x) \prod_e N_{\sigma_e}(v_{ie} - v_e(x))}, $$

where i is the index of an individual, v_{ie} are the traits describing its tolerance to the various environmental factors e (such as current velocity v, temperature t, oxygen o, pH p, and substrate size s; maybe also organic matter m), $v_e(x)$ are the corresponding longitudinal profiles of these environmental factors, $K(x)$ is the longitudinal profile of the carrying capacity density of organisms that are maximally adapted to location x, and $N_\sigma(d)$ is the normal function $\exp(-\frac{1}{2}d^2/\sigma^2)$ with standard deviation σ.

Downstream movement

Individuals drift downstream with a rate

$$ r_i = \frac{r_{max}}{1 + \exp(-\alpha(d_i - d_{th,i}))}, $$

where r_{max} is maximal drift rate, d_i is the death rate of individual i, $d_{th,i}$ is a corresponding threshold describing the death rate above which individual i is likely to drift, and α describes the sharpness of this onset of drift around $d_{th,i}$. Individuals drift for a duration Δt drawn from an exponential distribution,

$$ \Delta t \sim \sigma_{t,i} \exp(-\Delta t / \sigma_{t,i}), $$

where $\sigma_{t,i}$ is their average drifting duration. Their target location is found by integrating over the velocity profile $v_v(x)$.

Random movement

Individuals move randomly with a rate r_m, changing their position by drawing a new position from a normal distribution centered on their old position with standard $\sigma_{m,i}$.

Flight

At the end of each year, before reproduction, individuals may undertake a directed movement step along the stream. This describes the essence of their life phase as an adult, covering a distance

$$ \Delta x \sim \sigma_{x,i} \exp(-\Delta x / |\sigma_{x,i}|), $$

where $\sigma_{x,i}$ is their average flight distance. We interpret a negative value of $\sigma_{x,i}$ as upstream flight and a positive value as downstream flight.

Birth

At their target location, each individual produces $b\exp(-c\Delta x_i)$ offspring and dies. The discounting factor $0 < \exp(-c\Delta x_i) < 1$ imposes a cost of dispersal, with c measuring the strength of this cost. With probability μ, all offspring traits may undergo an incremental mutation relative to those of their parents; their trait values are then drawn from a normal distribution centered on the parental trait value, with different standard deviations for the different traits chosen so as to obtain in the population a stable coefficient of variation of about $1/2$ in each trait. Immediately after their birth, offspring undertake a random movement step as described above (so as to prevent artificial crowding).

Pollution

We consider pollution by incorporating point sources that release organic matter or other substances into streams and rivers, thus affecting the downstream longitudinal profiles of environmental factors. Non-anthropogenic pollution mostly affects pH, while anthropogenic pollution causes a low availability of oxygen. The impacts of pollution on environmental factors are modeled by changing the longitudinal profiles of these factors in accordance with data observed in Korean streams and rivers.

Empirical data

Environmental factors (temperature, dissolved oxygen, pH, and substrate size) and the densities of benthic macroinvertebrates were recorded monthly over a period of 10 years for various streams and rivers, both clean and polluted, in Korea. The data was then analyzed by determining the SAD for each stream or river (Qu et al. 2008; Tang et al. 2010). The longitudinal profiles of environmental factors will be obtained based on information in the published literature in conjunction with the aforementioned empirical data from Korean streams and rivers.

Work plan

The work plan is as follows:

- Add environmental factors (current velocity, temperature, oxygen, substrate size, and pH) one by one to the model and observe their effects on biodiversity patterns.
- Compare the modeled SADs to the empirical SADs.
- Introduce pollution events and observe their effects on biodiversity patterns.
- Also for the polluted streams, compare the modeled SADs to the empirical SADs.
- Adjust the model until a satisfactory match of model results with empirical data is achieved.

Relevance and link to EEP's research plan

This project extends work previously conducted as part of EEP's research project on *Evolving Biodiversity* (e.g., Doebeli and Dieckmann 2003; Heinz et al. 2009; Payne et al. 2011), interfacing these modeling approaches with empirical observations of the key ecological factors that promote or hinder the biodiversity of benthic macroinvertebrate communities in Korean streams and rivers.

Expected output

I intend to publish this work as a coauthored article in an international scientific journal. I also expect this work to be a part of my Ph.D. thesis.

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