Adaptation of aquatic insects to the current flow in streams

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ABSTRACT

Water velocity is one of the most important abiotic factors influencing the survival of aquatic insects in rivers and streams. The unidirectional water flow shaping their habitat and characteristically dividing it into alternating zones of high and low water velocity (riffles and pools) also imposes on them the special necessity to adapt to continual downstream drift. Here, we analyze an individual-based eco-evolutionary model parameterized with field data, and show how species adapted to riffles and pools, respectively, emerge if three basic processes are considered: density-dependent local competition, drifting, and adult flight. We also find that evolutionary branching in velocity adaptation is accompanied by an differentiation of drifting behavior. Generally, individuals drift either frequently and for only a short duration, or infrequently and for a longer duration. While riffle and pool species each exhibit both drifting strategies, a third species that can stably establish at intermediate water velocities (runs) exhibits exclusively the former. As the run species is therefore particularly susceptible to drift loss, long-range adult flight turns out to be crucial for its persistence. These insights highlight the ability of process-based eco-evolutionary models to generate testable hypotheses and stimulate empirical research.

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1. Introduction

Freshwater ecosystems fall into two major groups: still water systems like lakes and ponds, and running water systems like springs, streams, and rivers. In this study, we focus on the latter type (lotic ecosystems; Leopold et al., 1964; Ward, 1991; Allan and Castillo, 2007), which exhibit the characteristic feature of unidirectional water flow. To establish in such systems, species must adapt to downstream drift, which would otherwise wash the populations out (Needham, 1928; Müller, 1954; Elliott, 1971; Waters, 1972; Kopp et al., 2001; Svendsen et al., 2004). Some authors have argued that mechanisms of compensatory movement should be important to stabilize populations (Müller, 1954, 1982; Lutscher et al., 2010), while others have suggested that loss of individuals through drift is often compensated through overproduction of offspring (Waters, 1972; Anholt, 1995). These views are not mutually exclusive.

Aquatic insects play an essential role in the functioning of lotic ecosystems (Ward, 1991; Merrit and Cummins, 1996). Their larvae either graze producers (i.e., algae) or are the primary agents in

filtering and breaking down particulate organic matter; they occupy – roughly speaking – the trophic level between microorganisms and the larger vertebrates like fish, for which they serve as a major source of food (while small fish and tadpoles can also fall prey to the larger predatory insects). Because of their pivotal ecological function, aquatic insects are often used as indicators in the biological assessment of water quality (James and Evison, 1979; Hellawell, 1986; Rosenberg and Resh, 1993; Chon et al., 2013).

Descendant from terrestrial insects, at least 50,000 species from more than ten major orders have found their way back into the water, adapting to all kinds of ecological niches found in streams around the world (Williams and Feltmate, 1992; Merrit and Cummins, 1996; Lancaster and Briers, 2008). Yet many aquatic insect species share some characteristics that allow considering their function in a more abstract way. There are commonalities in their life cycles, and most taxa can be assigned to one of a handful of functional feeding groups (Cummins and Klug, 1979); their habitats can be characterized by only a few important abiotic factors, among which water velocity is one of the most important (Statzner et al., 1988; Merrit and Cummins, 1996; Allan and Castillo, 2007).

A typical aquatic insect life cycle consists of a relatively long aquatic larva stadium (up to several years) with numerous instars and molts (and mobile, active pupae for the holometabolous

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species), and a relatively short existence as a flying adult outside the water (down to a few days) with usually weak flight abilities (with the notable exception of the dragonflies, Odonata: Anisoptera). Sexual reproduction is the norm, but parthenogenesis is also common in some major groups. The short-lived adults often do not much more than find a mate, lay eggs, and die, while it is the long-lived larvae that assume an important role in the aquatic food webs (Williams and Feltmate, 1992; Merrit et al., 2009).

Downstream drift of aquatic insects is a common occurrence and was noted as early as by Needham (1928). Elliott (1971) found that drifting distances are well described by an exponential distribution, while the mean time spent in drift turned out to be remarkably constant over a range of flow velocities for individual taxa, and within some groups of taxa (Elliott, 2002a); there was, however, considerable variation between taxa (Otto and Sjöström, 1986; Allan and Feifarek, 1989). Other investigations revealed that drifting seems to depend on local density (Fonseca and Hart, 1996). Also, Elliott (2002b) argued that drift is not necessarily a passive process, but could be initiated by the larva, e.g., to escape from predators or local competition (Rader, 1997).

The flight ability of emerged adults allows them to quickly bridge larger distances. Adults typically remain close to the water body from which they emerged, often following it. At least in some taxa, adult flight appears to be directional – adult upstream flight may compensate larval downstream drift and so spatially stabilize the insect population in the stream (Hershey et al., 1993; Kovats et al., 1996).

The functioning of complex ecological systems cannot be understood without mathematical models, which, because of their complexity, are usually studied with numerical methods (Grimm and Railsback, 2005). The traditional approach to modeling ecosystems is exemplified by the CLEAN model for lake ecosystems (Park, 1974), which described the dynamics in a number of "compartments" representing abiotic and biotic resources through a system of coupled differential equations (Jørgensen and Bendoricchio, 2001). The "total stream model" of McIntire and Colby (1978) implemented a similar idea in discrete time. Aumen (1990) presented a comprehensive model of solute transport along streams based on differential equations. A model of stream ecosystems describing the flow of energy and abiotic agents through trophic layers was presented by Yang and Sykes (1998). Gertseva et al. (2004) focused on aquatic macroinvertebrates and explicitly consider the dynamics between the various functional feeding groups.

More recently, the easy availability of computational resources allowed computationally demanding approaches to analyzing ecological processes. Schleiter et al. (1999) used artificial neural networks to extract predictors of functional relationships between biological indicators and physico-chemical water properties in lotic ecosystems; Nisbet et al. (1997) considered, in addition to differential-equation models, an individual-based model in their study of the interplay of productivity and population dynamics at higher trophic levels. Rolff et al. (2001) already employed an individual-based model to study the co-evolution of damselflies and water mites. Large-scale community models, however, so far seem to have mostly neglected this evolutionary aspect, i.e., the construction and stabilization of the interacting species and their niches through an adaptive process of mutation and selection (Chave et al., 2002; Ulrich and Gotelli, 2007).

Here, we present a model that adds this evolutionary aspect to an ecological model of a simple stream community. We consider, albeit in simplified form, ecological interactions through resource utilization, movement, and inter- and intraspecific localized competition. In addition, we allow adaptation to a spatially continuous stream environment characterized by locally different water velocities ("riffles" and "pools"; Frissell et al., 1986) via various heritable traits. We investigate how, starting from a single ancestral line,

species adapted to different niches along a stream emerge and persist, and how this adaptive branching interacts with the evolution of larval drift and larval movement, as well as adult flight behavior. On a more general note, this study demonstrates how an abstract speciation model can be applied to answering system-specific questions.

2. Methods

To study the evolution of various traits of aquatic insects in a model stream, we construct a model that follows the general framework of abstract parapatric speciation models introduced in Doebeli and Dieckmann (2003) and Heinz et al. (2009), but strives for increased ecological realism by considering a specific environment (small streams) and a specific group of organisms (aquatic insects). The resulting model is individual-based, stochastic, continuous in time and one-dimensional space, and assumes asexual, nearly faithful reproduction once per year. Model parameters are based on empirical data.

2.1. Ecological model

We simplify the real ecological situation in the following manner:

- We reduce the number of environmental factors. Due to its pivotal ecological importance, we here consider only water velocity.
- We simplify the spatial structure along the stream, neglecting all differences over the cross-section of the stream. Each location along the stream is characterized by a single water velocity. Along the stream, velocity varies between high and low velocity (riffles and pools; see Fig. 3).
- We impose the same life cycle on all individuals, letting them all reproduce in the same week of each year and assuming a very short adult stage, during which each adult produces the same number of offspring.
- We limit the model mostly to the larval stage, treating the adult stage with summary assumptions.
- We do not consider any explicit resource dynamics, including effects of competition only via a generic local carrying capacity.
- We assume drift to be an active process, employed to escape both high population density and maladaptation, with all other movement processes occurring unconditionally (as a side effect of foraging, or through other instinctive behavior).

The individual-based model describes only the larval stage explicitly. We do not discern between different larval stages (instars, pupa, etc.), but simply assume that all larvae emerge as adults once per year at the same time. Adults immediately fly a certain distance along the stream to a new location, where they lay a number of eggs before they die. From the eggs, the new generation of larvae immediately hatches and resumes life in the stream. A conceptual diagram is shown in Fig. 1. Traits and events are described in detail below.

2.2. Heritable traits

The larvae are each characterized by five heritable quantitative traits, namely

- a velocity adaptation trait $v \geq 0$ that specifies the preferred water velocity (for whatever morphological or behavioral reason).
- a drifting threshold trait $t \geq 0$ that specifies the critical local mortality that causes the larva to try and improve its situation by drifting. This does not mean that we assume larvae can sense