

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 Feltsmate, 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

their own mortality directly, but rather, that they can sense the quality of the environmental conditions (maladaptation or local competition) that ultimately affect their mortality.

- a drifting duration trait $d \geq 0$ that specifies the average time the larva spends drifting before landing at a new downstream location.
- a larval movement distance $-\infty < s < \infty$ that specifies the expected distance covered by a larva over a certain period through movement other than drifting (see next section). The sign of this trait value indicates the directional preference: positive values mean downstream movement, negative values upstream movement.
- an adult flight distance trait $-\infty < f < \infty$ that specifies the expected flight distance along the stream of the emerged adult, before it produces its offspring and dies. Positive values mean downstream flight, negative values mean upstream flight.

2.3. Population state and events

The state of the whole population at every point in continuous time is fully specified by the current abundance N of larvae in the stream, their current locations x_i along the stream, and their trait values $v_i, t_i, d_i, s_i,$ and $f_i, i = 1, \dots, N$. The abundance changes via death and reproduction events, and the larva locations change via movement and drift events. Traits remain unchanged over an individual's life-time, but offspring inherits them only nearly faithfully, i.e., small mutations are introduced at reproduction. Over time, the distribution of trait values in the population therefore changes, subject to selection and random drift.

Events that alter the population state fall into two classes: there are events that directly affect the whole population simultaneously, and events that directly affect only single larvae (Fig. 1). We call these, respectively, population events and individual events. Events are characterized by the rates at which they occur and by the probability distributions of possible outcomes. Rates generally depend on traits and local environment (which includes the other larvae). In our model, we consider one kind of population event and three kinds of individual events, as follows.

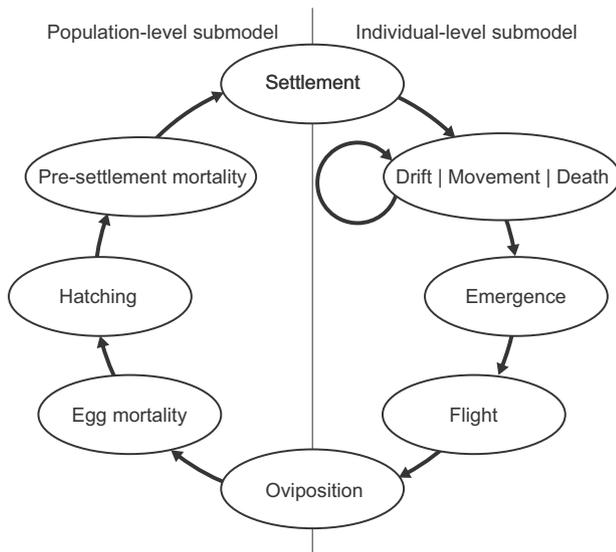


Fig. 1. The annual life cycle of aquatic insects is partly modeled explicitly, partly through summary assumptions on the population level. Drift, movement, and death of larvae that manage to settle at the beginning of the year are traced at the individual level. At the end of each year, adults emerge, lay eggs, and die after flying a certain distance along the stream. With a certain probability, which accounts for egg mortality and larval mortality before settling, the newly hatched larvae resume life in the stream.

2.3.1. Reproduction: the offspring generation replaces the parent generation

A reproduction event (population event) occurs once per year. All larvae emerge at the same time as adults at their current location, fly distances $\Delta x_i^{(f)}$ along the river, lay n_{off} eggs at their new location, and die. For each individual, the overall flight distance from its location of emergence is drawn from an exponential distribution,

$$|\Delta x_i^{(f)}| \sim \exp(-|\Delta x_i^{(f)}|/|f_i|). \tag{1}$$

The direction of the flight is determined by the sign of each individual's adult flight trait f_i . If $\Delta x_i^{(f)} = \text{sign}(f_i)|\Delta x_i^{(f)}| > 0$, the resulting step is taken downstream, otherwise upstream. We assume the probability to not survive flight over a short distance to be proportional to this distance, so the adult survives this flight event with a probability

$$p_i = \exp(-c_f|\Delta x_i^{(f)}|), \tag{2}$$

in which c_f represents a flight cost. If the adult survives, n_{off} offspring larvae immediately hatch at the resulting new location with trait values drawn from normal distributions centered on the corresponding parental trait values and variances chosen such as to produce trait distributions with coefficients of variation close to empirically known values (Table 1). If this would result in a negative value for one of the bounded traits, that trait value is set to zero. After hatching, the offspring larvae immediately attempt an undirected movement step to settle into their habitat. Survival of the egg and settling stage is described by a fixed probability q , so that effectively qn_{off} larvae per adult settle in.

2.3.2. Drift: larvae may let themselves be carried downstream by the current

Through a drift event (individual event), a focal larva drifts to a new downstream location. Drift events occur for each individual i with a drift rate $r_{d,\text{max}}$ if the currently experienced local mortality μ_i (see below) surpasses the larva's drifting threshold t_i ,

$$r_{d,i} = \begin{cases} r_{d,\text{max}} & \text{if } \mu_i > t_i \\ 0 & \text{otherwise} \end{cases} \tag{3}$$

The time τ_i spent drifting depends on the larva's drifting-duration trait d_i and is for each drift event drawn from a log-normal distribution as

$$\log(\tau_i/\text{unit}(d_i)) \sim \exp(-\tau_i^2/2d_i^2), \tag{4}$$

in which $\tau_i/\text{unit}(d_i)$ on the left-hand side just means that the resulting drifting time has the same time unit as used for d_i . From τ_i the distance $\Delta x_i^{(d)}$ drifted and thus the new location is calculated via the water velocity profile $v(x)$ by numerically solving

$$\tau_i = \int_{x_i}^{x_i + \Delta x_i^{(d)}} \frac{1}{v(x)} dx. \tag{6}$$

2.3.3. Directed movement: larvae continually move up- or downstream in small steps

Through a directed movement event (individual event), a focal larva changes its location via a small step. Individuals move with a fixed rate m . The step length $\Delta x_i^{(m)}$ depends on the larva's movement distance trait s_i and is drawn from an exponential distribution as

$$|\Delta x_i^{(m)}| \sim \exp(-|\Delta x_i^{(m)}|/|s_i|), \tag{7}$$

with the direction of the movement steps determined by the sign of the movement distance trait in the same way as for the flight steps (Eq. (1)).

Table 1
Parameter values taken from ^a Lisle (1979); ^b Frissell et al. (1986); ^c Brussock and Brown (1991); ^d Wilzbach et al. (1988); ^e Jowett (1993); ^f Elliott (1971); ^g Elliott (2003); ^h Merritt et al. (2009); ⁱ Fuller (2009); ^j Otto and Sjöström (1986); ^k Elliott (2002a); ^l Hershey et al. (1993), mostly for species of mayflies, stoneflies, and caddisflies. We found no literature values for the coefficient of variation of the drifting threshold, settling probability, and boundary-loss threshold distance, and so estimated values based on our own field experience. Reported results are robust with respect to variations around all values. Downscaling factors are discussed in the main text.

	Symbol	Value	Reference
Stream length (km)		100	a, b
Riffle density (1/km)		20	a, b, c
Water velocity (riffle) (m/s)	v_{riffle}	0.8	d, e
Water velocity (pool) (m/s)	v_{pool}	0.1	d, e
Velocity tolerance (m/s)	σ_v	0.2	e
Competition radius (m)	σ_s	3	f, g
Avg. root-mean-square dispersal distance at birth (m)		5	f, g
Carrying capacity (1/m)	K	50,000	c
Number of offspring	n_{off}	1000	h
Settling probability	q	2%	
Maximum drift rate (1/wk)	$r_{d,\text{max}}$	2	i
Larval movement rate (1/wk)	m	2	g
Coeff. of variation velocity adaptation		20%	j, g
Coeff. of variation drifting threshold		10%	
Coeff. of variation drifting duration		100%	j, k
Coeff. of variation larval movement distance		50%	g
Coeff. of variation flight distance		100%	l
Boundary-loss threshold distance (m)	y	50	
Length-downscaling factor	α	4	
Density-downscaling factor	β	5000	

2.3.4. Mortality: larvae may die if they are maladapted or suffer strong competition

Through a death event (individual event), a focal larva dies and is consequently removed from the population. Death events occur for each individual i with a variable rate μ_i (their current mortality), which depends on the quality of its local adaptation as well as on local competition,

$$\mu_i = \frac{r_r}{\sqrt{2\pi q n_{\text{off}} K \sigma_s}} \sum_{j \neq i} \exp\left(-\frac{(x_i - x_j)^2}{2\sigma_s^2}\right) / \exp\left(-\frac{(v_i - v(x_i))^2}{2\sigma_v^2}\right). \quad (8)$$

The sum in the numerator describes the effective density of competitors, with σ_s the width of the Gaussian spatial interaction kernel. The denominator describes adaptation to the local water velocity, with σ_v being the tolerance width. The pre-factor in Eq. (8), in which n_{off} is the number of offspring per year, $r_r = (q n_{\text{off}} - 1)$ the yearly reproduction rate in 1/y, and K the local carrying capacity (a one-dimensional density: the supported number of larvae per stream-length unit), ensures that, for a homogeneous population and in the absence of evolution, the geometric mean of global larva densities before and after the yearly reproduction event at demographic equilibrium equals exactly K . (This also defines precisely what we mean by “carrying capacity”).

2.3.5. Boundaries: movement beyond is not possible

Dispersal, be it by drift or directed movement of larvae, or by adult flight, that would lead beyond the source or mouth of the stream, deserves special attention, because the individuals thereby would leave the model stream, and their new locations as calculated via the equations above would be invalid. “Leaving a stream” into the downstream direction will typically result in arriving in a different, often much larger, body of water, which may have very different characteristics (as an extreme case, consider a stream discharging into the sea). We simply assume that in this case, neither larvae nor adults will find their way back into the model stream and consider them, for all practical purposes, lost; they are removed from the population.

The situation at the source is different insofar as larvae cannot leave the water, and thus remain at the extreme upstream location, shortening the movement step that would have led them beyond

accordingly. Adults, however, conceivably can fly past the source and explore beyond, and ultimately might find their way back. We therefore assume that, if a flight step leads beyond the source, the adult is lost only if it moves beyond a threshold distance y from the source, and otherwise reproduces at the extreme upstream location.

2.4. Downscaling

A challenge for implementing this ecological model as an individual-based model (IBM) is the large number of insects that exist and interact in real ecosystems. The number of individuals that can be considered in an IBM is in comparison, for computational reasons, rather low. To make sure that the IBM is representative of the ecological model, we therefore apply a systematic *downscaling* procedure, by which we reduce the total number of larvae that we should consider in the ecological model to the feasible number of individuals in the IBM. To do this, we

- reduce the length of the stream (and therefore the number of riffle–pool segments) by a factor $\alpha > 1$, and
- reduce the average local density of individuals (which relates to the carrying capacity) by a factor $\beta > 1$.

2.4.1. Length downscaling

Downscaling the stream length increases the influence of the boundaries on population and adaptive dynamics, and constrains the evolution of drifting and compensatory movement distances, while local dynamics remain mostly the same. Length-downscaling can be applied as long as the model stream remains sufficiently longer than the typical movement distances.

2.4.2. Density downscaling

Downscaling the carrying capacity increases local competition and thus mortality, resulting in lower abundance if all other parameters remain the same and the interpretation of model individuals as real individuals is retained. Reinterpreting the model individuals as *aggregates* of β real individuals (Scheffer et al., 1995), which together approximate the original spatial distribution of real individuals, however, restores the original abundance. With the understanding that this factor β is carried through all equations, rates and parameters remain unchanged. Evolved trait values and

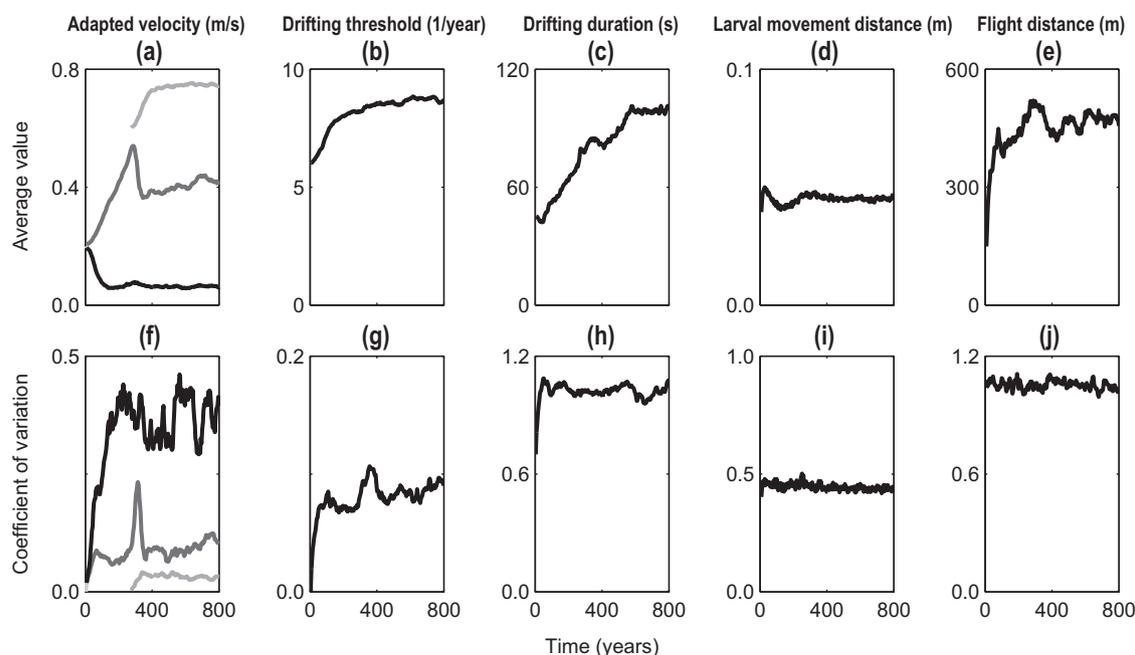


Fig. 2. Traits and their coefficients of variation evolutionarily stabilize over the course of several hundred generations. Panels (a)–(e) show the typical time evolution and eventual stabilization of the averages of the five heritable traits considered, and panels (f)–(j) show the evolution of the corresponding coefficients of variation. In panels (a) and (f), riffle (light gray), pool (black), and run (dark gray) populations (defined as subpopulations of individuals with velocity adaptation traits $v \geq 0.67$ m/s, $v \leq 0.33$ m/s, and 0.67 m/s $> v > 0.33$ m/s, respectively) are indicated separately, since we always observe evolutionary branching with respect to the velocity adaptation trait. For parameters, see Table 1.

their distribution correspond to the individual trait values. Density downscaling can be applied as long as enough model individuals remain to fairly represent the original spatial distribution. Care must be taken to not reduce the number of model individuals to the point where effects of demographic stochasticity manifest that have no counterpart in the original population (e.g., local random extinction, increased genetic drift etc.).

2.5. Stochasticity and scheduling

Our model as described above is inherently stochastic: the population configuration changes through the realization of certain events, which are specified via the rates at which they occur, and the probability distributions of the possible resulting configurations. Interactions among the larvae and between larvae and external environment are described through their effect on these probability rates.

Stochasticity in the model manifests on several levels. Dispersal stochasticity (due to drift, directed larval movement, and adult flight) leads to fluctuations in the local densities and fluctuating overall population sizes from year to year, i.e., demographic stochasticity, which introduces a random element to selection and drift that combines with the random effects of mutation and results in stochasticity on the evolutionary time-scale (which in turn feeds back to the ecological level).

We analyze our model as specified above numerically using the scheduling algorithm of Allen and Dytham (2009), which realizes events serially while advancing the time in steps drawn at random from an exponential distribution. This algorithm assumes maximum event rates, in our case specifically a maximum mortality, which conflicts with Eq. (8). We therefore cut off mortalities at a high value chosen so that there is no influence on outcomes. We ascertain the robustness of the results reported in the next section both by replicating model runs and by varying parameters around the values for which we report results. Table 1 summarizes the model parameters.

3. Results

We survey our model population much like a field researcher surveys a population of real insects (or better, since we have access to every single model larva); that is, we extract, at certain points in time, overall abundance, local densities, and current trait distributions. In addition, we also have access to quantities that can be inferred from field data only with difficulty (like current interaction strengths and mortalities for every single individual).

3.1. Eco-evolutionary models generate communities with realistic ecotype distributions

The evolvable traits and their coefficients of variation generally stabilize at certain values over the course of some hundred generations, indicating that this simulation time is long enough to observe the evolutionarily steady state (Fig. 2). We find as the most conspicuous result branching in the velocity adaptation trait (Figs. 2a, 3a), which we observe for a wide range of parameters (Figs. S1–S4), i.e., the population splits into a subpopulation that prefers high water velocity, and a subpopulation that prefers low water velocity. Individuals with these preferences dominate the riffle and pool zones of the stream, respectively; that is to say, they are mostly found in the parts of the stream to which they are adapted (Fig. 3). Under certain circumstances, which we discuss below, a subpopulation adapted to intermediate water velocities can also emerge.

3.2. Compensation mechanisms let ecological species emerge despite drifting

To investigate which circumstances promote or hinder evolutionary branching, we consider various limits (Fig. 4; also see Figs. S5–S8). While we observe no branching with global competition (Fig. 4a), local density-dependent competition allows two branches to coexist (Fig. 4b) in the absence of any movement (except for random larval movement before settlement). If larvae may drift,

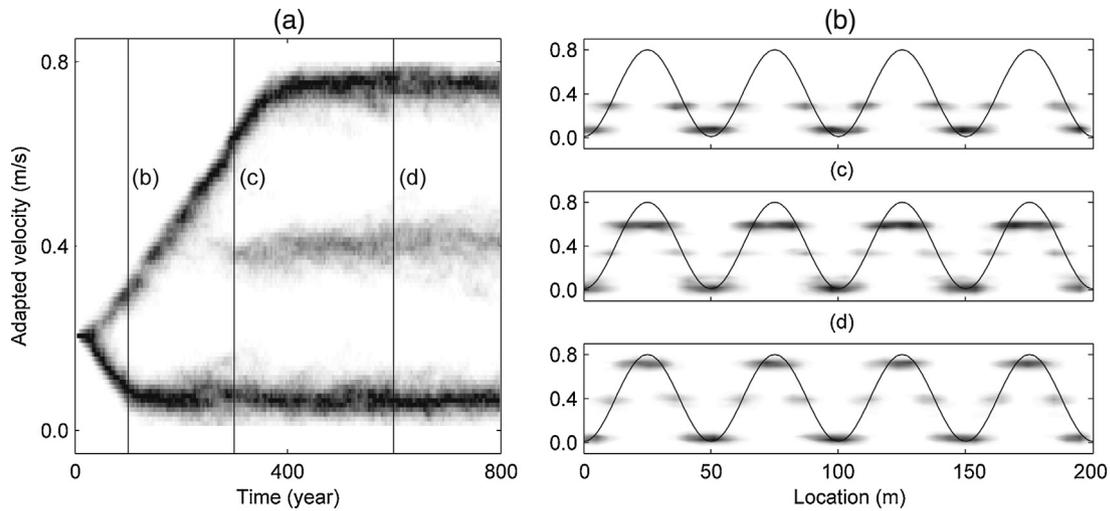


Fig. 3. Trait evolution is accompanied by the emergence of a distinctive ecotype distribution. Panel (a) shows the typical time evolution of the distribution of velocity-adaptation traits. Panels (b)–(d) show the spatial distribution of the population along a short part of the river (4 pool–riffle–pool sequences; continuous lines indicate the velocity profile of the stream, for simplicity assumed to be sinusoidal) in the years indicated by the thin vertical lines in panel (a). For parameters, see Table 1.

however, only one main branch can persist (Fig. 4c). Of the compensatory upstream movements considered, adult flight not only restores the two branches, but allows a third branch to emerge in the run zones between riffles and pools (Fig. 4d). While directed larval movement cannot restore branching on its own (Fig. 4e), it improves the stability of the run branch when acting together with

adult flight (Fig. 4f). In addition, branching disappears in two trivial limits (not shown), namely, if environmental variation along the stream is not sufficient (i.e., the number of riffles/pools per stream length becomes very small, which implies that riffles and pools are so far apart that newly deposited larvae cannot find them) or if variation occurs on such a small scale that the random movement

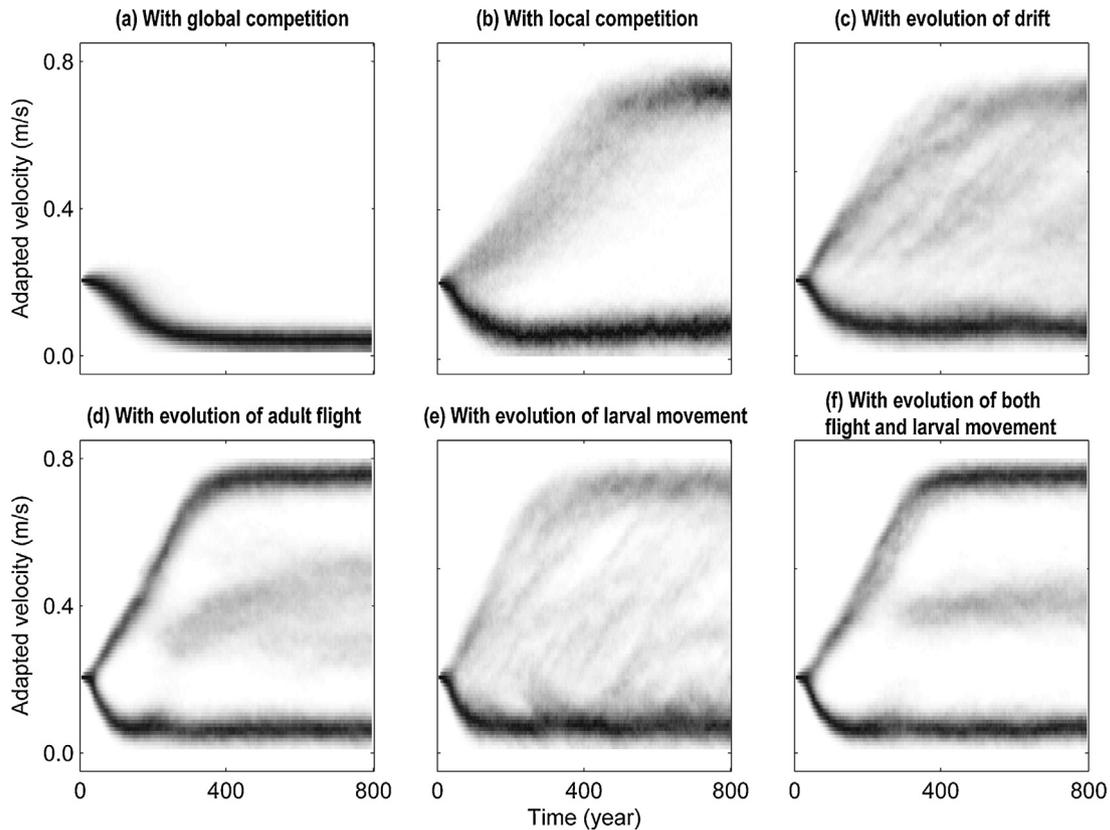


Fig. 4. Adult flight allows three branches to emerge despite drifting. (a) Global competition ($\sigma_s \rightarrow \infty$ in Eq. (8); no movement or drift) prevents branching, while (b) local competition without any movement by larvae or adults allows the emergence of two branches adapted to pools and riffles, respectively. (c) With local competition and drift (but still no directed larval movement or adult flight), branching is again suppressed, although a wide range of phenotypes can persist besides the main branch. Of the compensatory-movement possibilities considered to evolve, (d) adult flight is successful in restoring branching without directed larval movement, and even allows a third branch broadly adapted at the run zone to emerge, while (e) directed larval movement without adult flight is not sufficient. However, when (f) directed larval movement and adult flight are evolving together, this results in the clearest branching scenario. For other parameters, see Table 1.

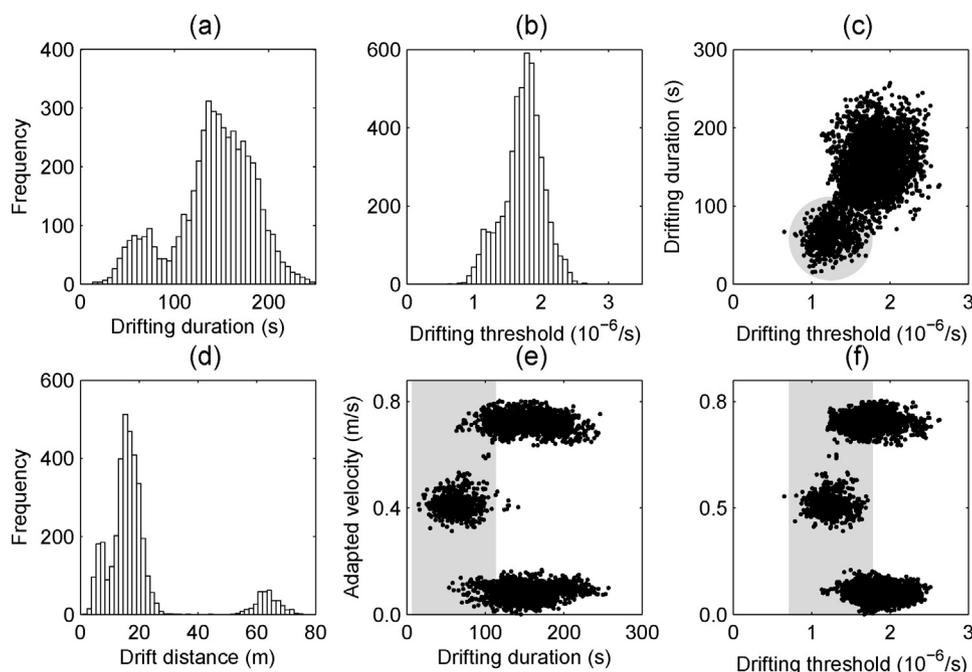


Fig. 5. An empirically testable typology of drifters. Panels (a) and (b) show the respective marginal trait distributions of drifting-duration and drifting-threshold traits in the population. Panel (c) shows the correlation of these traits in the population and reveals that there are two basic strategy groups: low-threshold short-duration drifters and high-threshold long-duration drifters. Panel (d) shows the distribution of drifting distances sampled over the course of 1 year after 800 years of evolution. Panels (e) and (f) show the correlation of the drifting traits with velocity adaptation and reveal that the run-zone population is made up of short-duration drifters only. Light gray shading in these two panels indicates the respective ranges of the low-threshold short-duration drifters likewise indicated in (c). For parameters, see Table 1.

of larvae effectively averages over the environmental variation so that only the average value is experienced (i.e., the number of riffles/pools per stream length becomes very high).

3.3. Two distinct drifting strategies emerge

Taking a closer look at the evolutionarily stable drifting trait distributions (Fig. 2b,c,g,h), we see that they do not simply peak around a single trait value (Fig. 5a,b). A correlation plot (Fig. 5c) of drifting threshold vs. drifting duration reveals an evolutionary split into two groups of drifting strategies: individuals that drift more easily and only for shorter durations, and individuals that drift less easily and for longer durations. These drifting strategies result in a clearly defined bimodal distribution of realized drifting distances in the population (Fig. 5d). Remarkably, individuals in the run zone only apply the first strategy (Fig. 5e,f).

3.4. Rare long-distance adult flight is required for species establishment in run zones

To investigate the influence of adult flight behavior on trait evolution and branching, we finally introduce costs of adult flight by considering a certain probability per flight distance that an individual would not survive its adult phase (Eq. (2)). High costs, as expected, suppress the evolution of longer flight distances, while a weak upstream tendency evolves without costs (Fig. 6a). We also find that the emergence of branching in velocity adaptation is connected to adult flight – only when the evolution of adult flight is not inhibited by high costs do we observe a third branch (Fig. 6b). Remarkably, the onset of three-way branching coincides with a slight broadening of the flight-distance distributions, i.e., with the appearance of rare individuals that undertake long flights, and not so much with the shape of the bulk region of those distributions.

4. Discussion

We have introduced an eco-evolutionary individual-based model of aquatic insects in streams that considers the most important elements of a typical life cycle, i.e., reproduction, larval movement, ecological adaptation to the local water velocity, localized competition, downstream drift, and adult flight. We have used this model to demonstrate the emergence of ecological species using a set of realistic model parameters taken, wherever possible, from the literature. Under realistic conditions, at least two evolutionary branches, corresponding to specialists adapted to high and to low water velocity, i.e., riffle and pool zones, respectively, emerge (Figs. 2 and 3) if the velocity tolerance is sufficiently small (Fig. S4).

A subpopulation adapted to an intermediate range of water velocities emerges if directed larval movement acts together with adult flight (Fig. 4f). Evolved movement distances are very low and show no clear bias for either the upstream or the downstream direction. Larvae depend mostly on a refined drifting behavior to displace themselves in reaction to adverse environmental conditions, which are often created by local crowding during the first part of the year.

It may come as a surprise that adult flight turns out to influence the evolution of the larval traits so strongly and even be requisite for evolutionary branching in the ecological trait, seeing how broad a distribution of flight distances emerges with a relatively small net movement upstream (Fig. 6). But clearly, ecological adaptation to certain niches in the stream can only be favored by evolution if at the same time mechanisms can emerge that make staying in this niche likely. This mechanism turns out to be a refined drifting behavior, which enables larvae to escape local competition if necessary, but still land in a downstream region to which they are adapted. Because drifting exclusively occurs in the downstream direction, evolution toward frequent drifting also means evolution toward increased overall downstream movement, which creates a selective disadvantage since individuals are lost when they reach the end of the stream.

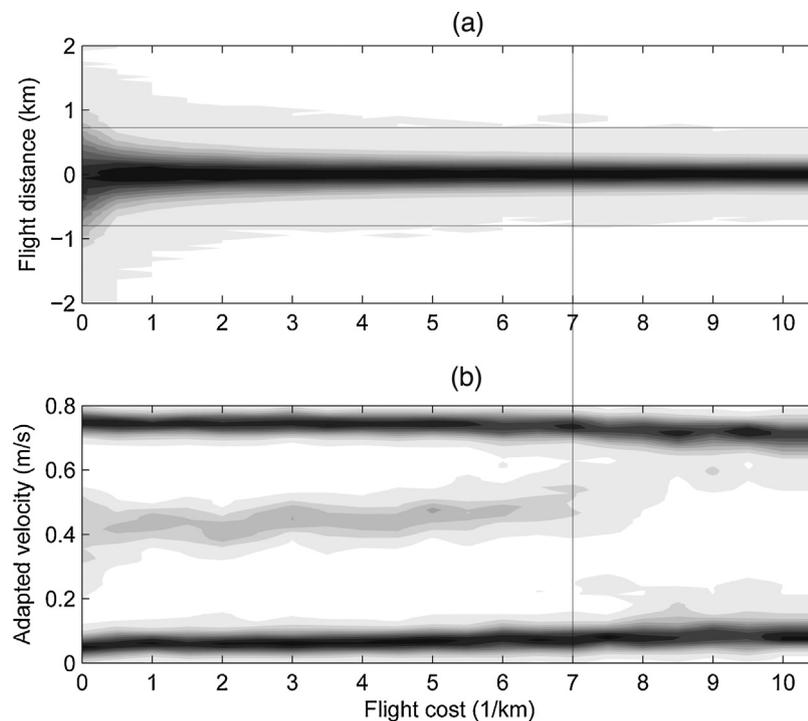


Fig. 6. The evolution of compensatory adult flight facilitates species establishment in the run zones. Panel (a) shows evolutionarily stable distributions of adult flight distances as a function of flight costs, while panel (b) shows the corresponding distributions of velocity adaptations. A thin vertical line indicates the largest flight cost at which the middle branch in (b) is sustained. Thin horizontal lines in (a) indicate the width of the flight distance distribution at this point, so that the widening of this distribution toward smaller costs can be perceived more easily. The cost-free case is the one depicted in Figs. 2, 3, 4f, and 5. High costs (which effectively switch off adult flight) create a case similar to the one depicted in Fig. 4e.

With the water velocity profile assumed here (Fig. 3), run zones make up only about 20% of the total stream length, while riffles and pools occupy nearly 40% each. Drifting is therefore risky for individuals adapted to run zones, since they may be exposed to higher mortality in riffle and pool zones before they find a good spot again. It may therefore seem surprising that the frequent-drifting strategy emerges as the dominant one within the run species. We suspect that the reason behind this is that water velocity changes more quickly along run zones than along riffle or pool zones, which makes the fine-tuning of locations through short-range drifting the locally superior strategy. However, frequent drifting also exposes the run species more strongly to drift loss than either the riffle or the pool species, which, together with the increased mortality in the stream incurred by frequent drifting, may be the reason behind its relative instability. This is consistent with the observation that many individuals that survive at the end of the year have drifted only a few times (not shown).

Adult flight as well as larval movement would allow subpopulations to remain, in a demographic sense, attached to a certain environment, compensating for drift loss (Kopp et al., 2001), which makes refined drifting behavior and local adaptation possible, and an evolutionarily successful strategy. Why does, in our model, adult flight appear to be more successful at this than larval movement? The reason is that on their way up the stream, larvae must traverse unfavorable environments, from which they escape through downstream drifting – unfavorable upstream environments thus present a barrier that they cannot pass, and little net movement upstream results. Larvae with an upstream movement bias essentially just fine-tune their location by repeated drifting and moving to find the optimal environment.

Flying adults, however, can cover relatively large distances without drifting back immediately. Even with the very broad distribution of flight distances assumed here, which implies that many adults may not be able to place their offspring in their favored

environment, the compensation effect resulting from a few successful re-colonizers of the upstream region appears to be enough to maintain even the fragile run species. This is also apparent from the fact that the disappearance of the run species is connected to the disappearance of rare long-distance fliers (Fig. 6).

One may question the relevance of our results for cost-free flight, since mortality of flying adults is usually high in nature. However, adults usually are able to sense their environment to some extent and pick a spot for oviposition that is somewhat favorable to their offspring (Peckarsky et al., 2000; Spencer et al., 2002), in contrast to our model assumption of a broad exponential distribution of flight distances that puts many adults in bad spots. In this sense, our model already imposes a substantial cost on adults, which counteracts to some extent the assumption of cost-free flight. To further increase realism, empirical data about costs due to adult mortality before oviposition and due to spot selection would be needed.

Our assumptions about the directedness of adult flight (Petersen et al., 2004; Hershey et al., 1993) mirror the typical situation in many taxa, but are by no means universally valid. However, based on our results we speculate that for local ecological adaptations to emerge, in general a form of directed movement that allows compensation of drift loss will be necessary. This also provides a new perspective on the so-called “drift paradox” (Humphries and Ruxton, 2002): compensatory movement may not be necessary to enable population persistence in a wider sense, but it may under certain conditions be necessary for ecological species to establish or coexist.

The compensation mechanism in our model works only in connection with evolving drifting strategies and should not be confused with exact compensation *sensu* Kopp et al. (2001) – the broad flight distance distribution in Fig. 5 already strongly hints at that. The reason is, we believe, simple: the exponential, and therefore very broad, distribution of realized flight distances (Eq. (1)) just does not permit exact compensation; even if the mean (i.e., the

value of the flight distance trait) were to be exactly equal to the total drift distance by some coincidence, the realized flight distance would still almost always be way off.

We have assumed asexual reproduction, which is clearly a simplification. Under sexual reproduction, evolutionary branching is not possible without additional mechanisms of non-random mating. If, however, adults mate immediately after emerging, which is not uncommon, some degree of assortativity may in fact already arise from habitat differentiation along the stream, which could then be promoted by selection against hybrids, with an overall similar outcome to the asexual case. Also, the simplified life cycle included here will not apply universally, although it should be a good model for many taxa.

To summarize, our simple model yields patterns that can be considered realistic, and provides insight into various stages of the evolutionary process. We highlight the importance of the possibility of compensation of drift loss for the emergence of locally adapted subpopulations, which can be considered ecological species, and formulate the hypothesis that the facility for directional upstream movement and the ability to persist in local niches go hand in hand.

Finally and on a more general note, we suggest that field biologists will benefit from providing quantitative descriptions of their observations, and also from characterizing the site/stream under consideration by measuring the handful of abiotic parameters that ecologists consider relevant (see Introduction), instead of just mentioning its name and location. For example, we surveyed a large body of literature to find information about water velocities to which various well-studied species are adapted, but found it often hard to extract actual velocity ranges from the descriptions, even if they are clearly based on very careful observation. Some methods also give information of questionable usefulness, e.g., velocity information sometimes seems to be obtained by putting nets in a stream at a point of known water velocity and collecting insects including drifting ones. However, if drifting is an active process employed to escape adverse conditions, this does not give any information about which velocities species prefer, or are adapted to, but only tells us that there is probably an upstream site they wanted to get away from – information that may be difficult to interpret if the stream layout upstream of the net site is not documented. Modern modeling tools allow us to analyze very complex and realistic systems, but good data about these systems is needed to tame their complexity and achieve this goal.

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Appendix A. Supplementary data

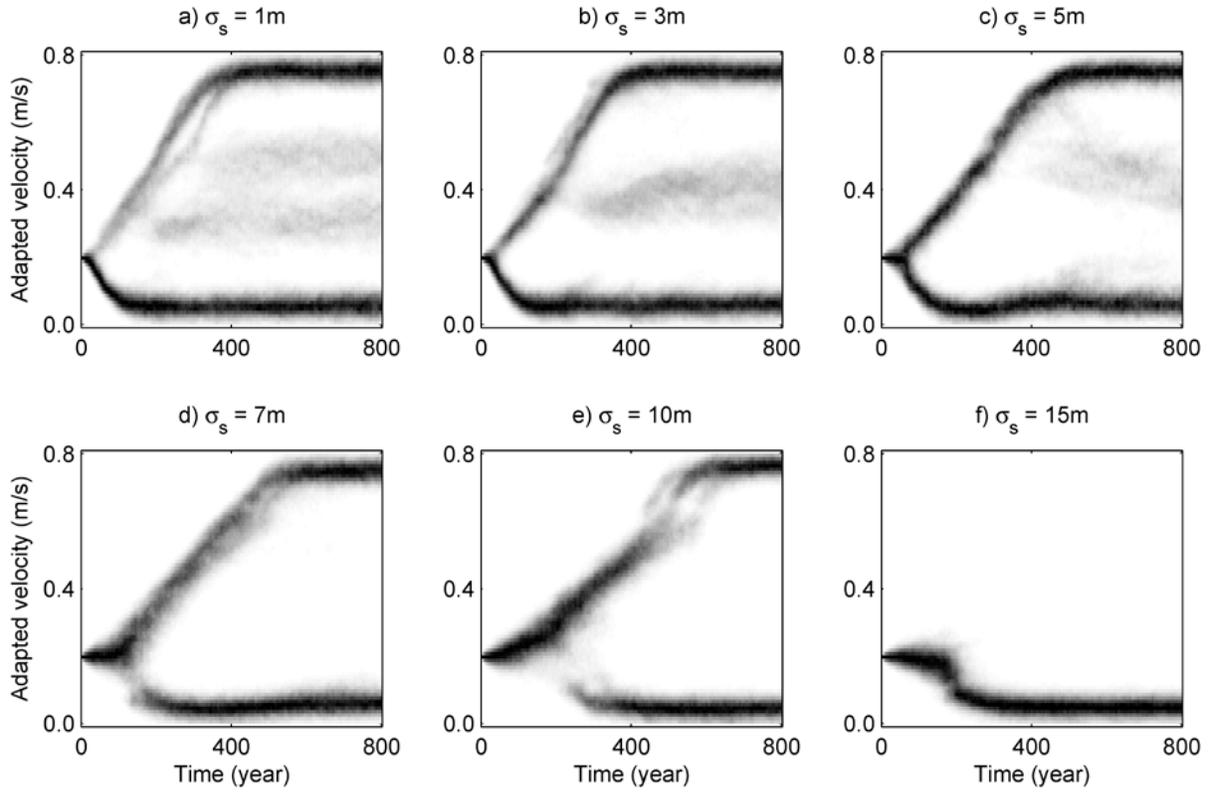
Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.04.019>

References

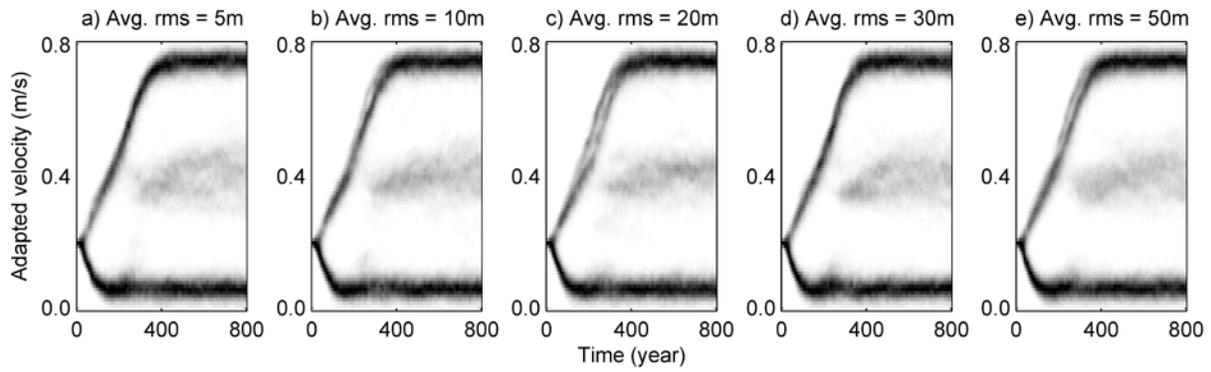
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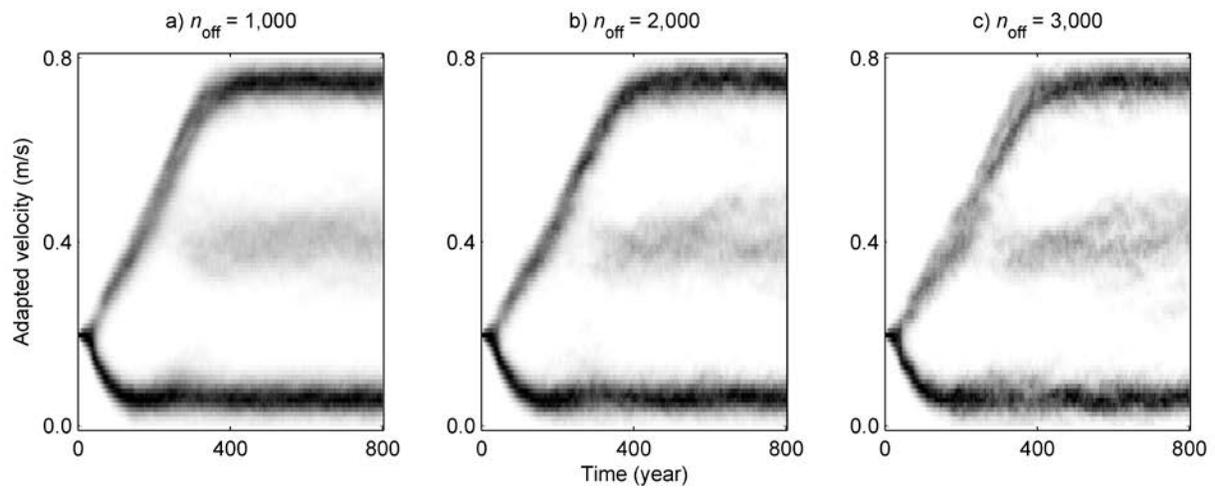
1 Supplemental figures



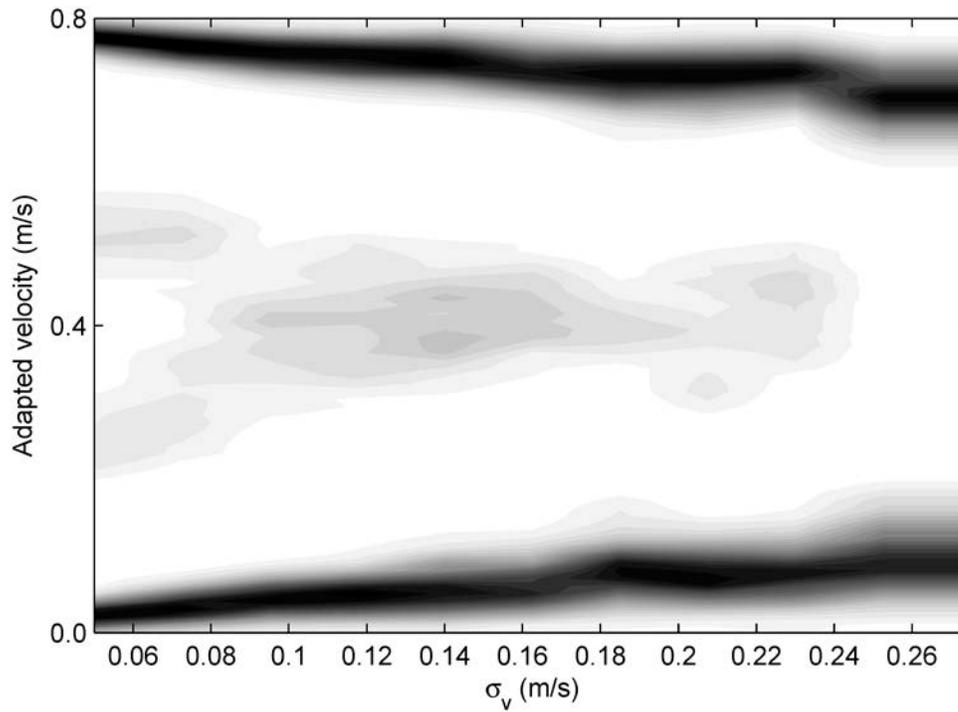
2 *Figure S1* Adapted velocity branching patterns as in Fig. 3a for different values of the spatial
3 competition radius σ_s . The disappearance of the run branch (d) and the disappearance of the riffle
4 branch (f) both coincide with competition from the neighboring branch becoming strong. (For
5 comparison, the distance between riffles and pools is 25 m, the distance between either and the run
6 12.5 m).
7



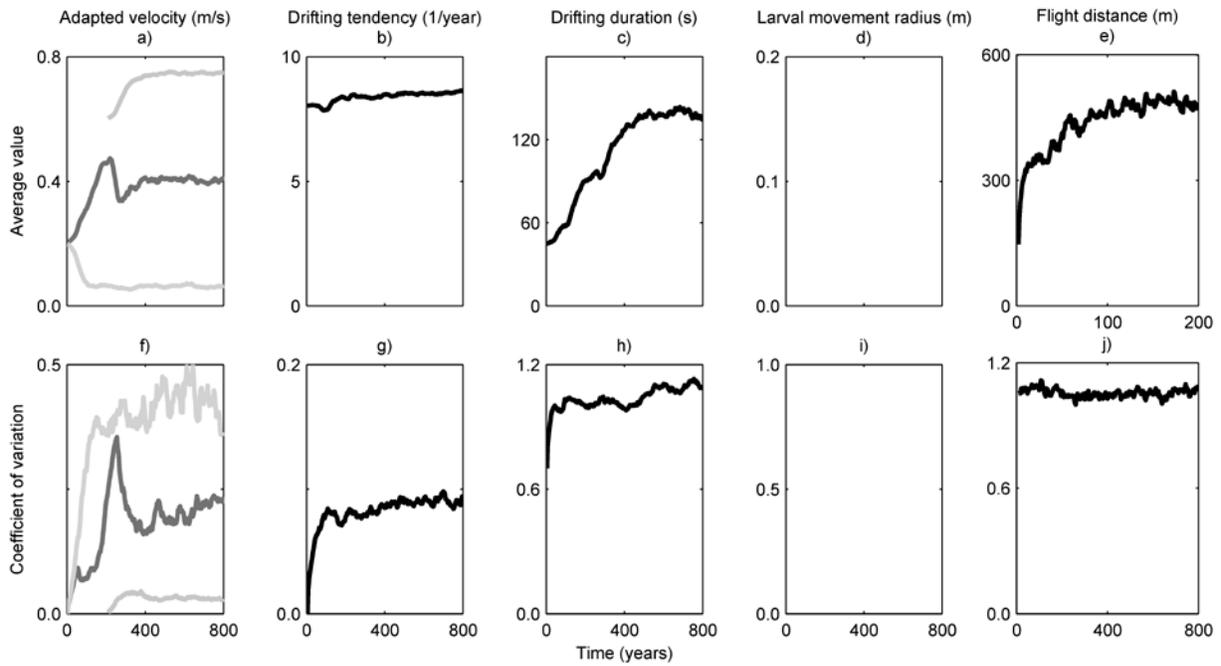
8 *Figure S2* Adapted velocity branching patterns as in Fig. 3a for different values of the average
 9 displacement distance at birth. Varying this parameter considerably has no effect, which is
 10 consistent with the very broad distribution of flight distances and the very weak upstream bias
 11 observed (compare Fig. 6). Offspring placement is essentially random.
 12



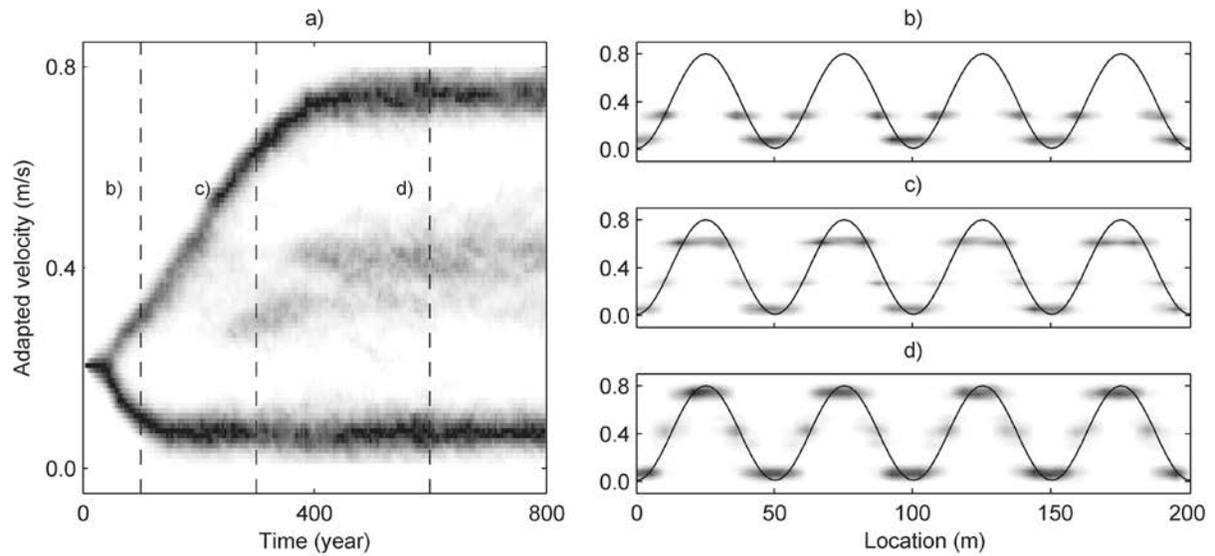
13 *Figure S3* Adapted velocity branching patterns as in Fig. 3a for different values of the number of
 14 offspring n_{off} . The main effect of increasing this number is to increase density-dependent
 15 competition during the first few weeks of the year, leading to more drifting and higher overall
 16 mortality, but there is little effect on the evolutionary dynamics.
 17



18 *Figure S4* Evolutionarily stable adapted velocity distributions as a function of the velocity tolerance
 19 σ_v . While a high tolerance prevents the middle branch from emerging, very low tolerances even
 20 allow four branches to persist. That pool and riffle branches become more narrow with decreasing
 21 velocity tolerance, but the run branch does not, is consistent with the high proportion of sedentary
 22 high-threshold drifters in the pools and riffles and the dominance of low-threshold drifters in the
 23 run (Fig. 5), as the latter also improves local adaptation by drifting, while the former can only
 24 evolve their adaptation trait.
 25

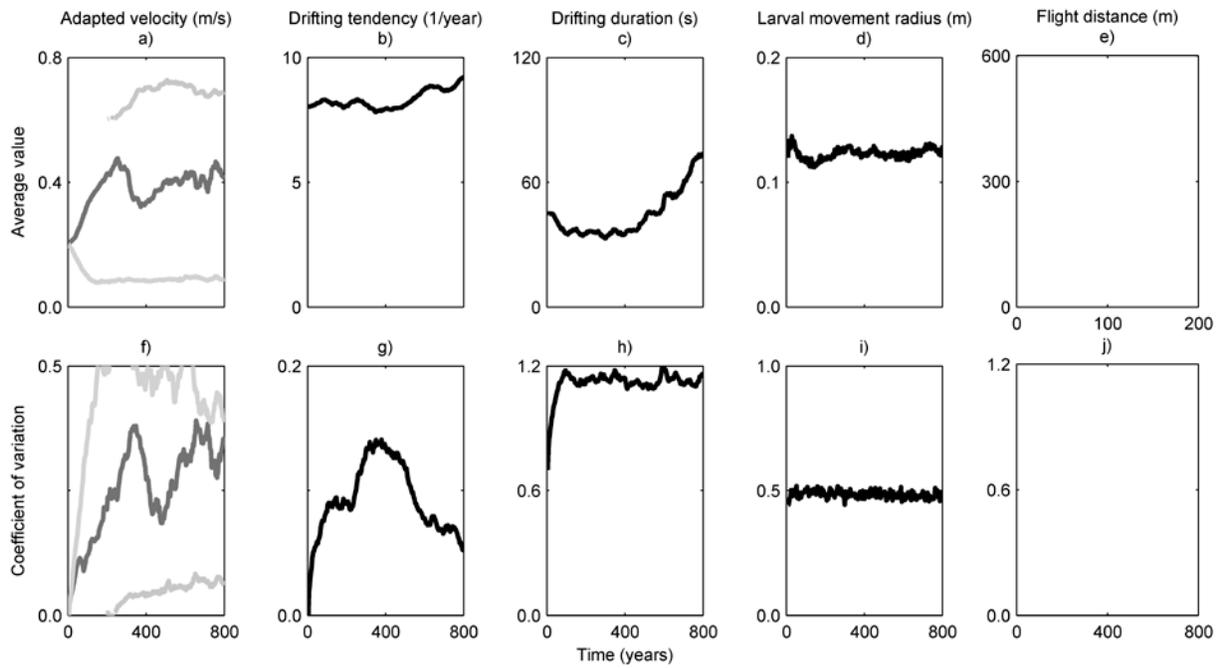


26 *Figure S5* Traits and their coefficients of variations as in Fig. 2 for the model variant shown in
 27 Fig. 4d including adult flight, but no directed larval movement.

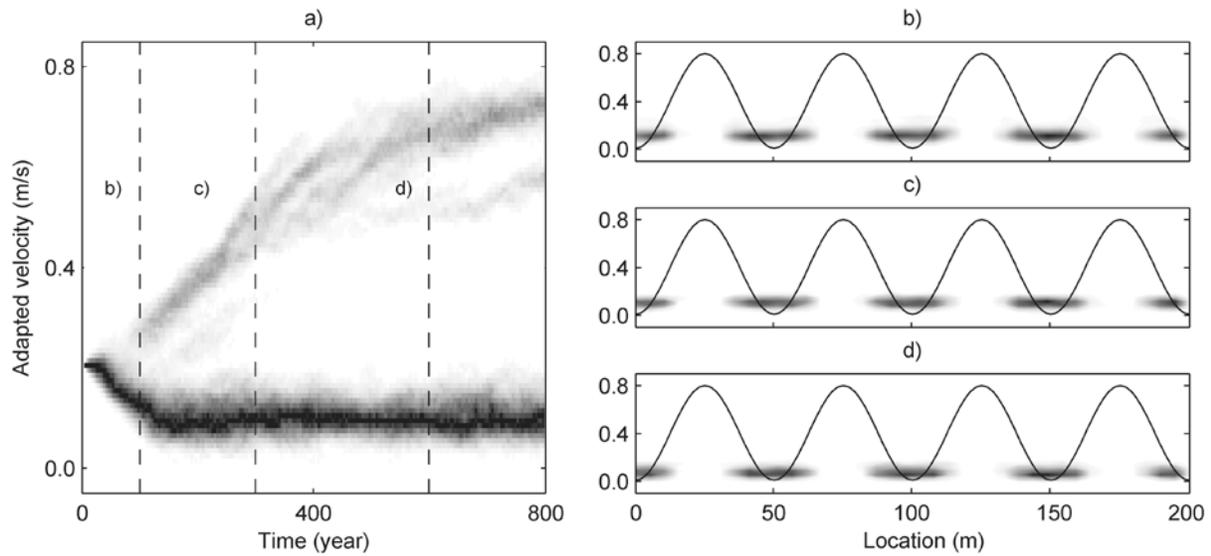


28 *Figure S6* Trait evolution and ecotype distribution as in Fig. 3 for the model variant shown in
 29 Fig. 4d including adult flight, but no directed larval movement.

30



31 *Figure S7* Traits and their coefficients of variations as in Fig. 2 for the model variant shown in
 32 Fig. 4e including directed larval movement, but no adult flight.



33 *Figure S8* Trait evolution and ecotype distribution as in Fig. 3 for the model variant shown in
 34 Fig. 4d including directed larval movement, but no adult flight.