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Current Opinion in Insect Science

Integrating behavioral, population and large-scale approaches for understanding stream insect communities

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Stream insects are ubiquitous in running waters, show high diversity in terms of species numbers, form and function, have key roles in ecosystem processes, and are thereby important components of ecological research. Here, we emphasize that the integration of behavior, population-level processes and large-scale constraints, such as the history of the regional species pool, drainage basin morphology and environmental conditions, may be key to increasing our understanding of how stream insect communities are assembled. We argue that as an alternative to analyzing the species composition of whole insect communities, focusing on variation in the composition of behavioral trait groups is likely to provide increased understanding of how stream insect communities are assembled, thereby linking behavioral, population and community ecology.

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Current Opinion in Insect Science 2014, **2**:7–13
This review comes from a themed issue on **Ecology**
Edited by **Ian Kaplan** and **Saskya van Nouhuys**
For a complete overview see the Issue and the Editorial
Available online 18th June 2014
http://dx.doi.org/10.1016/j.cois.2014.06.002

Introduction

The distribution and abundance of species comprising ecological communities result from multiple processes acting at various spatial and temporal scales [1,2]. A major challenge is to understand the relative importance of those processes, which would benefit from the integration of behavioral, population and community-level approaches. Such understanding also necessitates asking how spatial and temporal scales of observation affect the responses by individuals, populations and whole communities to the abiotic environment and to other organisms. Increased understanding of how ecological communities are assembled can hence be achieved through simultaneous considerations of small-scale processes (e.g., behavioral choices and organismal responses to the environment) and factors causing variation in community structure at larger scales (e.g., history of the regional species pool and dispersal limitation).

Stream insects are a suitable model group for examining the relative importance and appropriate scales of investigation of individual-level, population-level and community-level processes because they are ubiquitous in stream ecosystems (Box 1), have diverse behavioral, morphological and ecological traits [3], and are highly variable in community structure even between adjacent streams or consecutive riffles in a stream [4]. Such variation is likely to be generated by multiple processes (Figure 1), often acting simultaneously, including individual behaviors, responses of species to environmental gradients, metapopulation dynamics, and metacommunity dynamics [5,6].

While many studies examine the behavioral choices (e.g., selection of oviposition sites) of stream insects [7], the responses of single species to environmental gradients [8] and metacommunity-level patterns [9], few studies address local extinction-colonization dynamics of stream insects [10]. Furthermore, very few studies integrate behavioral-level, population-level and community-level approaches for understanding the distribution and abundance of species comprising stream insect communities [11]. This lack of integration likely stems from the logistical difficulty of combining small-scale behavioral and population approaches with large-scale community-level and biogeographical approaches. However, while studies on each level of biological organization and spatial scale remain important in advancing our knowledge of stream insect communities, we emphasize that progress toward understanding stream insect communities would benefit from integration of these organizational levels and relevant spatial scales [5,6].

In this essay, our aims are: (1) to describe examples of behavioral, population and large-scale studies necessary to advance our understanding of stream insect communities; and (2) to propose perspectives about how to integrate those approaches to increase our knowledge of stream insect communities at multiple spatial and temporal scales. Rather than providing a comprehensive review of stream insect communities, we focus on one

Box 1 Organization of stream insect communities in a nutshell.

Stream insect communities are composed of species belonging to a number of different taxonomic orders [3], the most common of which are mayflies (Ephemeroptera), stoneflies (Plecoptera), caddisflies (Trichoptera) and dipterans (Diptera). Those four orders are almost ubiquitous in streams, occurring from tropical to Arctic latitudes, from lowland to mountainous altitudes, and in widely variable environmental conditions. Different environmental conditions typically favor different insect communities, and this biological variation may be very high among drainage basins, among streams within a drainage basin, among riffle sites within a stream and among patches within a riffle (Figure 1). The fact that stream insect communities exhibit such high variation in structure and organization at multiple spatial and temporal scales may be caused not only by variation in abiotic environmental conditions, but also by biotic interactions and dispersal processes [4,5]. Biotic interactions mainly include predation by fish and predatory stream invertebrates on larval insects and by terrestrial predatory insects, lizards and birds on adult stream insects. Dispersal in stream insects occurs as: (1) downstream larval drift within riffles and between consecutive riffles in a stream, (2) adult aerial dispersal among riffles within a stream and (3) adult aerial dispersal among streams [5]. An important process potentially linking abiotic environmental conditions, biotic interactions and dispersal is the oviposition behavior of adult insect females [6]. In order to oviposit, an insect female either stays at its natal site or disperses from its natal stream site to another site with more favorable environmental conditions. A dispersing insect female faces multiple challenges before laying her eggs. Those challenges include avoiding terrestrial predators when dispersing and avoiding fish predators when ovipositing at a suitable location [5]. If oviposition is successful, the eggs will hatch and the larvae will develop in a stream. The hatching success and larval development may again vary depending on prevailing abiotic and biotic conditions, which affect realized larval population size and community structure at a locality [6].

example and emphasize the importance of investigating links between oviposition choices, dispersal and the responses to environmental conditions by stream insects to understand how those processes interact to influence stream insect communities.

The roles of behavioral, population and large-scale processes are typically studied in isolation

Behavioral, population and large-scale processes should be combined in studies of stream insect communities, because the behavioral choices of individuals may affect both populations and communities [12••]. Critical behavioral choices include how to avoid predators, how to find food, how to find mates, where and when to oviposit, and how and where to disperse. All those behavioral choices potentially affect communities and have been extensively studied [13], but here we focus on oviposition and dispersal processes. These two processes are likely to be interconnected (Box 1), but an important distinction can also be made. While the choice of an oviposition site is a small-scale phenomenon, dispersal processes transcend scales from local (i.e., larval drift dispersal within a stream) to regional (e.g., adult aerial dispersal between streams) [5,13].

Oviposition preferences by female stream insects may determine if a species is present at a site and affect realized larval population sizes [12••,14,15••,16]. Both the presence and abundance of a species are thereby mediated by the habitat characteristics of a site related to suitable structures for oviposition (e.g., protruding rocks), although in-stream drift dispersal of larvae can populate areas with no suitable oviposition habitat [15••]. Furthermore, oviposition behavior may be key for understanding population dynamics [17] and have consequences on local communities [5]. For example, if we concentrate only on larval insect habitat demands, we are likely to miss an important component linking adult behavior to realized larval population sizes. This component often overlooked in ecological studies may be better understood by considering local habitat features necessary for successful oviposition by adult insect females [6]. Consideration of oviposition behavior could hence contribute to understanding why some species are absent or at low abundance in seemingly suitable sites and why the proportion of variation in community structure explained by typically measured environmental and spatial predictors is often low [6,9,11,18].

The dispersal of stream insects has been studied widely [13], especially the relative roles of density-dependent and density-independent mechanisms triggering within-stream drift of larval insects in short sections of streams [19]. Although such smaller-scale dispersal may affect the abundances of stream insects in a local community [20], dispersal processes are most likely to influence the presence and abundance of species at larger spatial scales between riffle sites in a stream (larval drift and aerial adult dispersal) and between streams (aerial adult dispersal) [5,21–23]. Dispersal may be homogenizing (i.e., mass effects where high dispersal rates allow species to occur at environmentally suboptimal sites; [24]) or limiting (i.e., where species are absent in some sites due to large distances to the nearest occupied sites; [24]). Although the scales at which dispersal shifts from homogenizing to limiting are typically unknown, we assume that high dispersal rates between consecutive riffles in a stream lead to increasingly similar community composition [25,26], whereas dispersal limitation at across-streams scales results in increasing differences in community composition [27,28•].

Given that most dispersal of stream insects occurs within or a short distance beyond stream corridors [29,30], it is tempting to assume that large distances between streams promote relative isolation and thereby increase differences in community composition [27,31,32••,33]. However, although most individuals do not disperse far from their natal streams, some individuals may fly relatively long distances either actively or assisted by wind [25,30]. Such rare instances of long-distance dispersal may not only be important in countering local extinctions, but also allow colonization and establishment of populations in