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**Dispersal by terrestrial stages of stream insects in urban watersheds:
a synthesis of current knowledge**

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Dispersal by terrestrial stages of stream insects in urban watersheds: a synthesis of current knowledge

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Abstract. Adult dispersal and completion of life cycles by aquatic insects are essential for the persistence of populations, colonization of new habitats, and maintenance of genetic diversity. However, life-cycle stages and processes associated with the terrestrial environment often are overlooked when the effect of watershed urbanization on the persistence of insects associated with streams is examined. We reviewed and synthesized current literature on the known effects of watershed urbanization on the terrestrial stage of stream insects. Some research has directly examined the effects of watershed urbanization on dispersal, but much of the evidence we present is indirect and from related studies on aquatic insect life-history traits and dispersal abilities in nonurban watersheds. Our goal is to provide examples of potential impacts that warrant further study, rather than to provide a comprehensive review of all life-history studies. We discuss how watershed land use, riparian condition, and habitat quality affect: 1) adult fitness, 2) adult dispersal, and 3) habitat fragmentation, and 4) how these factors interact with species traits. In general, we found that the local- and landscape-scale changes to stream, riparian, and upland habitats that typically result from anthropogenic activities have the potential to prevent the completion of aquatic insect life cycles and to limit adult dispersal, and therefore, can affect population persistence. When considered within the spatial context of dendritic stream networks, these effects, particularly those on adult dispersal, might have important implications for design and assessment of restoration projects. We discuss a framework for how to determine the relative importance of effects on specific life-cycle stages and processes for the absence of larval populations from urban streams. Overall, more research on terrestrial life-cycle stages and processes and on adult dispersal is required to understand how urbanization might affect population persistence of insects in urban streams.

Key words: adult stream insects, watershed urbanization, flight, colonization, restoration.

Anthropogenic alterations to natural landscapes can lead to loss of native populations (Pickett et al. 2001, McKinney 2002). The change from natural to urban land use in watersheds generally degrades habitat and water quality for stream-dwelling insects (Sweeney 1993, Paul and Meyer 2001, Walsh et al. 2001, 2005, Roy et al. 2003). These effects can cause species loss, increased dominance of taxa tolerant of poor habitat, and decreased diversity at the community level (Allan and Flecker 1993, Paul and Meyer 2001, McKinney 2002, Walsh et al. 2005).

Degradation of the aquatic environment in urban streams has been linked to patterns of decreased diversity (Allan and Flecker 1993, Allan 2004, Moore and Palmer 2005, Urban et al. 2006), but direct effects

on the aquatic stage of stream insects do not represent all potential mechanisms involved in loss of insect taxa. All stages of the insect life cycle must be completed for a population to sustain itself, or the population must be rescued by immigrants from neighboring populations. However, research to date has focused on the effects of watershed urbanization on aquatic insect development, survival, and movement within the stream (e.g., Petersen et al. 2004), which excludes one or more life stages of many aquatic insects. The anthropogenic alteration of natural landscapes can affect both in-stream and terrestrial stages of aquatic insects. Terrestrial habitats of adult aquatic insects include stream banks, riparian areas, and upland areas, and aquatic insects interact with biotic and abiotic components of these habitats. Anthropogenic activities in a watershed can alter upland and riparian habitat structure and, thus, affect adult aquatic insect fitness and dispersal (McIntyre 2000).

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Understanding the effects of watershed urbanization on the entire life cycle of stream insects is important for conserving and restoring populations and communities in urban watersheds. Aquatic insects are important components of stream ecosystem function (Wallace and Webster 1996, Covich et al. 1999) and are important food resources for higher trophic levels in aquatic (Huryn and Wallace 2000) and terrestrial habitats (Gray 1993, Sabo and Power 2002, Kato et al. 2003, Briers et al. 2005, Fukui et al. 2006). Impacts to terrestrial adult stages might indirectly affect ecosystem function because adults play a vital role in population persistence. Stream insects also are used as bioindicators of stream health (e.g., Rosenberg and Resh 1993, Barbour et al. 1999, Karr 1999, Bonada et al. 2006), and a full understanding of how watershed urbanization affects population persistence has important implications for their utility for assessing stream health or restoration success.

The critical role of terrestrial life stages in regional adult dispersal makes understanding the effect of urbanization on the entire life cycle of stream insects particularly important (Petersen et al. 2004). Dispersal, defined by Bilton et al. (2001, p.160) as the "movement of individuals or propagules between spatially (or temporally) discrete localities or populations," can directly affect population dynamics (Palmer et al. 1996, Fagan 2002, Grant et al. 2007), as well as population genetic structure and local adaptation (Wright 1938). Drift by larval insects has been well studied (Waters 1972, Allan 1995, Huryn et al. 2008), and long distance movements between watersheds by drifting and crawling is unlikely (Jackson et al. 1999, but see Elliot 2003). Research on adult dispersal traditionally has focused on measuring distance, direction, and flight behavior in various terrestrial habitats (Bilton et al. 2001), and only a few studies have attempted to determine how terrestrial environments affect transport between 2 adjacent habitats (e.g., Macneale et al. 2005, Blakely et al. 2006). Even in species with very short adult stages, restricting terrestrial dispersal can constrict population growth or lead to population loss, independent of impacts to aquatic stages from instream habitat degradation (Power et al. 1988, Enders and Wagner 1996). On the other hand, dispersal can mitigate some negative effects of watershed urbanization by enabling recolonization of streams if habitat and water quality improve (Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). Ultimately, the loss or maintenance of populations related to insect dispersal ability will affect regional patterns of species biodiversity in streams (Vinson and Hawkins 1998).

We discuss the diversity of aquatic insect life cycles, with a focus on use of terrestrial environments by aquatic insects. We explored what is currently known about the effects of watershed urbanization on: 1) adult fitness, 2) adult dispersal, 3) habitat fragmentation, and 4) the interaction of these factors with species traits. We focused on direct effects to terrestrial stages of aquatic insects and did not cover impacts to larval stages that can influence dispersal ability (e.g., Stevens et al. 1999, Plaistow and Siva-Jothy 1999). We found that few studies have provided direct empirical evidence of urban landuse effects on the terrestrial stage of aquatic insects. As a result, we included relevant studies on dispersal and life-history traits of aquatic insect species in nonurban terrestrial habitats. We stopped short of providing a review of all instances of life-history traits and adult behaviors that could relate to potential impacts to adult insects in a typical urban watershed. Instead, we have provided examples of these potential impacts and suggested areas that require further study. We also discuss the role of the terrestrial environment for stream restoration and species conservation and a potential framework for identifying the effects of urbanization on developmental stages and life-cycle processes of stream-dwelling insects.

Aquatic Insect Life Histories and Dispersal

Life cycles and species traits

Aquatic insects have complex life cycles with distinct developmental stages that differ in their requirements to use aquatic and terrestrial habitats (Wilbur 1980, Werner and Gilliam 1984, Huryn et al. 2008). Figure 1 illustrates a generalized life cycle of an aquatic insect species and includes the life stages and life-cycle processes that, if affected by urbanization, could lead to population loss. In our review, we refer to aquatic insects as being in the *aquatic stage* or the *terrestrial stage*. Aquatic insects generally have an immature stage confined to living, feeding, and dispersing (e.g., drift or crawling) in the aquatic environment. Adult stages for most aquatic insect taxa are terrestrial, but some species in the orders Coleoptera and Hemiptera are exceptions (Polhemus 2008, White and Roughly 2008). Instream dispersal is possible by crawling, swimming, and drift during the aquatic stage. Dispersal during the terrestrial stage occurs by flight, crawling over land, and surface skating over the water. Aquatic coleopteran and hemipteran adults usually have the ability to leave the aquatic environment, disperse through the terrestrial environment, and colonize another aquatic habitat (Polhemus 2008, White and Roughly 2008).

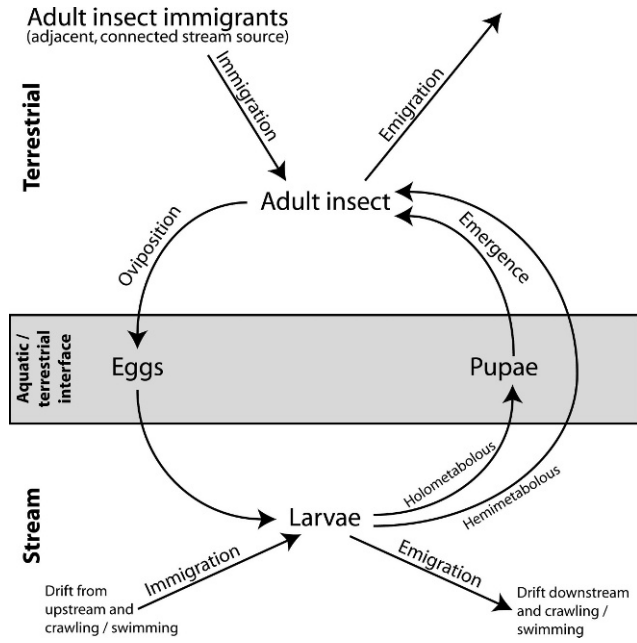


FIG. 1. Diagram of a generalized aquatic insect life cycle for holometabolous and hemimetabolous insects. The complete life cycle includes aquatic and terrestrial stages. The association of pupal and egg stages with the terrestrial and aquatic environments differs among species and often involves both stages. As a result, we describe these stages as being part of the aquatic/terrestrial interface. Any breakdown in the life cycle, increase in emigration, or barrier to immigration can contribute to population loss.

Thus, the adults of some taxa are aquatic-stage and terrestrial-stage dispersers simultaneously. Adults of other taxa of aquatic insects cannot return to an aquatic environment except to oviposit. The interactions of egg and pupal stages with the terrestrial and aquatic environments differ among species, but generally these stages are associated with the interface between aquatic and terrestrial environments (Huryn et al. 2008). In addition, adult oviposition behavior and emergence of larvae and pupae occur within or in proximity to the aquatic environment and represent processes responsible for bridging the aquatic-terrestrial interface during aquatic insect life cycles (Huryn et al. 2008).

The diversity of life cycles and dispersal habits limits our ability to generalize the effects of urbanization on terrestrial stages across all aquatic insects. Use of the terrestrial environment by adults and transport of adults among habitats differ among orders, among species within orders, and between adult and larval stages of the same species (Huryn et al. 2008). For example, some stream insects feed extensively as adults (e.g., Odonata; Corbet 1999), whereas others do not feed at all (e.g., Ephemero-

tera; Brittain 1982). All orders of aquatic insects possess some taxa that are capable of flying. However, flight capability can differ widely among species within an order and among individuals within a species (e.g, Plecoptera; Hynes 1976), or might change during the lifetime of an individual (e.g., wing histolysis in reproductive stages of species of Gerriidae; Kaitala and Huldén 1990). Some generalizations can be made at the order level, but exceptions are common and life-history strategies vary greatly at the species level.

From an instream perspective, aquatic stages respond to urbanization with increased mortality, decreased production, or increased drift out of the stream reach, which cause loss of the larval population from the stream regardless of impacts to terrestrial stages (reviewed by Paul and Meyer 2001). In contrast, terrestrial conditions and the aquatic-terrestrial interface might cause similar declines in population size by preventing successful adult emergence, mating, or oviposition, or by limiting adult survival. Expansion of our focus to include the entire insect life cycle suggests additional avenues by which watershed urbanization can lead to population loss, with or without affecting aquatic stages.

Function and extent of adult dispersal

Movement by aquatic insects at the regional scale is important for colonization of new habitats, escaping unsuitable habitats, and recruitment of neighboring populations. Recruitment occurs through immigration of adult or larval individuals or through addition of offspring from viable eggs to an uninhabited area or an existing population. Individual insects can be added to a population through movement of the aquatic stages, but most recruitment for successive generations of aquatic insect populations occurs by addition of eggs from adult female oviposition (Bunn and Hughes 1997). Most species of aquatic insects reproduce sexually, although parthenogenesis occurs in most aquatic insect orders (Chapman 1998) and is common in mayflies (Sweeney and Vannote 1987, Funk et al. 2006).

Dispersal also can be important for supplying recruits to upstream reaches that lose individuals through downstream drift. Adult aquatic insect flight often is oriented in an upstream direction (Pearson and Kramer 1972, Neves 1979, Coutant 1982, Winterbourn and Crowe 2001, Macneale et al. 2005) and might have evolved in response to the loss of immature individuals that drift downstream (Müller 1982). Hershey et al. (1993) found that the observed

preference of a mayfly species to fly upstream and oviposit compensated for the loss of individuals drifting from upstream reaches. Anholt (1995) found that persistence of populations in upstream reaches also could be explained by density dependence of birth and death rates upstream, but concluded that population persistence still required occasional movement of adult individuals upstream.

Dispersal that increases individual fitness acts as a selective force affecting persistence and spatial distribution of populations connected by gene flow (Gandon and Michalakis 2001). Gene flow, the transfer of alleles from one population to another, occurs when colonization or recruitment is followed by multiple generations of successful outbreeding (Bilton et al. 2001). Flow of novel alleles into a population is an important source of genetic variation, but even without new variants, gene flow maintains genetic diversity locally by increasing the effective size of the population and slowing the rate at which shared alleles are lost at random through genetic drift (Wright 1938). Limited gene flow can facilitate local adaptation, but small, isolated populations lose genetic variation through genetic drift and, over time, can become subject to the detrimental effects of inbreeding (Frankel and Soulé 1981). Urban environments couple human and aquatic insect populations in ways that produce selection pressures with complex effects on the fitness of members in both groups. In Cali, Columbia, insecticide applications to control the Dengue virus vector *Aedes aegypti* produced locally intense selection pressures that interacted with high levels of gene flow and resulted in rapid changes to mosquito population genetic structure, vector competence, and resistance to insecticides that varied independently among the sites and times evaluated (Ocampo and Wesson 2004). The prevalence of multiple, co-occurring insecticides in urban streams reported by Hoffman et al. (2000) indicates that insecticides are widely used in urban settings and similar effects on nontarget adults of aquatic insects are likely.

Research on the ability of aquatic insects to disperse has had varied results. Studies that have examined the movement of adult insects away from the stream generally have shown that most individuals stay close to or above the stream channel (Jackson and Resh 1989, Sode and Wiberg-Larsen 1993, Kovats et al. 1996, Collier and Smith 1998, Griffith et al. 1998, Petersen et al. 1999, Briers et al. 2002, Lynch et al. 2002, Petersen et al. 2004, Macneale et al. 2005, Winterbourn 2005, Chan et al. 2007, Winterbourn et al. 2007, Finn and Poff 2008). The rapid decline in abundance of adult insects caught with increasing

distance into the riparian zone and upland areas has been interpreted as evidence that long-distance dispersal by adults is rare (Sode and Wideberg-Larsen 1993, Griffith et al. 1998, Petersen et al. 1999, Briers et al. 2002). However, studies of genetic relatedness among some aquatic insect populations suggest that long distance migrations across drainage basins are possible and even occur commonly (Hughes et al. 2000, Kelly et al. 2001, Wilcock et al. 2001, 2003). Briers et al. (2004) labeled *Leuctra inermis* stoneflies (Plecoptera: Leuctridae) larvae with ^{15}N and were able to estimate that a small portion of adults migrated at least 1 km between streams. Kovats et al. (1996) used light traps and found inland movement by adult caddisflies up to 5 km from aquatic habitats. Light traps can artificially attract insects and, thus, might not represent typical dispersal distance, but these results show that long distance adult migrations on the scale of kilometers is physiologically possible. In addition, certain taxa can be passively transported long distances by wind (Kelly et al. 2001), especially those taxa, such as Plecoptera, that are weak fliers (Briers et al. 2004).

Observations that adult insects are most active over the stream channel often are interpreted as evidence that adults disperse between watersheds by traveling along stream corridors rather than in a direct path through upland areas. Petersen et al. (2004) and Sode and Wiberg-Larsen (1993) collected more aquatic insects from traps placed across the stream channel than perpendicular to it, a result that suggested more individuals were flying above and parallel to the channel than away from it. Movement along the stream corridor can be extensive. Hershey et al. (1993) estimated that 33 to 50% of adult *Baetis* mayflies (Ephemeroptera) traveled 1.6 to 1.9 km upstream from where they emerged, and Coutant (1982) found ^{65}Zn labeled caddisflies up to 16 km upstream from the point source causing the radioisotope labeling.

In contrast, recent work has shown that adults can move between watersheds along a direct path through upland areas. Larval drift downstream past the confluence followed by adult flight upstream along the neighboring branch could result in the exchange of individuals between adjacent stream branches, but has not been proven (Griffith et al. 1998). In addition, the upstream bias of adult flight might prevent individuals from flying long distances downstream to a node and then up another branch (Macneale et al. 2005). The genetic structure of *Calopteryx splendens* (Odonata) damselfly populations along river networks observed by Chaput-Bardy et al. (2008) suggested that dispersal between watersheds by this strong flier occurs through upland areas rather

than along networks, a pattern that might not be surprising for odonates. However, Macneale et al. (2005) found that dispersal patterns, dispersal distances, and capture rates of ^{15}N labeled adult *Leuctra ferruginea* stoneflies (Plecoptera) along the stream network indicated that individuals caught at an adjacent stream traveled through the upland areas to reach the adjacent stream rather than along the stream corridor, a result suggesting that size, strength, and flying ability are not the only determinants of cross-stream movement.

Urban Landscapes and Aquatic Insect Dispersal

Adult fitness

Terrestrial habitats altered by urbanization might be less hospitable than unaltered habitats to adult aquatic insects, and the alterations might directly affect adult development, survival, and mating success. In many geographic regions, riparian forests are important for adults of some species to complete development, feed, roost, and find mates (Sweeney 1993, Petersson and Hasselrot 1994, Smith and Collier 2000, Briers and Gee 2004, Winterbourn 2005). As such, riparian deforestation might impact adult development and mating success. In addition, the microclimate in remnant riparian patches might be altered by surrounding urbanization (e.g., a heat-island effect; Oke 1989, Pickett et al. 2001). Collier and Smith (2000) found that adult stoneflies had lower mortality in forested habitats with lower temperatures and higher humidity than pastureland, and Jackson (1988) and Smith and Collier (2005) found that experimentally altered higher air temperatures decreased adult longevity for several aquatic insect taxa.

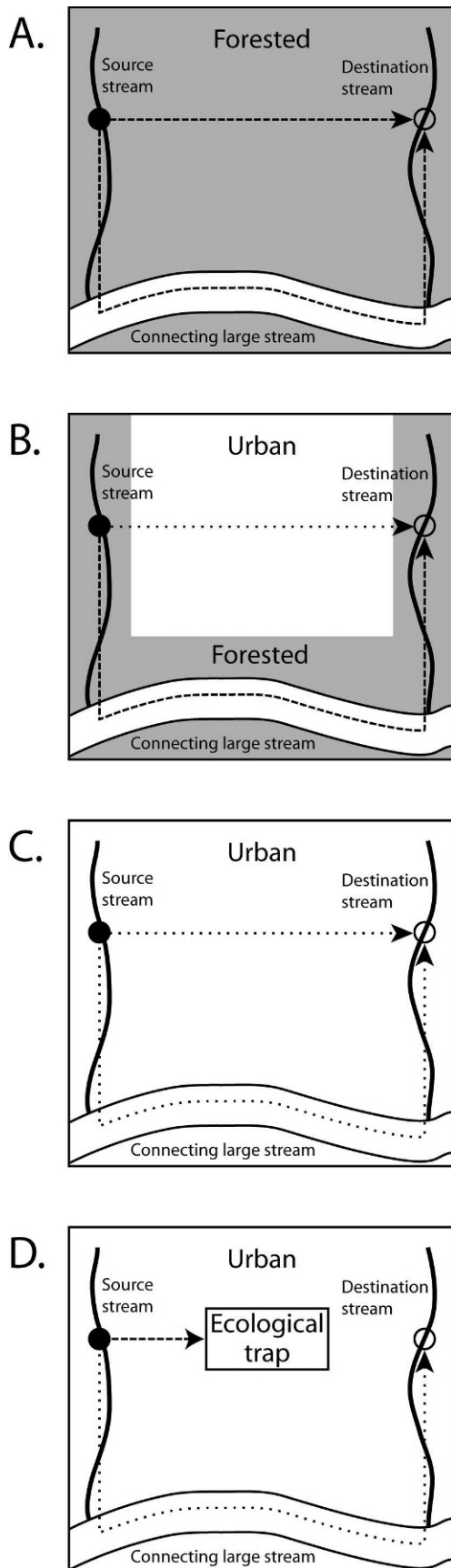
Deforestation of riparian areas also might lead to differences in types or abundances of natural enemies in urban landscapes and affect the level of predation on adult aquatic insects in remnant forest patches. Adult insects are important prey for animals, such as arachnids (Kato et al. 2003, Briers et al. 2005), birds (Gray 1993), bats (Fukui et al. 2006), and lizards (Sabo and Power 2002). Predation in the terrestrial environment can contribute to significant mortality in adult aquatic insect populations (Gray 1989, Werneke and Zwick 1992, Paetzold and Tockner 2005). Urbanization often leads to an overall decrease in specialist predators and an increase in generalist predators in early successional areas recovering from the impacts of urban development (McIntyre 2000) and could increase predation on certain taxa. In general, altered mortality resulting from changes in predator communities is likely to have species-specific effects on aquatic insect populations depending on the species

composition of predator assemblages (Paetzold and Tockner 2005) and individual species traits, such as adult life span (Jackson and Fisher 1986). For example, Faeth et al. (2005) found that increases in bird density and compositional shifts to more insectivorous species led to greater top-down control on herbivorous insect populations in urban areas than in the surrounding natural desert areas. In addition, greater top-down control was likely to occur with the conversion of other ecosystems to urban lands (Faeth et al. 2005). Increased predation on arthropods with increased urbanization is likely to decrease adult aquatic insect survival and decrease the probability of dispersing long distances among habitats.

Adult dispersal

Riparian deforestation and other changes to the riparian zone also might deter movement away from a natal stream (Sweeney 1993). Emigration frequently is triggered by environmental cues (e.g., wind speed or direction, light intensity, temperature or moisture gradients, presence or absence of trees or other vegetation) that can be altered or eliminated by urbanization (reviewed by Ims and Hjermann 2001). Harrison and Harris (2002) found greater diversity of aquatic insect adults in riparian areas with herbaceous vegetation and trees than in riparian areas consisting of grazed grasses. Collier et al. (1997) found a greater number of adult stream-insect taxa in native than in nonnative pine forests in the New Zealand hill country, and Smith et al. (2002) found a greater number of trichopteran species in native forests than in pasture land. However, factors affecting both larval community composition and adult dispersal in the aforementioned studies probably were controlling adult community composition. Winterbourn et al. (2007) found that adult Plecoptera, Ephemeroptera, and Trichoptera were more abundant in forested than in grassland habitat (although not significantly so for Trichoptera) and concluded that terrestrial habitat determined adult abundance in conjunction with larval distributions. Petersen et al. (1999) found that adult stoneflies were more abundant in the forested riparian zone than in the open riparian zone on the opposite side of the stream and clearly demonstrated the effect of terrestrial habitat type on adult dispersal.

For species that prefer to move through forested areas, migration among streams or reaches is subject to the location and distribution of forested patches. Adult dispersal can occur laterally through upland areas in intact forested watersheds (Fig. 2A), but might be limited to riparian corridors if upland areas are deforested (Fig. 2B). In watersheds with deforest-



ed uplands, increased dispersal distance among streams or reaches could increase energy use, risk of predation, desiccation, or encountering harsh habitats for migrating adult insects. Dispersal among streams might be constrained when both upland and riparian zones are deforested (Fig. 2C), but a natural affinity to stay above the stream might allow dispersal along the stream corridor.

Preference of some taxa to move into forested areas might not always translate into a greater amount of adult migration in forested than in open riparian and upland areas. Briers et al. (2002) found that whether an open riparian area discouraged, encouraged, or had no effect on movement away from the stream compared to a forested riparian zone depended on individual species. Furthermore, Delettire and Morvan (2000) found that chironomid flies tended to aggregate in vegetated areas rather than open areas near the stream, and as a consequence, isolated riparian forests surrounded by deforested watersheds actually might have discouraged emigration because insects were less likely to move from the preferred forested habitats into open habitats to migrate to another stream (Delettire and Morvan 2000). The tendency to seek forested habitat observed by Delettire and Morvan (2000) also might cause adult insects in open habitats (e.g., Fig. 2C) to disperse further to seek forested habitat. Higher temperatures from loss of riparian vegetation might decrease survival (Jackson 1988, Collier and Smith 2000, Smith and Collier 2005), but also might lead to greater flight activity (Briers et al. 2003) and potentially increased transport distances on short time scales for individuals in warm, deforested habitats. Thus, the actual effect of riparian vegetation on emigration is complex and requires further study.

The loss of natural structures from and the addition of anthropogenic structures to watersheds also can affect dispersal (Fig. 2D). Insect species that use

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FIG. 2. Diagram showing how transport between 2 adjacent headwater stream reaches flowing into a larger, main-stem stream could be affected by the loss of forested areas (shaded) in association with urbanization (unshaded). A.—Upland and riparian zones are forested and dispersal is not impeded. B.—Upland areas are deforested, but riparian zones remain forested. C.—Upland and riparian zones are deforested. D.—Upland and riparian zones are deforested and ecological traps, attractive to adult insects, exist in upland areas. Closed circles indicate the source of adults and the open circles indicate the destination. Dashed lines indicate a more likely pathway of dispersal and the dotted lines indicate a less likely pathway of dispersal.

highly specific stream or riparian structures as swarming markers (Savolainen et al. 1993, Tokeshi and Reinhardt 1996) or species that prefer shaded conditions (Pettersson 1989) might fail to remain at urban streams with simplified or artificial habitat conditions. Other taxa are at risk of encountering anthropogenic structures or areas in urban landscapes that attract individuals but are inhospitable to them or their offspring (i.e., ecological traps; Kristan 2003; Fig. 2D). For example, adults of many aquatic insects use polarized reflected light to locate aquatic habitats (Bernáth et al. 2002) and anthropogenic structures that reflect polarized light can attract dispersing aquatic insects (Horváth and Varjú 1997). The reflective surfaces of cars mimic the polarization of reflected light from streams, and as a result, parking lots are potential sinks for migrating insects in urban watersheds (Kriska et al. 2006). Asphalt and other road surfaces, which have a shape similar to that of streams, also reflect polarized light and attract mating swarms of mayflies (Kriska et al. 1998) and midges (Tokeshi and Reinhardt 1996). Other structures, such as glass buildings (Kriska et al. 2008) and black gravestones (Horváth et al. 2007), that reflect polarized light also have been identified as potential attractants of aquatic insects. Street lights might act as ecological traps for phototactic species dispersing at night (Eisenbeis 2006), but few studies have examined their impact on aquatic insects. The use of mercury vapor lamps and black lights by entomologists for nighttime trapping is proof that artificial lights can attract adult aquatic insects.

In contrast to ecological traps that can attract adult insects, some anthropogenic structures can block movement of adult aquatic insects. Impediments above the stream, such as culverts, might block movement of adult taxa flying upstream (Blakely et al. 2006). In contrast, structures, such as bridges and low head dams, are less likely to affect dispersal along streams (Blakely et al. 2006, Grenouillet et al. 2008). Roads and bare ground are sometimes barriers to ground (Mader et al. 1990) and aerially (Lövei et al. 1998) dispersing terrestrial arthropods. In general, few studies have demonstrated the potential for anthropogenic structures in upland areas to act as physical barriers to aquatic insect movement and could be an area of future study.

Habitat fragmentation

Taxa respond differently to habitat loss and fragmentation, but general patterns (reviewed by Ewers and Didham 2006) include lower population size, increased demographic stochasticity, reduced

levels of gene flow, loss of genetic diversity (Watts et al. 2004), and increased risk of extirpation or extinction (reviewed by Fahrig 2003). Degradation of matrix habitat can lead to spatial isolation of populations by impairing dispersal (Ricketts 2001). Degradation of the matrix of dendritic stream networks occurs when upland and riparian zones between stream reaches are altered (Grant et al. 2007). The combined effects of aquatic and riparian habitat loss can contribute to spatial isolation of populations by eliminating populations from the landscape and increasing the distance between suitable habitats (Lowe 2002). Thus, the effects of fragmentation might be particularly relevant to adult aquatic insect populations in headwater streams. If remnant and restored forest patches are limited to the riparian zone, formerly 2-dimensional forests (Fig. 2A) are reduced to 1-dimensional dendritic networks that follow stream corridors (Fig. 2B). The resulting dendritic forests might interact with the behaviors of flying stream insects (e.g., the propensity to aggregate or move into forested areas) to impose new constraints on dispersal, with consequences for population persistence. Dendritic habitat structure alters the dispersal, isolation, and population extinction probabilities of taxa (e.g., fish, salamanders) that move only within or along such networks (Lowe 2002, Fagan 2002, Fagan et al. 2005, reviewed by Lowe et al. 2006, Grant et al. 2007). In contrast, emergence as winged adults in fully forested watersheds permits insects to leave the channel and to move among stream habitat patches, unconstrained by the network's hierarchical structure. Thus, even when riparian zones are intact, upland habitat alteration can isolate populations or patches within a stream network by imposing novel spatial constraints on terrestrial dispersal.

In addition to riparian corridors, habitat fragmentation that restricts terrestrial dispersal might be particularly important for populations in headwater streams. Headwaters often have unique habitats with assemblages of endemic insect populations (Gomi et al. 2002, Finn et al. 2007, Gooderham et al. 2007, Meyer et al. 2007, Richardson and Danehy 2007, Clarke et al. 2008, Smith and Lamp 2008, but see Heino et al. 2003, 2005). Dispersal into headwaters is limited to flying adults because no upstream sources of stream residents are available from drift. As a result, the unique characteristics and location of headwaters in stream networks might contribute to natural isolation. Conversion of headwater streams to buried underground drainage systems in urban watersheds and the loss of ephemeral and intermittent headwaters caused by altered hydrology (Elmore and Kaushal 2008, Roy et al. 2009) can increase the

isolation of headwater populations by eliminating headwater habitat and increasing the distance among remaining populations in urbanized watersheds. As a result, the headwater populations in urban watersheds might be connected only to populations in the adjacent main-stem stream (Smith and Lamp 2008). Thus, headwaters might experience even greater isolation from fragmentation in urban watersheds than larger streams.

Interaction with species traits

The interaction of species' characteristics (e.g., habitat specificity, dispersal ability) and landscape properties (e.g., physical obstacles, loss of habitat) can determine the extent to which aquatic insect populations are affected by fragmented urban environments. Species traits, such as larger overall size, greater thoracic mass, greater wing loading, and greater wing size, are related to greater population range sizes (Malmqvist 2000, Hoffsten 2004, Rundle et al. 2007) and flight ability (Rankin and Burchsted 1992, Marden 2000, Berwaerts et al. 2002). These traits also might be correlated with a greater ability to avoid or withstand harsh terrestrial habitats in urban watersheds, but to our knowledge, this possibility has not been examined. However, Sato et al. (2008) detected greater population genetic structure (but no significant loss of genetic diversity) in 3 highly mobile damselfly species in urban than in rural ponds in Japan. Even though this study examined lentic species, population differentiation was greatest in the species with the most specific habitat requirements and indicated that population fragmentation is dependent on species traits in addition to dispersal ability (Sato et al. 2008).

Interspecific differences in dispersal ability might result from adaptations to specific habitats and thus be associated with species-specific affinities for certain habitat types. Thus, any decrease in colonization potential in urban watersheds results from a complex interaction between the type of habitat affected by watershed urbanization and the preferred habitat and dispersal ability of the insect species. For example, Wilcock et al. (2007) compared the genetic structure of 2 species of caddisflies in streams and found that *Plectrocnemia conspersa* (Trichoptera:Polycentropodidae), which inhabits smaller intermittent streams, dispersed more than *Plectrocnemia flavomaculatus* (Trichoptera:Polycentropodidae), which inhabits larger perennial streams. Selection for strong dispersal ability in headwater taxa adapted to living in intermittent habitats might allow these taxa to persist longer in urban landscapes than poorer

dispersing taxa adapted to living in more permanent, large streams (Wilcock et al. 2007). However, loss of small, intermittent streams in urban watersheds (Elmore and Kaushal 2008) could mean that those species adapted to greater dispersal have no habitat to colonize in urban watersheds.

Applications

Data on terrestrial stages, life-cycle processes, species traits, and adult dispersal of aquatic insects are difficult to obtain, but might be necessary to identify the mechanisms by which populations lack persistence in urban streams. Moreover, interactions among species traits, landscape variables, and specific human impacts might be difficult to observe, and even more difficult to relate to different life stages. Life-history, dispersal, morphological, and ecological traits are being used to explain larval presence/absence in urban streams and to predict community composition in streams (Poff et al. 2006, Horrigan and Baird 2008, Statzner et al. 2008, Verberk et al. 2008). Incorporation of species traits into these types of studies would further enhance restoration and conservation initiatives.

Restoration

Success of community redevelopment in stream restoration projects depends on the ability of species to disperse to and recolonize restored stream ecosystems (Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). The potential for long-distance dispersal across terrestrial habitats makes aquatic insects likely candidates to colonize restored streams (Hughes 2007) as is evidenced by Masters et al. (2007), who found 8 species of acid-sensitive Ephemeroptera, Plecoptera, and Trichoptera adults beside acid streams where larvae had not been observed in 21 y of benthic sampling. Some investigators assume that flight-capable insects have extensive enough dispersal that restoration of local habitat should be the focus of restoration and that restored local habitat is sufficient to promote recolonization and community development (Palmer et al. 1997). However, recolonization is controlled by: 1) species life-cycle and dispersal traits, 2) the spatial structure of source populations, stream networks, and remaining urban land use, and 3) the temporal patterns of project completion and the interactions among them (Mackay 1992, Palmer et al. 1997, Bond and Lake 2003, Lake et al. 2007). Identifying and conserving dispersal pathways could help mitigate the effects of urbanization on stream insect communities and encourage dispersal (Lowe 2002), but doing so will require a better understand-

ing of the adaptive behaviors of species to past and present spatial structures of stream ecosystems and of how differences in the matrix affect dispersal and movement of individuals in fragmented stream systems (Ricketts 2001, Davies et al. 2001).

Predicted outcomes and assessments of stream restoration projects probably would improve if species traits, spatial population structure, dispersal pathways, and spatial characteristics of stream networks were considered during project design (Jansson et al. 2007, Lake et al. 2007, Spänhoff and Arle 2007). The slow recovery of communities in urban environments with constrained dispersal also might require adjusting the timeline for determining the success of restorations of aquatic insect communities (Lake et al. 2007). Ideally, assessments of restoration success should consider potential dispersal limitations when bioassessments based on aquatic insects are used (Purcell et al. 2002). Surveys of potential source populations might be helpful because the probability of colonization increases with a greater number of and a shorter distance to source populations (Fuchs and Statzner 1990, Huxel and Hastings 1999, Ahlroth et al. 2003). Loss of source populations, rather than failed restoration of local habitat, could be the reason a species fails to recolonize a restored reach (Suding et al. 2004). Urban stream restoration methods also might have to address specifically the impacts to life-cycle process that are responsible for species loss. Even more radical approaches, such as stocking insects into restored streams, might be possible when recolonization is unlikely, but research is needed on this approach (Brady et al. 2002). However, we think that managers should not simply give up on restoring streams in situations where dispersal is severely impeded and colonization is unlikely. In situations like this, designers of assessments of restoration success might find using direct measures of functional and geomorphological attributes of stream health more practical and more informative than using bioassessments based on stream insects.

Framework for identifying stage-specific urban effects

Estimates of movement of adult aquatic insects from one stream to another are difficult, generally require expensive methods to label individuals (but see Payne and Dunley 2002) or sequence genetic samples, and often are impractical to include in assessments of impacts from urbanization. Surveys that use malaise traps, light traps, or sweep nets can provide some estimate of dispersal ability and presence/absence, but do little to indicate actual levels of movement among habitats (Macneale et al.

2004). In lieu of these approaches to measuring dispersal, patterns of adult and larval presence/absence can be used to determine how impacts to terrestrial stages are influencing population persistence in urbanized streams.

Table 1 illustrates how surveys of aquatic larvae and terrestrial adult populations in different habitat types within a region can help to identify potential mechanisms that are linked to population dynamics. In this case, we consider populations in urban and rural headwater streams. Each line represents a presence/absence scenario and a potential mechanism based on the assumption that dispersal between the 2 habitats is possible. We think the mechanisms that structure larval communities in urban headwaters can be grouped into 2 categories: 1) mechanisms that influence population dynamics of tolerant larval taxa able to survive in urban headwaters and 2) mechanisms that lead to and maintain the absence of larval taxa from urban headwaters. The 1st category includes species that occupy urban headwater streams as larvae and, by default, are found there as adults (scenarios 1, 4, and 7, Table 1). These taxa usually are tolerant of habitat degradation and are able to complete their life cycle. If adults do not emerge from the natal stream then recruits from adult immigrants rescue the population (e.g., source-sink dynamics; Caudill 2003).

The 2nd category includes species whose larvae occupy rural headwater streams but are absent from urban headwater ecosystems (scenarios 2 and 3, Table 1). This category is of greater interest for determining if impacts on adults lead to the persistent loss of populations from stream communities and for determining the potential for the community to return following restoration. Scenario 2 (Table 1) indicates that dispersal barriers are not likely to lead to the absence of larvae because adults of that taxon can migrate to the reach, so high egg mortality, some barrier to successful mating, or a lack of oviposition sites or cues are the cause of larval absence. High mortality of early instar larvae also might result in an apparent absence of larvae from the stream community. Presence of even 1st-instar larvae generally is representative of scenarios 1, 4, and 7. High mortality of early instars generally has the same effect as high egg mortality and should be considered in the presence or absence of scenario 2. The pattern in scenario 3 (Table 1) indicates that a dispersal barrier is present, and that a lack of adult immigrants was partly responsible for the lack of colonists. However, some effect occurring in the stream (e.g., early instar or egg mortality) or at the terrestrial/stream interface (e.g., preventing oviposition) cannot be ruled out and

TABLE 1. Potential mechanisms controlling species presence/absence from the focal habitat (in this example, an urban headwater) for various combinations of species presence/absence in the regional species pool for the focal habitat and in the focal habitat itself. This framework is a starting point for hypothesis generation and further investigation and includes only relevant presence/absence scenarios. Species with low abundances might be rare and undetected by surveys.

Scenario	Present in regional pool of similar habitats? (e.g., rural headwaters)		Present in focal habitat? (e.g., urban headwater)		Possible mechanisms affecting presence/absence in the urban headwater
	Larvae	Adults	Larvae	Adults	
1	Yes	Yes	Yes	Yes	Species is ubiquitous and able to survive in poor habitat or larval mortality rescued by adult immigrants (i.e., source-sink dynamics)
2	Yes	Yes	No	Yes	Immigration of adults occurs but poor habitat prevents successful reproduction (mating and oviposition) or causes egg or early instar mortality to prevent detection
3	Yes	Yes	No	No	Immigration of adults does not occur; mechanisms in scenario 2 might occur if immigration were restored
4	No	Yes	Yes	Yes	Species tolerant of poor habitat; source-sink dynamics possible
5	No	Yes	No	Yes	Species not suited for this habitat (not a headwater or stream species); mechanisms in scenario 2 might occur, but less likely
6	No	Yes	No	No	Immigration of adults does not occur; mechanism from scenario 5 might occur if immigration occurs
7	No	No	Yes	Yes	Species tolerant of poor habitat; source-sink dynamics possible
8	No	No	No	Yes	Species not suited for this habitat (not a headwater or stream species); mechanisms in scenario 2 might occur, but less likely

could result in a lack of colonists even if migrants arrived. The mechanisms are not definitively identified from this conceptual model, but the patterns of adults and larvae could be useful for resource management and restoration activities.

Comparing adult and larval presence/absence (Masters et al. 2007) and the interaction between regional- (e.g., dispersal) and local-scale processes that affect population dynamics (Palmer et al. 1996) is not a novel idea. The model in Table 1 is a simple framework for identifying how local and regional processes can affect communities. Collecting data on adult presence/absence can reveal the occasional movements of adult individuals over long distances that probably are important for population rescue and persistence (Bunn and Hughes 1997, Macneale et al. 2005). Only a few studies have experimentally examined the conditions under which regional or local processes are the more important regulators of community structure for stream insects (e.g., Sander-son et al. 2005) or how pre- and postrecruitment processes drive population dynamics (e.g., Peckarsky et al. 2000, Reich and Downes 2004).

Local processes important for colonization include more than just the survival of larval stages. Specific structures often are required for pupal attachment (Hoffmann 2000), emergence (Petersen and Hildrew 2003, Jáimez-Cuéllar and Tierno de Figueroa 2005), oviposition, or egg attachment (Hoffmann and Resh

2003, Lancaster et al. 2003, Reich and Downes 2003a, b, Encalada and Peckarsky 2006). Changes to stream geomorphology and hydrology that result from watershed urbanization might eliminate these physical factors. Elimination of structures might present a barrier to colonization, but evidence that only a few individual adults are responsible for most recruits (Bunn and Hughes 1997) and that larval density (Reich and Downes 2004) and emergence density (Peckarsky et al. 2000) are unrelated to oviposition site abundance suggests that limited availability of oviposition sites might not necessarily be a barrier to recruitment. Regardless, the framework we present still allows potential identification of terrestrial (i.e., limited migration) and aquatic effects, which include the rest of the insect's life cycle (oviposition to emergence).

Conclusions

Urbanization probably hinders completion of life cycles in terrestrial habitats and constrains adult dispersal of stream insects, but the specific effects of urbanization on population demography and dispersal are relatively understudied (Strayer 2006). We recommend that future studies of stream urbanization incorporate new strategies that differ from the traditional focus on larval stages and instream effects to confront confounding aquatic and terrestrial effects

on population persistence. We presented an approach to provide a starting point for determining the role of specific life-cycle stages or processes for insect population dynamics in urbanized streams. However, further work is required to define and quantify changes to terrestrial habitats that have negative consequences for adult insect fitness and dispersal. Areas that require new or continuing work include: 1) understanding dispersal patterns of adult aquatic insects in urban watersheds, 2) identifying dispersal barriers and ecological traps affecting movement of adult aquatic insects in urban environments, and 3) understanding the long-term consequences of changing landscapes on population genetics and species persistence. In addition, these studies should be conducted in a variety of urban ecosystems (e.g., deserts, coniferous forests, subtropical and temperate regions). An understanding of how watershed urbanization affects terrestrial life stages and adult dispersal will lead to a better understanding of anthropogenic activities that affect stream insect populations, conservation measures that might help preserve populations, and restoration methods to improve urban stream structure and function.

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