

# Fluxes of terrestrial and aquatic carbon by emergent mosquitoes: a test of controls and implications for cross-ecosystem linkages

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**Abstract** Adult aquatic insects are a common resource for many terrestrial predators, often considered to subsidize terrestrial food webs. However, larval aquatic insects themselves consume both aquatic primary producers and allochthonous terrestrial detritus, suggesting that adults could provide aquatic subsidy and/or recycled terrestrial energy to terrestrial consumers. Understanding the source of carbon (aquatic vs. terrestrial) driving aquatic insect emergence is important for predicting magnitude of emergence and effects on recipient food web dynamics; yet direct experimental tests of factors determining source are lacking. Here, we use *Culex* mosquitoes in experimental pools as an exemplar to test how variation in general factors common to aquatic systems (terrestrial plant inputs and light) may alter the source and amount of energy exported to terrestrial ecosystems in adult aquatic insects that rely on terrestrial resources as larvae. We found strong sequential effects of terrestrial plant inputs and light on aquatic insect oviposition, diet, and emergence of *Culex* mosquitoes. Ovipositing mosquitoes laid ~3 times more egg masses in

high terrestrial input pools under low light conditions. This behavior increased adult emergence from pools under low light conditions; however, high input pools (which had the highest mosquito densities) showed low emergence rates due to density-dependent mortality. Mosquito diets consisted mainly of terrestrial resources (~70–90 %). As a result, the amount of aquatic carbon exported from pools by mosquitoes during the experiment was ~18 times higher from low versus high light pools, while exports of terrestrial carbon peaked from pools receiving intermediate levels of inputs (3–6 times higher) and low light (~6 times higher). Our results suggest that understanding the interplay among terrestrial plant inputs, light availability and biotic responses of aquatic insects may be key in predicting source and magnitude of emergence, and thus the strength and effects of aquatic–terrestrial linkages in freshwater systems.

**Keywords** Allochthonous input · Aquatic–terrestrial linkages · *Culex restuans* · Food web · Habitat selection · Resource subsidies · Stable isotopes

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## Introduction

Animals that cross aquatic–terrestrial boundaries as part of their life history (i.e., active resources; sensu Kraus et al. 2011) form strong and ubiquitous connections between freshwater and terrestrial food webs (Nakano and Murakami 2001; Marczak et al. 2007; Gratton and Vander Zanden 2009). In particular, animals with complex life cycles such as aquatic insects are thought to form an important part of this connection by moving aquatic resources from water, where aquatic insects spend their larval period, to land where they live as adults and

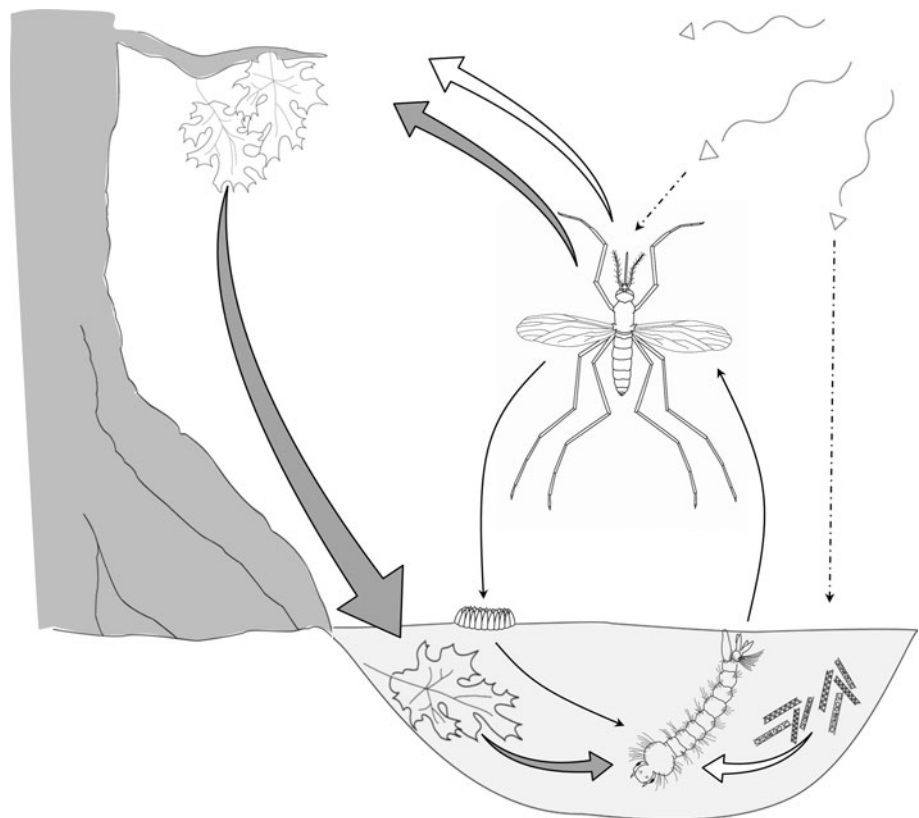
subsidize dynamics of a variety of consumers across a wide array of ecosystems (headwater streams, Nakano and Murakami 2001; Kato et al. 2003; Marczak and Richardson 2007; Benjamin et al. 2011; rivers, Sabo and Power 2002; Power et al. 2004; lakes, Gratton et al. 2008; and ponds, Kraus 2006). In this role, aquatic insects are considered the conduit by which aquatic ecosystems “feed” the forest (Nakano and Murakami 2001; Sabo and Power 2002). However, although adult aquatic insects do provide a major source of energy to many terrestrial predators, this analogy does not always hold. Larval aquatic insects in the water feed on both aquatic and terrestrial resources (i.e., periphyton or phytoplankton and terrestrial plant matter; Rounick et al. 1982; Merritt et al. 1992). Thus, newly emerged adult aquatic insects provide both an aquatic subsidy (aquatic ecosystem “feeding” the forest) and recycled terrestrial energy to terrestrial food webs (forest “feeding” the forest; Iwata 2007; Gratton et al. 2008; Fig. 1). For example, adult insects with herbivorous aquatic larvae such as mayflies may be mainly an aquatic subsidy to birds, spiders, and bats, while adults of detritivorous larvae such as midges and mosquitoes are more likely to represent a recycled terrestrial resource to those same predators (Nakano and Murakami 2001; Sabo and Power 2002; Power et al. 2004). This duality poses a problem for predicting adult insect flux (in this case, flux is driven by both aquatic and terrestrially-fixed carbon) and

for predicting the effects of these prey on terrestrial food webs. Thus, understanding the factors that influence source of energy exported from aquatic systems in emerging aquatic insect adults should help in predicting the strength and types of effects these cross-ecosystem linkages.

Correctly assigning sources of production driving adult aquatic insect emergence from aquatic systems helps us predict two important aspects of this link between aquatic and terrestrial food webs. First, it increases our ability to predict magnitude of emergence flux because we understand which ecosystem is providing the energy to produce the organisms (Polis et al. 1997; Marczak et al. 2007). For example, forested headwater streams are often not very productive in terms of aquatic primary production, but the flux of emerging aquatic insects from these streams can be quite large (Nakano and Murakami 2001; Marczak and Richardson 2007). At first, this pattern seems counterintuitive (Polis et al. 1997), but occurs because of the large contribution of terrestrial leaf litter to aquatic food webs in forested headwater streams (Wallace et al. 1997). Without understanding the contribution that terrestrial production makes to aquatic insect emergence, i.e., that the terrestrial ecosystem donates some of the energy driving patterns of “aquatic” resource flux, we would be unable to accurately predict emergence.

Second, correctly assigning the source of energy producing adult aquatic insects helps us predict effects of this

**Fig. 1** The flow of aquatic and terrestrial carbon between pond and forest ecosystems. Our focus is on the effects of light availability and terrestrial plant inputs on magnitude of aquatic and terrestrial carbon flux from small pools by adult *Culex* mosquitoes. *Dark arrows* represent flux of terrestrially fixed carbon; *white arrows* aquatically fixed carbon. *Dashed lines* show inputs of sunlight and *solid lines* the transition among mosquito life stages, from adult to eggs to larvae and back to adult



prey on terrestrial food webs, because it guides us in appropriately applying either subsidized or traditional food web theory to the problem (Polis et al. 1997; Huxel and McCann 1998; Huxel et al. 2002; Takimoto et al. 2002). For example, Polis and Hurd (1995, 1996) first described subsidized resource dynamics on desert islands where terrestrial predator abundance was found to be “extraordinarily” high compared to in situ prey. They concluded that this pattern was driven by the availability and use of marine-derived resources, which decoupled predator dynamics from the dynamics of prey derived from terrestrial production. Later models of both the desert–marine and forest–stream interfaces suggested subsidized consumers altered both food web dynamics and food web stability from dynamics of food webs driven by in situ resources alone because subsidy dynamics were driven only by the donor system (i.e. donor-control; Huxel and McCann 1998; Takimoto et al. 2002). Because their larval diet can be derived from both terrestrial and aquatic production, aquatic insect adults may represent both an aquatic subsidy and an in situ terrestrial resource to terrestrial consumers; As a result, the effects of these prey on terrestrial food webs may change depending on the extent to which larvae (either as individuals or as a community) rely on terrestrial production (Huxel et al. 2002; Paetzold and Tockner 2005; Schreiber and Rudolf 2008). Thus, understanding the factors driving source and magnitude of emergence should move us towards a more predictive ecology of food web dynamics at the aquatic–terrestrial interface.

Several factors may strongly alter source of energy and production of aquatic insects emerging from freshwaters. First, inputs of terrestrial plant matter to aquatic systems can alter abundance, distribution, and diet of aquatic insects by providing an important basal resource to larvae (Wallace et al. 1997). Experimental manipulation of terrestrial leaf inputs altered ecosystem function, community composition, individual diet, colonization, and survival in headwater streams and woodland ponds (Rounick et al. 1982; Wallace et al. 1997; Reiskind and Wilson 2004; Rubbo et al. 2006; Tiegs et al. 2008). Second, light availability, which often negatively co-varies with terrestrial plant inputs in temperate biomes, can also alter diet and distribution of aquatic insects by altering aquatic primary production and habitat selection by ovipositing adults (Binckley and Resetarits 2007). Finally, behavioral choices made during oviposition may determine source and magnitude of emergence by setting initial larval densities, which can lead to subsequent effects on mortality, resource use, and emergence of adults (Reiskind and Wilson 2004; Resetarits et al. 2004).

Mosquitoes are a globally distributed aquatic insect colonist of small pools; they can use both terrestrial and

aquatic resources as larvae (Merritt et al. 1992), and are prey for terrestrial spiders, birds, and bats (Walkinshaw 1935; Dabrowska-Prot et al. 1968; Anthony and Kunz 1977). *Culex* mosquitoes, in particular, often utilize detritus-based habitats (Merritt et al. 1992; Yee et al. 2010), including ephemeral ponds, puddles, containers, and tree holes. *Culex* mosquito larvae are predominantly filter-feeders that eat detritus and micro-organisms (Merritt et al. 1992), but like many aquatic insect larvae show some flexibility in their feeding depending on resource availability and preference (Merritt et al. 1992; Yee et al. 2010). Light availability, resource availability, and conspecific larval density can all have strong effects on oviposition site selection by adult *Culex* females (Reiskind and Wilson 2004; Yee et al. 2010), which can in turn affect growth and survival of larvae, and can alter adult recruitment (Fish and Carpenter 1982; Reiskind and Wilson 2004). Because *Culex* and the habitats they colonize are distributed across the landscape (Kitching 1971), their life cycles are short, and they are easy to manipulate, they are a good model species for studying ecological processes (Srivastava et al. 2004) including cross-ecosystem linkages.

Our goal was to test the general hypothesis that factors influencing resource base and production of aquatic insects would control the source and ultimately the amount of energy exported to the terrestrial food web by emerged adults. Since terrestrial plant inputs and light can both alter resource base and aquatic insect assemblage composition and dynamics in freshwater ecosystems, we expected these factors to alter both the amount and source of carbon in emerging insects in a predictable way. Specifically, we expected that increasing terrestrial inputs would increase the proportion of energy of terrestrial origin in emerging aquatic insects both by altering individual diet and the number of detritivores colonizing the pools. Light often covaries negatively with terrestrial inputs and is necessary for aquatic primary production; thus, we expected light to be used as a cue indicating the relative availability of aquatic versus terrestrial carbon to aquatic consumers. Specifically, for taxa whose larvae utilize algal-based resources, we expected light to be an attractant (Binckley and Resetarits 2009), while we expected light to deter oviposition for those with more detritivorous larvae (Yee et al. 2010). To facilitate study of the independent and combined effects of these factors over a gradient of terrestrial plant inputs, we used a well-studied case where terrestrial resources (detrital plant matter) and light control aquatic consumer dynamics: *Culex restuans* mosquitoes in small pools. Specifically, we manipulated both light and terrestrial plant matter inputs to artificial pools in the field, and measured how oviposition and diet responses to these factors altered source and amount of emergent adult *Culex* mosquitoes.

## Materials and methods

Because light and terrestrial input are often negatively correlated in nature (Wallace et al. 1997, Karlsson et al. 2009), we used a field experiment to independently manipulate light availability and terrestrial plant inputs in small artificial pools and test their separate and combined effects on oviposition, larval density, diet, and emergence of insects naturally colonizing small ( $\sim 40$  L) pools. The study took place at the Inger and Walter Rice Center for Environmental Life Sciences at Virginia Commonwealth University, about 32 km (20 miles) south of Richmond, Virginia in Charles City County, USA. The experiment was run in a mowed field (1.78 ha) surrounded by mixed pine–hardwood forest (dominated by *Pinus taeda*, *Quercus alba* and *Liquidambar styraciflua*). In late August 2009, we arranged 60 experimental pools (blue plastic bins, L  $\times$  W  $\times$  H: 48  $\times$  31  $\times$  34 cm; Sterilite, Massillon, OH, USA) in a split-plot design and randomly assigned them to one of two levels of light (whole plot factor), and one of three levels of terrestrial input (split-plot factor) for six total treatments ( $n = 10$  replicates per treatment). The pools were arranged 1 m apart in complete spatial blocks  $\sim 15$  m from other blocks and at least 20 m from the forest edge, and filled with well water. We manipulated light (65 and 30 % of ambient photosynthetically active radiation, PAR) using shade cloth attached to the top of a PVC frame (6.1  $\times$  4.9  $\times$  1.5 m). PAR was measured in high and low light treatments and adjacent to the experimental plots for three blocks under sunny/partly sunny conditions using Li-Cor 190S quantum sensor attached to a LI-1400 data logger (Licor Biosciences, Lincoln NE, USA; mean  $\pm$  SE, high light =  $890 \pm 186$   $\mu\text{mol photon/s/m}^2$ , low light =  $412 \pm 96$   $\mu\text{mol photon/s/m}^2$ , and ambient levels =  $1365 \pm 232$   $\mu\text{mol photon/s/m}^2$ ). We manipulated terrestrial plant inputs by adding  $16.85 \pm 0.26$ ,  $33.55 \pm 0.23$ , and  $67.01 \pm 0.18$  g wet mass (mean  $\pm$  SD) of a commercially available C<sub>4</sub> grass (*Eragrostis tef*) to the pools which approximated 0.5, 1 and 2 $\times$  mean ambient wet biomass of leaf litter on the ground at the forest edge during the summer (converts to 113, 226, and 450 g wet mass/m<sup>2</sup>;  $15.92 \pm 0.24$ ,  $31.70 \pm 0.21$ , and  $63.31 \pm 0.17$  g dry mass/pool; and 8.0, 15.9, and 31.7 mg/L nitrogen since grass was 2 % N by mass). Plants using the C<sub>4</sub> photosynthetic pathway have a different carbon isotope signature than C<sub>3</sub> plants, a natural difference we used here to distinguish carbon from terrestrial inputs versus from aquatic primary producers such as phytoplankton and periphyton (C<sub>3</sub> photosynthetic pathway). Grass used in this experiment fell into the range of C:N and color leaching found in natural litter at this site (with the exception of maple litter, Kraus et al., unpublished; Elser et al. 2000). Pools were seeded with a plankton inoculum from outdoor rain-filled tanks and opened to natural colonization by

aquatic insects on August 21. The experiment ran for  $\sim 3$  weeks. We kept the experiment relatively short to focus on the direct effect of our manipulations on primary consumers, before strong effects of community assembly (including large predators) indirectly affected behavior and survival of those organisms (Kraus and Vonesh 2010). Furthermore, this length of experiment likely captured the full larval period (egg–larvae–adult) of most aquatic insects that colonized the pools during the first 2 weeks of the experiment, since the major primary consumer (*Culex* mosquitoes) began emerging  $\sim 9$  days after the pools were first colonized.

To understand the factors driving aquatic insect response to light and terrestrial input, we followed the insect community from colonization to emergence. Since the majority aquatic insects that colonized the pools were *Culex* mosquitoes (Culicidae: Diptera), we focused on their responses and the responses of their potential resources. To measure colonization, we counted egg rafts (*Culex*) laid in the pools every 2–3 days from August 21 to September 9 by visually examining the pool surface and edges of the bin as well as by agitating any floating grass. We sampled aquatic insect larvae in the pools without replacement on August 28 using a modified aquarium net (net opening 5.8  $\times$  7.2 cm, mesh size 0.11 mm). Emerging aquatic insects were sampled using floating emergence traps (0.25  $\times$  0.25-m PVC base supporting a pyramid of mosquito netting, mesh size 0.87 mm; cover  $\sim 60$  % of pool surface area) which were emptied every 2 days from August 26 to 28 (before any mosquito or midge pupae were observed), and from August 31 to September 7. The large proportion of pools covered by the traps suggests we captured the majority of emergers, although traps may have reduced rates of oviposition. Emergent mosquitoes from each pool were dried for at least 24 h at 60 °C, and partially homogenized for <sup>13</sup>C isotope analysis at the UC Davis Stable Isotope Facility. To provide a basis for interpreting the  $\delta^{13}\text{C}$  signatures of emerging aquatic insects, we measured  $\delta^{13}\text{C}$  of three basal resources in the pools: particulate organic carbon (POC, or seston), periphyton, and terrestrial grass (Appendix A in Electronic supplementary material).

We also attempted to mitigate effects of large predaceous insects we knew to colonize these small pools (Binckley and Resetarits 2009; Kraus and Vonesh 2010) by removing adults (mainly predaceous diving beetles, Family: Dytiscidae) as soon as they were observed (within 0–3 days of their colonization). Our observations of pools throughout the experiment and destructive samples of pools at the end of the experiment indicated that we were reasonably effective at finding and removing adult beetles. Adults were found in 37 % of pools (mean  $\pm$  SD,  $1.14 \pm 0.35$  adults per pool that had adults) and successfully removed from 86 % of those pools. Of the pools



where we removed adults, only 1 of 19 (5 %) were found to have an adult at the end of the experiment, and of the pools where we did not find adults, 75 % of them showed no signs of having contained an adult. Despite these efforts, however, we were not as effective at removing adults before they had reproduced: 53 % of pools where we found and removed adults later contained larvae (35 % of the total pools). Because dytiscid larvae can also be voracious predators of mosquito larvae (Lundkvist et al. 2003; Yee 2010), we performed a post hoc analysis of the data to test for effects of dytiscid presence on the results obtained during the experiment.

To estimate relative gross primary production in the pools, we measured the change in dissolved oxygen (DO) in the pools during the night and day, adding the amount lost at night (an indicator of ecosystem respiration) to the amount gained during the day (net ecosystem productivity, NEP; Lovett et al. 2006; Rubbo et al. 2006). We measured DO and temperature in the bins on September 3 and 4 in the afternoon (~1300–1600 hours), morning (~0630–1000 hours), and afternoon (~1300–1600 hours) using a YSI 650 MDS sonde (YSI, Yellow Springs, OH, USA). These values likely slightly underestimate daily gross DO production because, although afternoon time was previously suggested to be near peak DO at this site, morning occurred slightly after the trough (Kraus and Vonesh, unpublished). We include here a qualitative estimate of biofilm on the surface of the pools by ranking pools as having no visible surface biofilm (1), slight film (2), and thick film (3) every 2–3 days, and measured pool temperatures twice in the morning (August 24, September 4) and afternoon (September 3 and 4). Samples were sent to a microbial ecology laboratory to obtain a more quantitative estimate of bacterial production, but problems during processing led to non-inclusion of the data. Colonization of the experiment was terminated on September 10 at which point all macroinvertebrates in pools were removed, identified, and weighed; the water was saved for analysis.

### Statistical analyses

We used generalized linear mixed models (GLMM) to test the independent and combined effects of light and input on all measured responses of aquatic insects and their resources. GLMMs are more appropriate than general linear models for analyzing data whose errors are non-normal and of known distribution (Bolker et al. 2009), and where random effects are included (in this case spatial blocks). They are especially useful for handling count data that contains many zeros, and for data constrained between two values (i.e., proportions). Error distributions were specified as expected for each dependent variable (e.g., Poisson or negative binomial for counts), data were square-root

transformed if it improved fit and the best-fit distribution was selected (using AIC values and over-dispersion parameter). Random effects of spatial block and block  $\times$  whole plot (i.e. light) were included where the mean estimates were non-zero, as indicated in the results. For all variables measured over time (egg masses, emergence, bacteria), we performed the analyses on summed data. One limitation of the GLMM approach is that we were restricted to univariate analyses of all dependent variables. To help correct for this, we used Bonferroni adjusted  $\alpha$ -values for statistical tests of strongly related dependent variables (e.g., counts from sequential life stages). All GLMMs were performed using SAS statistical software (SAS 9.1, © 2002–2003; SAS Institute, NC, USA).

To calculate proportion carbon from aquatic and terrestrial sources in the emergent mosquitoes, we applied a linear mixing model to mean source and consumer  $\delta^{13}\text{C}$  data using the program Isoerror (Phillips and Gregg 2001). Isoerror uses both source and mixture error to calculate a standard error for the mixing model estimates of proportion diet from each source. For these models, we assumed fractionation during metamorphosis was negligible (i.e., that signatures of emerged adults reflected larval diet; Mihuc and Toetz 1994), but that the trophic fractionation of  $\delta^{13}\text{C}$  ( $\Delta^{13}\text{C}$ ) was 1.0 ( $\pm 1.0$ ) ‰, the mean and SD of carbon isotopic fractionation found for freshwater animals (Deniro and Epstein 1978; Vander Zanden and Rasmussen 2001). This range approximates other potentially relevant values for  $\Delta^{13}\text{C}$ , including  $0.4 \pm 1.2$  ‰ for aquatic organisms (mean  $\pm$  SD; McCutchan et al. 2003),  $0.25 \pm 1.4$  ‰ for invertebrates (Vander Zanden and Rasmussen 2001), and  $+2.8$  ‰ for mosquito larvae from the genus *Aedes* feeding on plant tissue with similar C:N to the grass used in our study (beech tree flowers; Kaufman et al. 2010). Given the warming effects of light on pools, we also accounted for effect of temperature on trophic fractionation ( $\sim 0.1$  ‰ increase in  $\Delta^{13}\text{C}$  for every 1 °C increase in temperature; Power et al. 2003). Lipid concentrations in the consumer can also alter  $\delta^{13}\text{C}$  values; we corrected for these differences if necessary using C:N ratios as a surrogate for lipid concentration (Logan et al. 2008; Smyntek et al. 2007). Preliminary analysis of  $\delta^{13}\text{C}$  data showed that POC from low input pools would be our best surrogate for phytoplankton (signature was least similar to *E. tef* grass; Appendix A in ESM). Since phytoplankton is the more likely aquatic source of carbon for the majority of mosquito larvae in the study (*C. restuans* appear to filter-feed in open water; Reiskind and Wilson 2004), we used POC from low input pools as the aquatic carbon source. To calculate total biomass of carbon exported from experimental pools in emerging mosquitoes, we multiplied the estimated proportion of emergent adult carbon (reflective of larval diet) coming from carbon fixed from terrestrial and aquatic sources by the biomass and % C

of the mosquitoes emerging from each pool and averaged by treatment.

To explore the effects of density on survival of mosquito larvae to adult stage, we performed a regression on number of eggs laid per pool and the number of mosquitoes emerging from the pools during the experiment or found as pupae the day following final emergence trapping. Pupae were included to account for effects of delayed metamorphosis under more crowded conditions. Number of eggs per pool was estimated based on number of egg rafts deposited multiplied by mean number of eggs per raft for the predominant species in the experiment (*Culex restuans*,  $164 \pm 7.9$  SE,  $n = 20$ ; Reiskind and Wilson 2004). The analysis was performed on egg rafts laid from August 21 to September 4, adults emerged from August 31 to September 9 and pupae in pools on September 10 to best represent a correspondence between egg and adult cohorts (based on larval period of  $\sim 9$  days, from this study). Percent survival data were  $\log_{10}$ -transformed.

## Results

Mosquitoes of the genus *Culex* were by far the most abundant aquatic insect that colonized the pools during the experimental period (80 % of insects in pools at the end of experiment). Based on identification of larvae, the vast majority of mosquitoes were *C. restuans* (>99 %). *Culex quinquefasciatus* complex and *C. territans* comprised the remaining <1 % of mosquitoes found in the pools. We identified 942 *Culex* egg rafts from 50 pools, 306 larvae from 36 pools and 1,639 adults which emerged from 37 of 60 pools during the experiment. First *Culex* egg rafts were laid on Aug 24 and first adults were captured emerging on September 2.

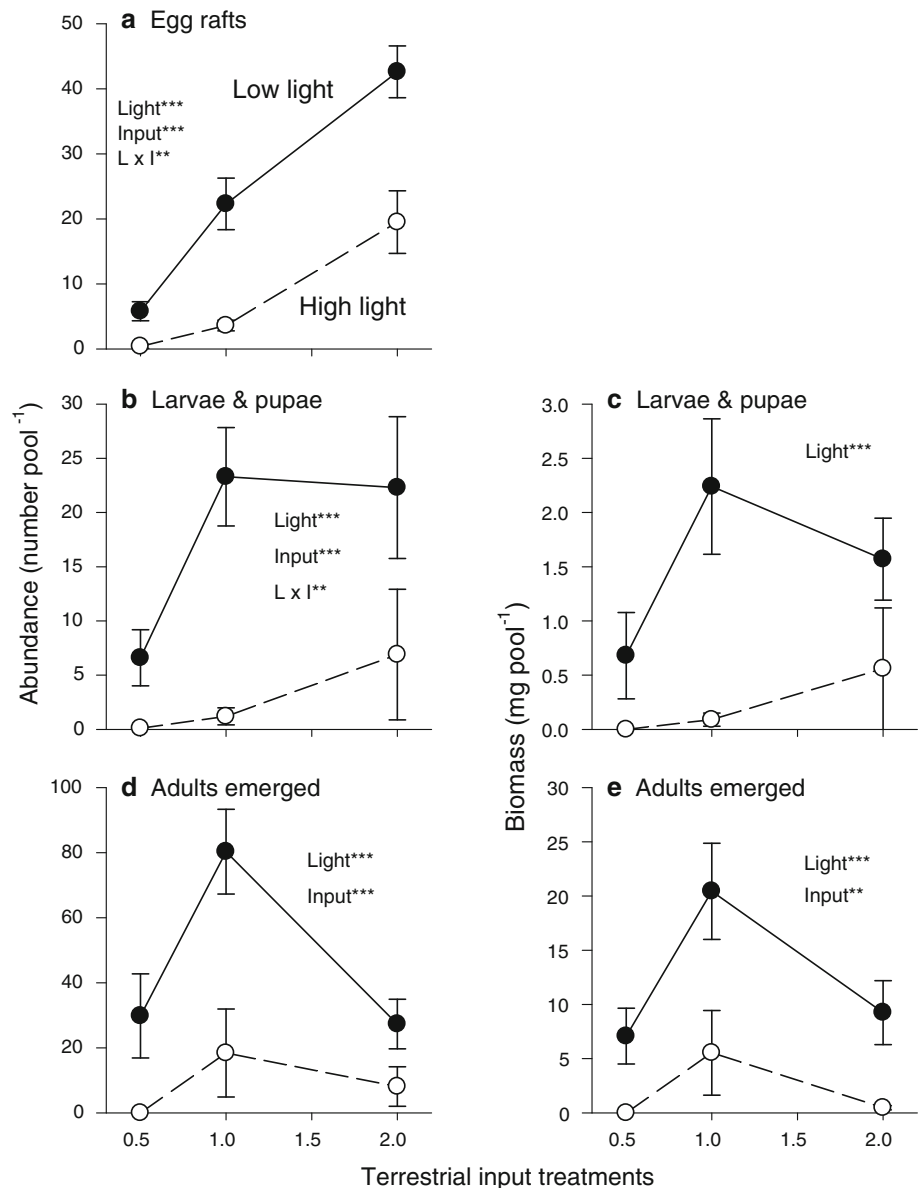
Ovipositing *Culex* mosquitoes preferred pools that received more terrestrial plant inputs in low light conditions: females laid  $\sim 2$ –4 times more egg rafts per pool as terrestrial plant inputs doubled and 3 times more egg rafts in pools receiving low versus high light ( $P < 0.001$ ; Fig. 2a; Table 1). However, the oviposition response to terrestrial inputs depended on light conditions, leveling off sooner across a gradient of input in low versus high light pools (light  $\times$  input,  $P = 0.006$ ; Fig. 2a; Table 1). Mosquito larvae and pupae were also present in significantly higher numbers (6.4 times) and biomass (6.9 times) in low light pools ( $P < 0.001$ ), but showed a saturating response to terrestrial plant inputs in low light conditions ( $P < 0.001$ ; light  $\times$  input; Fig. 2b, d; Table 1). Finally, adult mosquitoes emerged in greater numbers and biomass from low light pools (5–6 times higher,  $P < 0.001$ ) and mid-levels of terrestrial input ( $\sim 3$ –4 times higher,  $P < 0.001$ ; Fig. 2c, e; Table 1). Numbers and biomass of mosquitoes in pools at the termination of the experiment showed similar effects of

light and input as found during the experiment (abundance<sub>sqrtpoisson</sub>, Input:  $F_{2,36} = 10.62$ ,  $P < 0.001$ ; Light:  $F_{1,18} = 16.26$ ,  $P < 0.001$ ; Input  $\times$  Light:  $F_{2,36} = 8.55$ ,  $P < 0.001$ ; biomass<sub>sqrtpoisson</sub>, Input:  $F_{2,36} = 4.06$ ,  $P = 0.03$ ; Light:  $F_{1,18} = 10.59$ ,  $P = 0.004$ ; Input  $\times$  Light:  $F_{2,36} = 3.52$ ,  $P = 0.04$ ), suggesting that extending the experiment to allow emergence of animals that had previously colonized the pools would not have drastically changed our results. Survival of mosquitoes from egg to pupal or adult stages over the experiment was on average low ( $\sim 4$  %), but variable (range 0–15 %). This variance in survival can be explained by egg density in pools under low light conditions receiving mid- and high levels of terrestrial input; in pools receiving the most eggs over the experiment ( $\sim 7,000$ ), survival was near zero, whereas when egg density was low (<1,000) survival was at the upper end of the range (L1:  $F_{1,8} = 9.63$ ,  $P = 0.015$ ,  $R^2 = 0.55$ ; L2:  $F_{1,8} = 7.63$ ,  $P = 0.025$ ,  $R^2 = 0.49$ ; Fig. 3).

Aquatic and terrestrial basal resources differed in their  $\delta^{13}\text{C}$  signatures (GLMM,  $F_{2,20} = 32.47$ ,  $P < 0.001$ ; Tukey HSD, all pairwise comparisons,  $P < 0.01$ ; Appendix A in ESM), confirming their usefulness as a tracer of diet source in this experiment. Both particulate organic carbon (POC, block mean  $\pm$  SE, SD,  $-18.74 \pm 0.42$ , 1.31 ‰,  $n = 10$  blocks) and periphyton ( $-15.74 \pm 0.43$ , 1.36 ‰,  $n = 10$  blocks) when averaged across treatments were significantly less enriched than terrestrial *E. tef* grass ( $-12.45 \pm 0.08$ , 0.14 ‰,  $n = 3$  samples). The  $\delta^{13}\text{C}$  signature of emerging mosquitoes was more enriched (i.e., more similar to terrestrial grass) at higher levels of terrestrial inputs ( $P = 0.004$ ; Fig. 4a; Table 1). Using a two-source mixing model with terrestrial grass ( $\delta^{13}\text{C}$  mean  $\pm$  SD,  $-12.45 \pm 0.14$  ‰,  $n = 3$ ) and low POC from pools with low terrestrial plant input ( $-19.70 \pm 1.3$  ‰,  $n = 3$ ) as sources and the fractionation assumptions outlined above, we estimated that the source of production of *Culex* adults was mainly terrestrial in all treatments (on average  $\sim 70$ –90 %; Fig. 4b), but most aquatic in low terrestrial plant input pools. Varying the isotope discrimination estimate for carbon by  $\pm 1$  ‰ shifted the diet range  $\sim \pm 15$  % (84–100 % terrestrial at 0 ‰ fractionation and 56–82 % terrestrial at 2 ‰), but the treatment effects were qualitatively similar. In all cases, the estimated biomass of terrestrial carbon exported by emerging aquatic insects was calculated to be highest from low light pools that received intermediate inputs of terrestrial plant matter ( $P < 0.001$ , 0.002 for main effects respectively; Fig. 4c; Table 1). The estimated biomass of aquatic carbon exported from the pools in adult mosquito biomass was also highest from low light pools, but not affected by inputs of terrestrial plant matter ( $P < 0.001$ ; Fig. 4d; Table 1).

Aquatic net ecosystem production in the pools, as estimated by the change in dissolved oxygen (mg/L) during the

**Fig. 2** Response of *Culex* mosquitoes to inputs of terrestrial plant matter and light availability. **a** Number of egg rafts, **b** number and **c** biomass of larvae and pupae, and **d** number and **e** biomass of adults emerging from pools (mean  $\pm$  1SEM). Terrestrial input treatments represent 0.5, 1 and 2 times the typical biomass of fall leaf litter in a nearby forest edge. In *all* panels, significant effects for low versus high light pools (*L* Light,) and litter input treatments (*I* Input) are indicated as \*\* $P < 0.01$ , \*\*\* $P < 0.001$



day, increased significantly with increasing terrestrial plant input, and was not affected by light (Table A1 in ESM). A positive relationship between NEP and *E. tef* inputs suggested that N and P mineralized from the grass fertilized the pools, while the relatively colorless leachate ( $0.09 \pm 0.04$  absorbance and  $2.1 \pm 0.9 \text{ m}^{-1}$  color at 440 nm  $n = 24$  pools; Pace and Cole 2002) apparently did not cause the light limitation seen in more tannin-rich DOC-driven aquatic systems (Karlsson et al. 2009). Thus, relative availability of aquatic and terrestrial resources did not differ among treatments in our experiment. Similarly, our qualitative estimate of biofilm cover increased with terrestrial input, but was not affected by light (Table A1 in ESM). Relative quality of aquatic and terrestrial resources was also fairly consistent across treatments: based on C:N ratio, aquatic basal resources were a consistently higher

quality resource than terrestrial grass inputs for larval mosquitoes. Periphyton and POC had a significantly lower C:N ratio (mean  $\pm$  SE  $7.1 \pm 0.3$ , and  $6.1 \pm 0.3$ , respectively) than terrestrial grass ( $24.2 \pm 0.8$ ; Tukey HSD for all pairwise comparisons,  $P < 0.05$ ). However, periphyton C:N decreased with higher terrestrial plant inputs, perhaps due to N mineralizing from the grass (Appendix A in ESM). Light availability and inputs of terrestrial plant matter had no effect on % C ( $\sim 45\%$ ) and % N ( $\sim 12\%$ ) of emerging mosquitoes ( $P > 0.05$ ), but C:N ratios of emergent mosquitoes were lower in high light (3.6) versus low light (3.7) pools ( $P = 0.04$ ; Table 1). High light pools averaged  $\sim 1.8^\circ\text{C}$  warmer than low light pools (GLMM,  $F_{1,9} = 641.9$ ;  $P < 0.001$ ), and  $0.5\times$  and  $1\times$  input pools were also slightly warmer ( $\sim 0.2^\circ\text{C}$ ) than  $2\times$  input pools ( $F_{2,36} = 3.58$ ;  $P = 0.04$ ; Table A2 in ESM). Dissolved

**Table 1** Generalized linear mixed model (GLMM) statistical output testing effects of light and terrestrial plant inputs on *Culex* mosquitoes and the source of energy exported by emerging mosquitoes in experimental pools

Effects	Emergent adults <sup>sqr, norm, block</sup>			Larvae + pupae <sup>poiss, block, b × wp</sup>			Egg rafts <sup>nb, block</sup>		
	df	F	P	df	F	P	df	F	P
Abundance									
Light	1,45	36.93	<b>&lt;0.001</b>	1,9	39.56	<b>&lt;0.001</b>	1,45	61.30	<b>&lt;0.001</b>
Terr. inputs	2,45	8.96	<b>&lt;0.001</b>	2,36	26.35	<b>&lt;0.001</b>	2,45	53.72	<b>&lt;0.001</b>
Light × Inputs	2,45	1.86	0.167	2,36	18.80	<b>&lt;0.001</b>	2,45	5.78	<b>0.006</b>
Biomass									
Light	1,43	18.10	<b>&lt;0.001</b>	1,45	15.26	<b>&lt;0.001</b>			
Terr. inputs	2,43	6.17	<b>0.004</b>	2,45	2.52	0.092			
Light × Inputs	2,43	1.00	0.376	2,45	1.85	0.170			
Carbon exported									
Light	1,16	2.60	0.127	1,43	34.41	<b>&lt;0.001</b>	1,52	25.14	<b>&lt;0.001</b>
Terr. inputs	2,15	7.95	<b>0.004</b>	2,43	10.82	<b>0.002</b>	2,52	0.28	0.757
Light × Inputs	1,15	0.05	0.824	2,43	1.29	0.286	2,52	0.40	0.671
Adult quality									
Light	1,16	0.45	0.511	1,16	1.36	0.260	1,22	4.84	<b>0.039</b>
Terr. inputs	2,14	1.15	0.346	2,14	1.54	0.249	2,22	0.90	0.420
Light × Inputs	1,14	3.48	0.083	1,14	3.60	0.078	1,22	0.19	0.665

Significant effects for each taxon are in bold. Random effects of spatial block and block × whole plot (b × wp, i.e. light) were included where the mean estimates were non-zero as indicated. Superscripts indicate error distribution used for each response: *nb* negative binomial, *norm* normal. *Sqr* indicates the data were square-root transformed before analysis. Estimates of *F* statistics are analogous to type 3 SS in ANOVA

oxygen was higher in high light pools (GLMM,  $F_{1,45} = 14.09$ ;  $P < 0.001$ , afternoon average), and pools with highest amount of input ( $F_{2,45} = 10.54$ ;  $P < 0.001$ ; Table A2 in ESM).

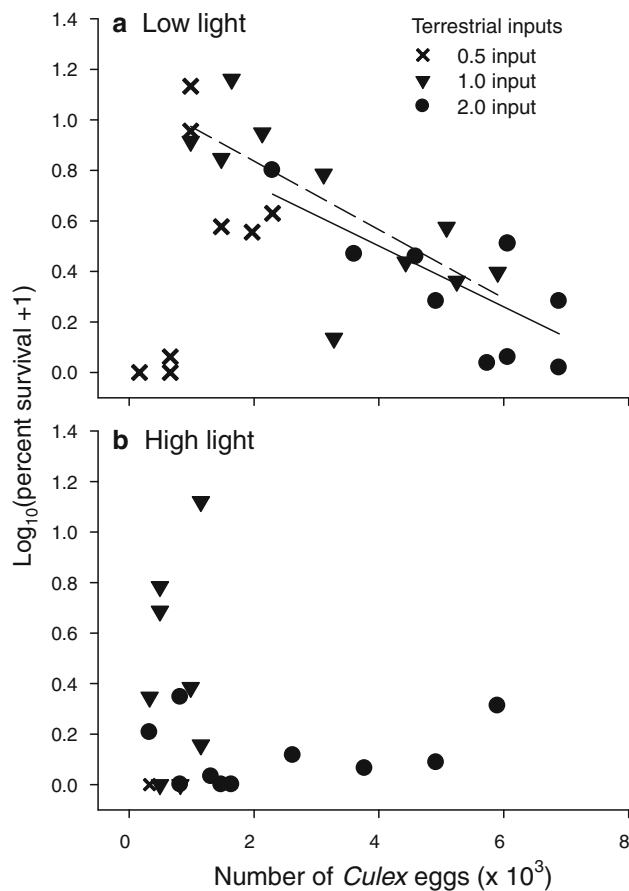
Dytiscid larval presence did not significantly affect response of *Culex* mosquitoes during the experiment after accounting for variance in mosquito response due to planned treatment effects (*Culex* egg rafts,  $F_{1,53} = 1.94$ ,  $P = 0.17$ ; *Culex* larvae,  $F_{1,35} = 3.11$ ,  $P = 0.09$ ; *Culex* adults,  $F_{1,44} = 1.38$ ,  $P = 0.25$ ). Mosquito larvae plus pupae abundance and biomass in pools at the end of the experiment (not pictured), however, was significantly lower (3- and 6.5-fold, respectively) in pools containing dytiscid larvae, after controlling for planned treatment effects (mean ± SE; GLMM, abundance<sub>sqr,poisson</sub>,  $F_{1,35} = 62.8$ ,  $P < 0.001$ ; biomass<sub>sqr,poisson</sub>,  $F_{1,35} = 38.1$ ,  $P < 0.001$ ). Combined with the lack of relationship between dytiscid larval presence and treatments, this result suggests that had the experiment run longer predators would have potentially reduced the magnitude of mosquito flux from the pools but not the relative difference among treatments (Ngai and Srivastava 2006). Although none had emerged as adults, there were a few dytiscid larvae in pools at the end of the experiment (mean no. ± SD,  $1.8 \pm 1.4$  larvae per pool where present, 31 total) apparently as a result of cannibalism (Yee 2010; J. Kraus, personal observation). In total, 2,467

mosquito larvae in 36 pools and 807 pupae in 25 pools were found at the end of the experiment. Other insect taxa found included 345 chironomid larvae and 39 pupae (from 13 pools), 13 dytiscid beetle adults (8 pools), 4 hydrophilid beetle adults (all in different pools), 2 unknown pupae, 1 unknown adult beetle, and 410 planktonic (hatchling) dragonfly larvae in 1 pool.

## Discussion

The purpose of this study was to test the hypothesis that terrestrial inputs and light would control source and amount of energy exported from aquatic systems in emerging aquatic insects. Specifically, we examined the effects terrestrial plant input and light on the source and amount of carbon exported by detritivorous *Culex* mosquitoes emerging from naturally colonized experimental pools. We found that increasing inputs of terrestrial plant matter initially increased then decreased total terrestrial carbon exported in emergent mosquitoes from pools, but had no effect on aquatic carbon exported. Also, somewhat counterintuitively, reducing ambient light exposure of pools increased both total terrestrial and total aquatic carbon exported by mosquitoes during the experiment. These patterns can be explained by the oviposition responses of





**Fig. 3** Percent of mosquitoes surviving from egg to pupae or emerged adult with 0.5, 1, and 2 times ambient inputs of terrestrial leaf litter in **a** low light and **b** high light pools. Data includes egg rafts laid from August 21 to September 4, pupae in pools on September 10, and adults emerged from August 31 to September 9. Regressions are shown for low light mid-input pools (dashed line  $R^2 = 0.55$ ) and for low light high-input pools (solid line  $R^2 = 0.49$ ). Percent survival is  $\log_{10} (+1)$ -transformed

adult *Culex* mosquitoes (selecting high terrestrial input and low light pools), density-dependent larval mortality, and the diets of *Culex* larvae in the pools. Given that terrestrial plant inputs and light are both broadly important in explaining variation among aquatic insect communities, we think interplay among effects of terrestrial inputs, light, and species life histories are likely to occur in and help shape aquatic–terrestrial linkages in other systems.

The relationship between oviposition behavior and habitat quality occurs in many animals with complex life histories (mosquitoes, Ellis 2008; Vonesh and Blaustein 2010; beetles, Binckley and Resetarits 2007; amphibians, Resetarits et al. 2004; mayflies, Richards and Minshall 1988). Although females often oviposit in habitats most beneficial for their larvae (Rauscher 1979; Kiflawi et al. 2003a, b; Rieger et al. 2004), many animals including mosquitoes do not exhibit perfectly optimal behavior in their oviposition choices (Thompson 1988; Heard 1994;

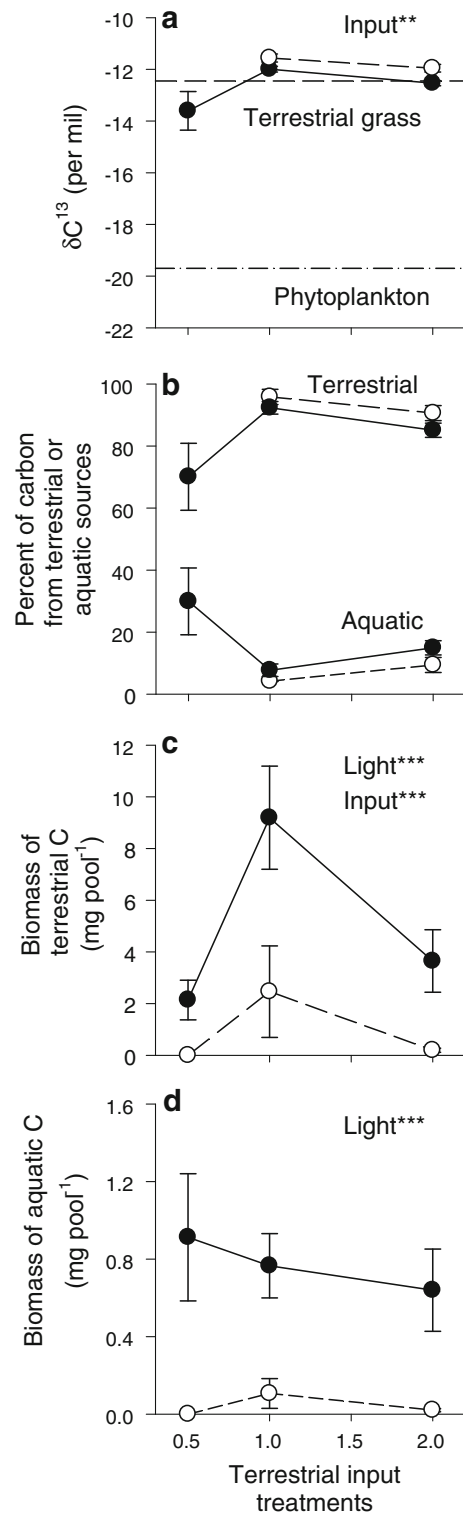
Kiflawi et al. 2003a, b; Rieger et al. 2004). Non-optimal choices can occur for many reasons, including imperfect information or conflicting cues of habitat quality (Parker and Smith 1990; Schlaepfer et al. 2002). Consistent with previous findings (Bentley and Day 1989; Reiskind and Wilson 2004), in our study the most *Culex* egg rafts were laid in pools that likely had highest initial resource availability (high terrestrial inputs and low light). However, pools receiving the largest number of egg rafts did not have the highest emergent mosquito production. Our results suggest that this pattern is most likely due to strong density-dependent mortality in the larval stage. Strong density-dependent resource competition in the larval stage is common in aquatic insects and amphibians in general and occurs in our study species specifically (Wilbur and Collins 1973; *C. restuans*, Reiskind and Wilson 2004) and can lead to reduced survival and size at metamorphosis. A disconnect between oviposition habitat selection and adult recruitment in our study could thus occur as the habitat quality shifted from being determined by initial resources to conspecific density as the communities in the pools assembled (Kraus and Vonesh 2010). Had the pool communities continued to assemble, our results and previous work suggest that colonizing predators would also play a potentially large role in determining larval densities and adult oviposition behavior. Specifically, before we removed them, adult dytiscid beetles showed similar colonization patterns to ovipositing mosquitoes, suggesting that had we not removed them they and their larvae may have augmented the patterns we found by further reducing biomass of mosquitoes emerging from high input/low light pools. As it was, larval dytiscid presence in pools did not differ among treatments and did not affect the results we found during the experiment; thus, dytiscid larvae likely would have reduced emergence flux equally across treatments had the experiment run longer. Although oviposition habitat selection is common, the natural effects of oviposition habitat selection on emergence are rarely directly measured for aquatic insects. Further study of how choices made during oviposition alter amount and source of emergence will be important for understanding aquatic–terrestrial linkages in other systems.

In freshwater systems, variation in use of aquatic primary production and terrestrial detritus can occur at both the individual and community levels (Rounick et al. 1982; Wallace et al. 1997). This variation is often related to resource availability and preference (Cummins 1973; Wallace and Merritt 1980; Rounick et al. 1982); thus, factors such as terrestrial plant inputs and light that affect or indicate resource availability can have large effects on source of carbon fueling the aquatic food web (Karlsson et al. 2009). In temperate systems, aquatic habitats receive less light and more terrestrial inputs as canopy cover

**Fig. 4** Source and biomass of carbon exported from low and high light pools in emergent *Culex* mosquitoes as a function of terrestrial inputs 0.5, 1, and 2 times ambient levels. Emergent adult mosquito **a**  $\delta^{13}\text{C}$  stable isotope signatures, **b** percent carbon from terrestrial or aquatic sources, and biomass of carbon fixed from **c** terrestrial and **d** aquatic sources (mean  $\pm$  1SEM). Estimated average signature for aquatic and terrestrial sources of carbon most likely used by mosquito larvae in pools are calculated from POC values in low terrestrial inputs pools (“phytoplankton” estimate, *dot-dashed line*) and dried *E. tef* grass (terrestrial estimate, *dashed line*). Solid symbols and lines represent low light treatments and open circles and dashed lines represent high light treatments. No adult mosquitoes were captured emerging from high light pools with low levels of terrestrial inputs. Significant effects for low versus high light pools (*Light*) and litter input treatments (*Input*) are indicated as \*\* $P < 0.01$ , \*\*\* $P < 0.001$

increases, shifting the resource base towards terrestrial detritus (Minshall 1978; Cummins et al. 1989; Skelly et al. 2002). In streams and ponds receiving more leaf inputs, community composition consisted of more detritivorous versus herbivorous larvae (Wallace et al. 1997; Binckley and Resetarits 2007), individual species showed more reliance on terrestrially fixed carbon (Rounick et al. 1982), and the ecosystem as a whole became more heterotrophic (Rubbo et al. 2006). In our study, we found that the stable carbon isotopes of emerged adult mosquitoes became more similar to the terrestrial grass and less like aquatic POC and periphyton as we added more terrestrial grass to pools (from low to mid amounts). Light did not alter aquatic primary production in our pools: 30 % of ambient light may have saturated algal photosynthesis, or, more likely, based on the increase in NEP with increased grass inputs, primary producers were nutrient-limited in our pools. Light also did not lead to a significant shift in mosquito diet. However, lower light levels did attract ovipositing females of the mainly detritivorous *Culex*. As a result, both light and terrestrial inputs altered the amount and source of carbon exported in mosquitoes from pools.

Given the variability of terrestrial plant inputs and light availability in nature and their potential effects on use of basal resources by aquatic larvae, these factors are also likely to affect cross-ecosystem flux in other ecosystems (Wallace et al. 1997; Rubbo et al. 2006; Binckley and Resetarits 2007). Our results suggest that terrestrial plant inputs and light can alter mosquito oviposition response and larval diet leading to cascading effects on source and amount of energy exported from an experimental aquatic system. Although exact patterns vary, many aquatic organisms respond to terrestrial plant inputs and light both during oviposition and in the larval environment (Wallace and Merritt 1980; Fish and Carpenter 1982; Wallace et al. 1997; Binckley and Resetarits 2007). For example, the river continuum concept predicts larval insect functional feeding groups to shift towards those using terrestrial plant detritus (shredders, collector-gatherers) as terrestrial inputs increase and aquatic primary productivity and light decrease



(Vannote et al. 1980). Thus, in forested headwater streams, where terrestrial inputs are high and emerging aquatic insects are an important resource to terrestrial predators (Nakano and Murakami 2001), exported secondary production is driven by terrestrial energy (Iwata 2007). Thus, predicting emergence and the strength of aquatic to

terrestrial linkages in these systems would require measuring terrestrial production, terrestrial inputs, and the behavioral response of aquatic insects to these resources.

Prey that move across ecosystem boundaries can play a large role in driving local food webs patterns and processes. We found that light and terrestrial inputs can alter the amount and source of energy exported from experimental pools in emergent mosquitoes by affecting oviposition behavior, larval densities, and larval diet. Correct identification of which ecosystem drives production of emerging insects, or any prey crossing ecosystem boundaries, allows better prediction of the magnitude of resource flux (Polis et al. 1997; Marczak et al. 2007), and will help us apply the most appropriate model for understanding how these prey will affect recipient food web dynamics. Thus, understanding how environmental conditions and animal behavior combine to shape the extent to which emerging insects are an allochthonous subsidy versus a recycled recipient resource for terrestrial consumers will be critical for predicting the strength and possibly effects of these aquatic–terrestrial linkages. This study highlights a need for greater understanding of energy source and the role of animal behavior in transforming that energy to animal production when evaluating cross-ecosystem linkages, especially those involving living prey.

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