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Canopy cover affects habitat selection by adult dragonflies

Sarah K. French · **Shannon J. McCauley**

Abstract The mechanisms structuring aquatic communities across environmental gradients are often difficult to distinguish from one another and can produce similar patterns of species distributions. In freshwater systems, the amount of canopy cover from surrounding trees is often associated with transitions in local community structure. These community changes could be driven by habitat selection prior to colonization of the aquatic habitat and/or species-sorting post-colonization. To assess the contributions of pre- versus post-colonization processes in structuring larval dragonfly assemblages, we tested the impact of artificial and natural canopy cover on the selection of experimental aquatic mesocosms by adult dragonflies, and monitored the performance (i.e. growth and survival) of larval dragonflies that were placed in mesocosms under a gradient of natural canopy cover. We found that greater levels of canopy cover resulted in fewer adult visits to mesocosms, and more natural canopy cover decreased the species richness of visitors. There were no effects of canopy cover on the growth and survival of larvae added to the mesocosms. Our results suggest that adult habitat selection plays a dominant role in structuring larval dragonfly assemblages across a canopy cover gradient, and that canopy cover can be an important environmental filter on species distributions.

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Introduction

Heterogeneous landscapes can affect species' establishment within habitats and their resultant distributions across environmental gradients by influencing dispersal, individuals' choice of habitat, and post-colonization processes (Lima & Zollner, 1996; Leibold et al., 2004; Keller et al., 2012). Animals dispersing to new patches may select habitats across gradients of available resources, refuges, or other environmental conditions (e.g. Boyce et al., 2003; Rieger et al., 2004). Alternatively, animals may have a

limited ability to detect particular habitats (Schooley & Wiens, 2003; Schtickzelle et al., 2007). Following the colonization of a habitat, colonist or offspring persistence can depend on differential performance (e.g. variable mortality) along environmental gradients, affecting community assembly and structure in the process (i.e. species-sorting; Leibold et al., 2004; Logue et al., 2011).

Studies on community assembly across heterogeneous habitats generally focus on two mechanisms, dispersal and species-sorting, while overlooking habitat selection as a critical link between the two (i.e. Fig. 1; Binckley & Resetarits, 2005; Resetarits, 2005). Individuals can choose and establish at habitats that
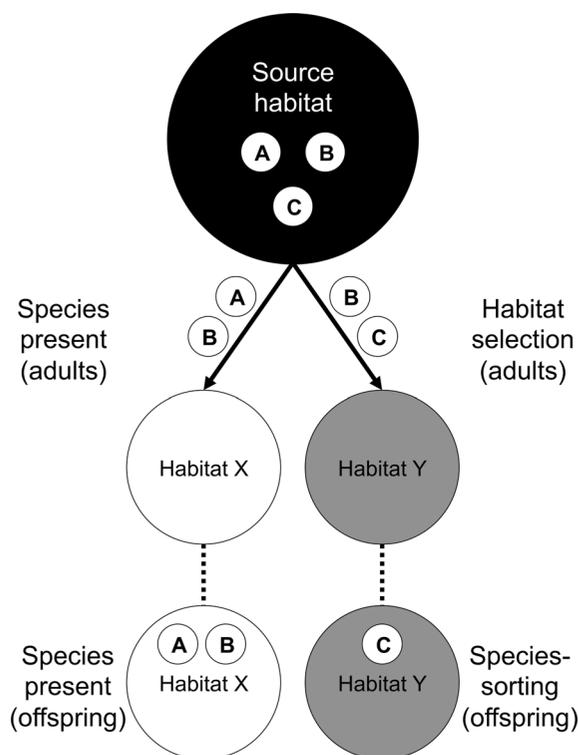

Fig. 1 Species selecting habitat following dispersal. Adults of species A, B, and C, disperse from a source habitat and select between two reproductive habitats (X and Y) of varying quality. Adults of A select X, adults of C select Y, and adults of B select both habitats. The offspring of A and B survive in X, and those of C survive in Y. Unsuitable conditions in Y lead to mortality in the offspring of B due to species-sorting. Without observations of both adult habitat selection and offspring species-sorting, we could not determine the mechanism generating patterns of offspring distributions. For example, we might infer that offspring of A and B cannot persist in Y. However, adults are simply not arriving at Y, and we have no indication of whether their offspring could survive in Y

they perceive to be of high quality (Binckley & Resetarits, 2005, 2007). This individual-level behavioural strategy of selecting habitats potentially minimizes the risks posed by colonizing low-quality habitats, and decreases the extent to which post-colonization species-sorting acts on community structure. Habitat selection to avoid predators occurs in a number of groups (e.g. Binckley & Resetarits, 2003, 2005; Brodin et al., 2006). For example, some *Chaoborus* spp. (Diptera: Chaoboridae) use chemical cues to avoid reproductive habitats with fish predators, where their offspring would experience greater mortality (Berendonk, 1999; Garcia & Mittelbach, 2008). However, not all animals can detect predators within the juvenile habitat (e.g. adult odonates; McPeek, 1989; McCauley, 2005a; Knorp & Dorn, 2016), and consequently may be limited in their ability to use habitat selection to improve post-colonization performance. The extent to which colonists acquire and use information about habitat quality, whether based on predators or other factors, is an important determinant of whether pre- or post-colonization processes dominate in shaping species distributions across environmental gradients.

In aquatic species with a dispersing terrestrial stage, a common life-history for many aquatic insects, the conditions in the terrestrial environment at both local and regional scales are important for adult dispersal and colonization, whereas local aquatic conditions determine larval performance (Rothermel & Semlitsch, 2002; Remsburg & Turner, 2009). The focal taxa in our study, dragonflies (i.e. infraorder Anisoptera), have an aquatic larval stage and a terrestrial adult stage, with habitat choices by adults potentially leading to reproduction across a gradient of habitat quality (Switzer, 2002). Adult dragonflies disperse and may select aquatic habitats in response to visual cues from both aquatic and terrestrial environments (Bernáth et al., 2002; Corbet, 2004; Remsburg et al., 2008; Knorp & Dorn, 2016). Habitat selection by adults can occur across a hierarchy of spatial scales: among ponds at the landscape scale, to among sites within a single pond (Buchwald, 1994 in Corbet 2004; Wildermuth, 1994 in Corbet, 2004).

Forest canopy gradients provide an important context in which to examine the effects of adult habitat selection versus larval performance on community structure in aquatic systems. Forest cover has dramatically changed in many regions of North

America, including widespread deforestation in some regions (Hansen et al., 2013) and significant forest regrowth in others (Foster et al., 1998). Forest regrowth following the abandonment of agricultural land in parts of eastern North America has led to the highest levels of forest cover in 200 years (Foster et al., 1998). Reforestation in this region is particularly likely to have large effects on small freshwater habitats such as ponds, as these habitats can be more fully shaded than lakes. Canopy cover over aquatic habitats can decrease light availability and water temperature, while increasing organic input, all of which can impact community structure within these habitats (Richardson, 2008). In temperate regions, tree cover near aquatic habitats can also restrict visitation and colonization rates at ponds by amphibians (Skelly et al., 2014), adult dragonflies (Remsburg et al., 2008), and beetles (Binckley & Resetarits, 2009). Canopy cover may decrease the amount of polarized light reflected from aquatic surfaces, a visual cue commonly used by dragonflies to detect oviposition habitats (Wildermuth, 1998), as well as the amount of sunlight available for adult thermoregulation (Horváth et al., 2007; Remsburg et al., 2008; De Marco et al., 2015). Low light availability at these habitats may affect the composition of a dragonfly assemblage by constraining adults' detection of habitat or limiting their persistence in the area, thus reducing colonization success (e.g. Remsburg et al., 2008; De Marco et al., 2015). In highly shaded ponds, eggs and larvae may develop more slowly due to lower temperatures (Pritchard et al., 1996; Corbet, 2004; Frances et al., 2017), potentially decreasing survival in these often desiccation-prone habitats.

Greater levels of canopy cover are also associated with changes in larval dragonfly assemblages. In temperate regions in the northern hemisphere, where more sunlight is reflected off surfaces than in tropical regions, dragonfly species that are not generally forest associated experience reduced larval abundances and diversity with increasing canopy cover (McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data). However, it is difficult to discern whether reduced dragonfly diversity in closed habitats is driven by adult habitat selection or by poorer performance (i.e. growth and survival) and species-sorting imposed on larvae by within-pond habitat conditions. Indeed, empirical studies aimed at teasing apart these two mechanisms in freshwater systems have been limited

(e.g. Binckley & Resetarits, 2005; Vonesh et al., 2009; Knorp & Dorn, 2016). Our study assessed the extent to which larval dragonfly distributions were related to adult habitat selection behaviour versus differences in larval performance across varying canopy conditions. Because polarized light is important in the visual detection of aquatic habitats by dragonflies (Wildermuth, 1998; Briscoe & Chittka, 2001; Bernáth et al., 2002), we predicted that more adults would visit open versus closed canopy habitats, resulting in more larvae in open canopy habitats. We also expected that larvae would have greater survival and growth rates in open canopy habitats because they are warmer and more productive (Schiesari, 2006). Adult arrivals (abundance and diversity) at a habitat were therefore expected to be strongly related to canopy cover, with subsequent larval distributions being principally shaped by the arrival of adult colonists, but reinforced by improved larval performance in open environments.

Materials and methods

To determine how adult dragonflies respond to canopy cover while selecting aquatic habitats, field experiments using aquatic mesocosms were performed at the University of Toronto's Koffler Scientific Reserve (KSR; King City, ON, Canada, 44.03 N, 79.53 W). Approximately 24 species of dragonflies are found at KSR (French & McCauley, unpublished data). Three separate field experiments tested whether shading (i.e. artificial cover) and canopy cover (i.e. natural tree cover) reduced the abundance and diversity of adult and larval dragonflies at artificial ponds. Each experiment used twenty mesocosms (100-gallon cattle tanks) as artificial ponds for potential dragonfly visitors during each experiment. Mesocosms were filled with filtered pond water, and in the case of the shading experiment, covered with netting until observations began to prevent aquatic insects from colonizing prior to starting the experiment. After approximately 25 days for the shading experiments and 1 day for the natural canopy experiments, all mesocosms were inoculated once with zooplankton collected from Gazebo Pond (Fig. 2), including cladocerans and copepods, to serve as a food source, particularly for early insect colonists. Four pieces of rabbit food were also added to serve as a nutrient base
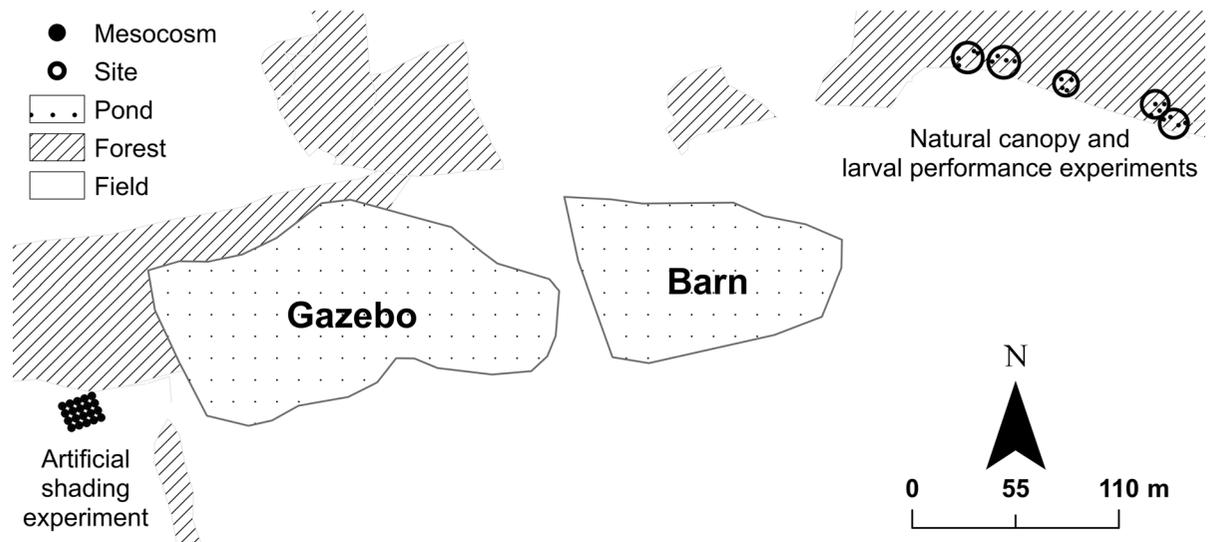
Fig. 2 Map of experimental sites at Koffler Scientific Reserve, with the arrangement of mesocosms used for the artificial shading, natural canopy, and larval performance experiments.

Landscape cover around the experiments is shown, as are the potential source ponds (Gazebo Pond and Barn Pond)

for algal growth for both experiments, and two handfuls of leaves collected from the terrestrial environment were added to the mesocosms of the shading experiments to serve as a nutrient base and to add structural complexity (these are standard conditions for colonization arrays; e.g. McCauley, 2006). Other aquatic invertebrates were allowed to naturally colonize the mesocosms, which also provided a food source for larval dragonflies. An artificial perch (a 1.2-m-long square dowel weighted at the bottom and extending past the water surface) for adult dragonflies to land on was added to each mesocosm (McCauley, 2006). Artificial vegetation was added to provide structural complexity, and consisted of two frayed rope bundles approximately 60 cm in length that were weighted to the mesocosm bottom and extended to the water surface, which larval dragonflies have been shown to use (McCauley, 2006, 2008). Observations started approximately 20 days after the zooplankton inoculation for shading experiments and five days for the natural canopy experiments. All observations of adult dragonflies, both at mesocosms and ponds, were conducted by sight and using binoculars, and the number of individuals and their species and sex were identified when possible.

Mesocosms were located near two ponds that contain fish (Gazebo Pond and Barn Pond; Fig. 2), which were potential source habitats. One fishless

pond is also present at KSR (Dufferin Pond, 509 m from nearest fish pond), but was a less likely source of visitors due to isolation by distance. There was an open field landscape between Gazebo/Barn Ponds and the mesocosm locations, making access to mesocosms under varying levels of canopy cover more standardized. Only the nearest pond for each experiment was surveyed for dragonflies, since identifying the regional pool of potential visitors was prioritized over knowing their exact source, and visitors may have stopped over at the nearest pond before visiting the mesocosms. Additionally, the larval and adult dragonfly assemblages at these two ponds with fish appeared to be identical (French & McCauley, personal observation).

Artificial shading experiment

To test the effects of artificial shading, water temperature, and their interaction, on the arrival of dragonfly visitors and subsequent colonization, we manipulated both in a fully factorial design. This setup allowed us to isolate the effects of shading (i.e. light availability and temperature) on dragonfly distributions from other water quality parameters influenced by canopy (e.g. nutrient input). There were four mesocosm treatments consisting of shaded, heated, shaded plus heated, and no shade or heat (i.e. control), and each treatment was replicated five times. Four rows, with five mesocosms

per row, were set up parallel to and moving away from a boundary of nearby trees (approximately 7.1 m away from the nearest row). Four replicates of each treatment were randomly assigned to a mesocosm in each row, such that at least one of every treatment was found in every row. A fifth replicate of each treatment was randomly assigned to the remaining mesocosms, independent of row. The trees did not shade the mesocosms during peak hours, and only shaded approximately a third of each mesocosm in the final row by 16h00. These conditions limited the potential for edge effects but nonetheless we wanted to control for any effects of this extra shading. Mesocosms in the shaded treatment had light blocked by dark green shade cloth, which reduces light penetration by 50% (Fig. S1 in Online Resource 1; note that this photo was taken prior to starting the experiment when mesocosms were still covered by netting). Mesocosms in the open canopy treatment had structure above them similar to that of the light-blocking cloth in the shade treatment but made of an open weave netting that allowed most incoming sunlight to reach the water's surface (Fig. S1). The overhang from both covers was approximately 1.8 m off the ground. The shade cloth shaded an entire mesocosm during hours of peak dragonfly activity and allowed adults to fly underneath, as flight paths of < 2 m above the ground have been observed in the field (Remsburg et al., 2008). Adults flew beneath both open and closed canopy cover, and were not observed to fly through the open netting; thus the weave density of the shade cloth likely did not deter dragonflies from arriving at the mesocosms. In addition to the potential naturally occurring effects of shading on water temperature, temperature was artificially manipulated with aquarium heaters (300 W, EHEIM JÄGER thermostatic heater, Deizisau, Germany) to test whether the warmer temperatures associated with open canopy conditions were preferred by adults, potentially because of positive effects of temperature on larval performance (e.g. faster growth rates, accelerated development; Flenner et al., 2010), and to identify any confounding influence of shading on pond temperature.

The mesocosms were observed by researchers for visiting adult dragonflies. A dragonfly was considered to be visiting a mesocosm if it was observed perching, hovering, or dipping at a mesocosm. Adults flying through the study area without stopping at a mesocosm were counted separately. We were conservative in our estimates of females by considering all adults independent of sex, because the arrivals were generally male-biased, a pattern which has been observed in other studies using mesocosms as artificial ponds (McCauley, 2006), and many females could not be definitively identified because in many species they resemble juvenile males. However, the abundance of males at a site can be positively related to the number of visiting ovipositing females and mating pairs (Van Buskirk, 1986; Corbet, 1962 in Horváth et al., 1998), and in a previous colonization experiment using mesocosms, male-biased adult arrivals predicted larval diversity (McCauley, 2006). In some instances, males arrive at aquatic habitats before females (Jacobs, 1955; Switzer & Walters, 1999) and remain for longer (Foster & Soluk, 2006). Males may also perch near oviposition sites and intercept approaching females (Jacobs, 1955; Switzer & Walters, 1999), or escort females to an oviposition site (Michiels & Dhondt, 1990). In addition, males and females likely use similar polarized light cues to find pond habitats where they encounter each other (e.g. Horváth et al., 1998; Wildermuth, 1998).

Observations were conducted twice a week for 6 weeks from July to August 2013, during hours of peak dragonfly activity (11h30–15h00), and when weather was suitable for dragonfly flight (no rain, zero to light cloud cover, and low wind). An observation period lasted an hour and involved the same two observers (SKF and SVLC) monitoring each of the four rows for 15 min. Two observers were situated at opposite ends of the rows, with each starting at a random row at the beginning of the period and continuing in one of two randomized directions. Two observation periods took place per day, for a total of 48 person-h of observations over 12 days. In between observation periods, we conducted a 40 person-min survey of adult dragonflies at the nearest source pond (Gazebo Pond, 39 m from nearest mesocosm) to determine the regional species pool, as even 20–40-min weekly surveys of adults can capture 87–96% of the representative species pool (Bried et al., 2012). The mesocosms were sampled for live dragonfly larvae and other colonizing insects (i.e. potential prey) after 10 weeks, with standard collection techniques across mesocosms. Prey density was calculated based on the total number of individuals from the most abundant prey families in a subsample (i.e. Chaoboridae, Chironomidae, and Baetidae).

Water temperatures were measured in between observation periods, within the hours of 12h30–13h40, using an OAKTON pH/CON 10 meter (Vernon Hills, Illinois, USA). Water temperatures (average of measurements taken from the bottom and top of mesocosms) were different among treatments (Kruskal–Wallis rank sum test, $\chi^2_3 = 16$, $P = 0.001$). A Nemenyi post hoc test (PMCMR package; Pohlert, 2014) indicated that shaded treatments (22.7 ± 0.2°C) had lower temperatures than heated treatments (26.6 ± 0.3°C; $P = 0.002$) and shaded plus heated treatments (26.0 ± 0.3°C; $P = 0.03$), but did not differ from control treatments (23.3 ± 0.1°C; $P = 0.7$). Heated treatments were marginally warmer than control treatments (no shade or heat; $P = 0.05$). Shaded plus heated treatments did not differ from control ($P = 0.3$) or heated treatments ($P = 0.9$). When treatments were pooled based on temperature manipulation, heated treatments (26.3 ± 0.2°C) had greater temperatures than non-heated treatments (23.0 ± 0.1°C; Wilcoxon rank-sum test, $W = 100$, $P < 0.001$). Heating treatments were therefore deemed effective.

We tested the effects of the presence and/or absence of heating and shading on the number and species richness of adult dragonfly visits to the mesocosms, and on the number, richness, and diversity (using the Shannon–Wiener index) of larvae within mesocosms. Separate generalized linear mixed-effect models (GLMMs; lme4 package; Bates et al., 2015) were run with adult abundance and species richness using a Poisson distribution, and with larval diversity using a Gaussian distribution. We also tested the effects of our treatments on larval abundance and richness using a GLMM with a negative binomial distribution due to overdispersion (glmmADMB package; Fournier et al., 2012; Skaug et al., 2012). Row was included as a random factor in each test. GLMM models with and without an interaction term were compared using likelihood ratio tests and the simplest model was selected. We separately tested the effect of prey density on larval abundance using a GLMM with a negative binomial distribution. All analyses were conducted in R (version 3.4.0; R Core Team, 2017).

Natural canopy experiment

To test the effects of a natural canopy cover gradient on the arrival of dragonfly visitors and subsequent colonization, mesocosms were placed under a range of canopy cover levels. These levels were based on natural ranges (32–91% cover) measured at the Edwin S. George Reserve (ESGR) in southeast Michigan, where earlier long-term surveys of larval dragonfly assemblages found decreased abundances and diversity with increasing forest canopy cover (McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data). This experiment allowed us to consider several components of canopy cover that our previous shading experiments did not capture (e.g. nutrient input). Twenty mesocosms were placed across five sites. At each site, one mesocosm was situated under each level of 30–40, 55–60, 70–75, and 90–100% canopy cover. Canopy cover above each mesocosm was estimated using a spherical densiometer (Model-C, Forest Densiometers, Rapid City, South Dakota, USA). Each mesocosm was observed for visiting adult dragonflies for 10 min by a single observer (SKF) approximately two days a week, depending on weather. Observations were repeated for a total of 10 weeks between July and September 2014, resulting in 70 h of observations over 21 days across all mesocosms. The nearest source pond (Barn Pond, 112 m from nearest mesocosm) was also surveyed for adults halfway through each observation day, for a period of 20 min (timing based on Bried et al., 2012). Again, visits were male-biased, but were assumed to predict the number of ovipositing females arriving (Van Buskirk, 1986; Corbet, 1962 in Horváth et al., 1998) and larval diversity (McCauley, 2006). The mesocosms were sampled for live dragonfly larvae and other colonizing insects (i.e. potential prey) after 12 weeks, with standard collection techniques across mesocosms. Prey density was calculated based on the total number of individuals from the most abundant prey families in a subsample (i.e. Culicidae, Chironomidae, and Baetidae).

I-Buttons (DS1921G-F50 Thermochron, Maxim Integrated, San Jose, California, USA) were placed in two mesocosms per site to measure water temperature, resulting in 2–3 i-Buttons per level of canopy cover, between July and September 2014. The i-Button in one mesocosm malfunctioned and the data could not be recovered. The i-Buttons collected data every 2 h between 10h15 and 18h50, resulting in approximately four measurements per day. The temperatures from a single canopy level treatment were averaged across all sites and days for subsequent analyses.

Water chemistry was measured in July–September 2014 using an Exo Sonde Probe (EXO2, YSI Inc., Yellow Springs, Ohio, USA): chlorophyll was averaged over 3 days, turbidity over 2 days, and dissolved oxygen, pH, and conductivity were measured once.

GLMMs tested the effects of natural canopy on the number and species richness of adult dragonfly visits to the mesocosms using a Poisson distribution, and on the presence/absence of larvae within mesocosms using a binomial distribution. Separate GLMMs tested the effects of canopy and prey density on larval abundance using a negative binomial distribution due to overdispersion (glmmADMB package). Site was included as a random factor. GLMM models were compared using likelihood ratio tests and the simplest model was selected.

A principal component analysis (PCA) was conducted using the princomp function to assess variation among mesocosms based on dissolved oxygen, pH, conductivity, chlorophyll, and water temperature, after scaling the variables. The first principal component axis explained 75% of the variance among mesocosms, with moderate to strong loadings (|0.36–0.5|; Table S1), and was the only axis retained based on a scree plot of the components. The PCA grouped 30–40 and 55–60% canopy cover separately from 70–75 and 90–100% canopy cover based on water chemistry (Fig. S2), indicating that the extreme levels of canopy were different. These results were confirmed using a one-way ANOVA on the PC1 component scores ($F_3 = 17$, $P < 0.001$; see Table S2 for all pairwise comparisons using Tukey's test); however, in this case, 55–60 and 70–75% canopy cover were marginally similar ($P = 0.09$), as were 70–75 and 90–100% canopy cover ($P = 0.07$).

Larval performance experiments

To determine how larval performance was affected by conditions within aquatic habitats that vary with canopy cover, we conducted experiments testing performance among mesocosms distributed across the same gradient of canopy cover as in the natural canopy experiment described above. These experiments allowed us to better assess the effects of post-colonization processes (i.e. growth and survival) on larval presence and abundance. Three species within the family Libellulidae, that occur across the shaded/unshaded gradient of canopy cover (McCauley et al.,

2008), were placed in cages made of insect screening within mesocosms and monitored for survival and growth (measured as head width, a standard metric of larval odonate size). Growth was calculated as ln((final–initial head width) + 1) divided by the number of days of each trial (e.g. McCauley, 2005b).

For the first trial, larval *Leucorrhinia intacta* were collected in September 2014 from Dufferin Pond at KSR and caged in the 20 mesocosms from the natural canopy experiment (under levels of 31–96% natural canopy cover). Across this performance trial, the mesocosms under 30–40 and 55–60% canopy cover had warmer water temperatures (10.5 ± 0.1 and $10.1 \pm 0.1°C$, respectively) than the mesocosms under 70–75 and 90–100% canopy cover (8.9 ± 0.1 and $9.0 \pm 0.1°C$, respectively; Kruskal–Wallis rank sum test, $\chi_3^2 = 144$, $P < 0.001$; $P < 0.001$ for all significant pairwise comparisons based on a Nemenyi post hoc test). Three cages containing *L. intacta* were placed in each mesocosm. One cage, which was approximately 89 cm × 75 cm in size with a plastic colander and dowels providing structural support within the cage, and which contained two pieces of artificial vegetation ranging between 10 and 20 cm long, held five larvae. The remaining two cages, which were approximately 25 cm × 25 cm in size with support provided by PVC piping with screening on one end, and which contained one piece of artificial vegetation, contained a single larva each. Larvae were checked biweekly for survival and photographed over a 5-week period from September to November 2014. Afterwards, head widths were measured from these photographs in ImageJ (version 1.46r; Schneider et al., 2012). For the cages containing five individuals, average growth was calculated. This value was then taken with the growth of individuals to determine average growth for each mesocosm. Growth across canopy cover levels was tested using a one-sided Wilcoxon signed-rank test.

A second experiment on larval performance was conducted in the summer of 2015 when water temperatures were warmer, to test for differences in survival and growth at the extremes of natural canopy cover (31–37 and 90–96%), which were shown to have different water chemistry conditions (Fig. S2). Across these performance trials, the five mesocosms under open canopy had warmer average water temperatures ($26.1 \pm 0.3°C$) than the five closed canopy mesocosms ($18.0 \pm 0.3°C$; Wilcoxon rank-sum test,

$W = 2500$, $P < 0.001$), a pattern also observed among natural ponds that vary in canopy cover levels (Werner & Glennemeier, 1999; Skelly et al., 2002). *Sympetrum* hybrids (i.e. combinations of *Sympetrum obtrusum*, *Sympetrum rubicundulum*, and possibly *Sympetrum internum*, which can all hybridize; Catling, 2007), which are found in more temporary ponds (McCauley et al., 2008), were collected in May–June 2015 from Dufferin Pond and placed in mesocosms. Larvae were checked weekly for survival and their head widths measured using digital calipers over a 4-week period from June to July 2015. *Sympetrum vicinum*, which occur across a wide range of pond permanence levels (McCauley et al., 2008), were collected in July 2015 from Gazebo Pond and placed in mesocosms. Larvae were checked weekly for survival and their head widths measured over a 4-week period from July to August 2015. In these two trials, three 25 cm × 25 cm cages, containing one larva each, were placed in a total of 10 mesocosms. Water temperatures were measured at the mesocosm bottoms within the hours of 15h00–17h30. The number of days between the beginning of the experiment and the date when larvae began their eclosion process (i.e. emergence time) was also recorded. We tested for differences in growth using Wilcoxon rank-sum tests, and differences in emergence times using two sample *t* tests, between open (31–37% canopy) and closed (90–96% canopy) mesocosms for each species. Growth across canopy cover levels was tested using one-sided Wilcoxon signed-rank tests.

Results

Across experiments, adult dragonflies showed strong habitat selection responses to canopy cover and shading. However, these conditions had no effect on larval presence, abundance, or performance.

Artificial shading experiment

In the artificial shading experiment, the nearest source pond had 11 species present over the course of the experiment, with all 11 observed in the experimental area, but only six species visiting the mesocosms (Table S3). Mesocosm conditions are summarized in Table S4. Of the individuals visiting the mesocosms ($N = 23$), 11 were male, 4 were female, 6 were female

or teneral (juveniles in which sex cannot be definitively determined, as females and male tenerals share similar colouring), and the sex of 2 could not be identified. Five individuals dipped, 16 perched, and 2 individuals did both at mesocosms. Under artificial shading (50% shade cloth), the mean number of adult visits per mesocosm was 28% lower than at open canopy mesocosms ($P = 0.008$; Fig. 3a, Table 1). However, shading only marginally lowered the species richness of visitors ($P = 0.08$; Table 1). Heating did not affect visitor abundance or species richness (Table 1).

Only three species of larvae (Libellulidae) were found within the mesocosms compared to six species of adults visiting the mesocosms. *Libellula pulchella* larvae were found in all 20 mesocosms, *Libellula luctuosa* larvae were found in 17 mesocosms, and *Tramea lacerata* were found in 2 mesocosms. Heating and shading treatments did not affect larval abundance (Fig. 3b), richness, or diversity ($P > 0.1$ in all cases; Table 1). Prey density was not related to larval abundance ($P = 0.08$; Table 1).

Natural canopy experiment

In the natural canopy experiment, we observed eight species at the nearest source pond over the course of the experiment, 10 species in the experimental area where mesocosms were located, and six species visiting the mesocosms (Table S3). Mesocosm conditions are summarized in Table S5. Of the individuals visiting the mesocosms ($N = 39$), 13 were male, 2 were female, 2 were female or teneral, and 4 were mating pairs (where 1 pair = 1 visit). The sex of 18 *Aeshna* individuals could not be determined. Three individuals dipped, 23 hovered, 11 perched, and 2 individuals both hovered and perched at mesocosms. In this experiment, an increase in natural canopy cover was associated with a significant decrease in the number of adult visits per mesocosm ($P = 0.001$; Fig. 4a, Table 2) and a decrease in the species richness of visitors ($P = 0.03$; Table 2).

Libellula pulchella larvae were found in 6 of the 20 experimental mesocosms, across a range of 34.5–89.9% canopy cover (Table S5). No other species of larvae were found in the mesocosms. Natural canopy cover was not associated with larval presence ($P = 0.4$) or abundance ($P = 0.8$; Fig. 4b,
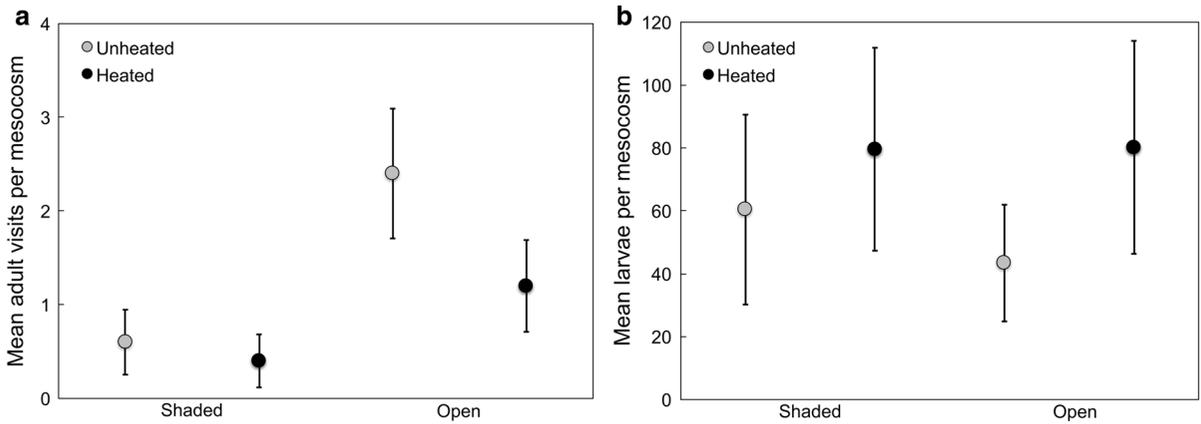
Fig. 3 a Mean number of visits (± 1 SE) by adult dragonflies and **b** mean abundance of larvae per mesocosm, based on a fully factorial design of no heating (grey circle) and heating (black circle), and shaded and open treatments. Open treatments had more adult visits than shaded treatments ($P = 0.008$), but no differences were found between temperature treatments or in larval responses

Table 1 Statistical test results for the artificial shading experiments

Variables	Response	Mean present | absent	Estimate	Standard error	z value	P value
Shading	Adult abundance	0.5 | 1.8	− 1	0.5	− 3	0.008
Heating		0.8 | 1.5	− 0.6	0.4	− 1	0.2
Shading	Adult richness	0.5 | 1.2	− 0.9	0.5	− 2	0.08
Heating		0.7 | 1	− 0.3	0.5	− 0.7	0.5
Shading	Larval abundance	70 | 62	0.03	0.5	0.06	1
Heating		80 | 52	0.5	0.5	1	0.3
Prey density	Larval abundance	n/a	− 3	2	− 2	0.08
Shading	Larval diversity	0.4 | 0.4	0.05	0.1	$t = 0.5$	0.6
Heating		0.5 | 0.3	0.2	0.1	$t = 1$	0.1
Shading	Larval richness	1.6 | 1.6	< 0.001	0.4	0	1
Heating		1.8 | 1.4	0.3	0.4	0.7	0.5

Each test was conducted using a GLMM, with 20 observations per test

Table 2). Prey density was not significantly related to larval abundance ($P = 0.3$; Table 2).

Larval performance experiments

There were no effects of canopy cover on larval survival in any species. There was no mortality of caged *L. intacta* larvae (138/139 survived: one individual was accidentally crushed by the PVC structure). There was no growth observed in the larvae in these trials ($P = 1$; Table 3), likely due to the colder seasonal temperatures. In the *S. vicinum* trials, all individuals survived the larval period ($N = 30$), whereas in the *Sympetrum* hybrid trials ($N = 29$), 27 individuals survived the larval period, and 2 individuals died (in mesocosms with 91.9% and 94.5% canopy cover). Both *Sympetrum* hybrids and *S. vicinum* exhibited growth across treatments ($P < 0.001$ and $P = 0.01$, respectively; Table 3), but no differential growth between open and closed canopy conditions ($P > 0.4$ in both cases; Table 3). The *Sympetrum* hybrids reached emergence faster in open mesocosms ($P = 0.03$; Table 3); however, there was no difference among treatments for *S. vicinum* individuals ($P = 0.8$; Table 3).
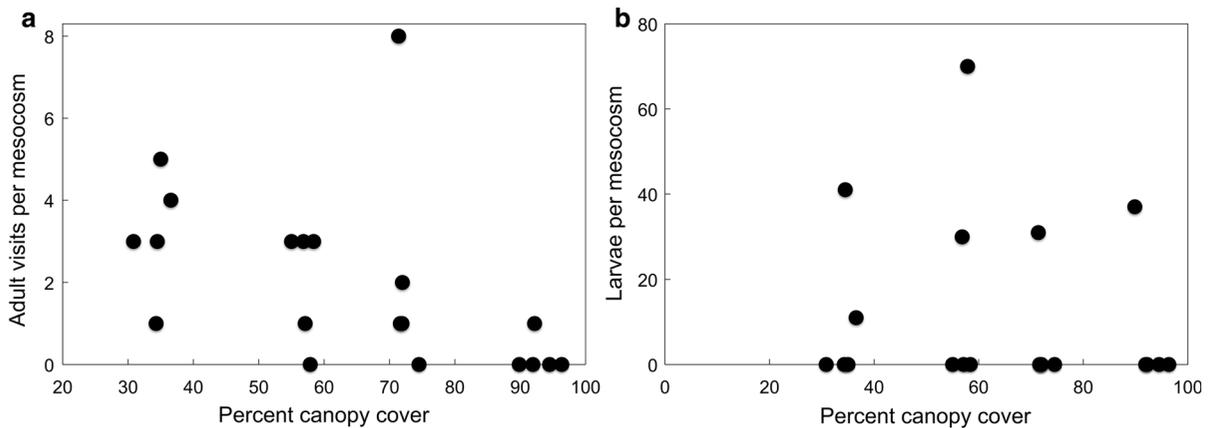
Fig. 4 With an increase in natural canopy cover, **a** the total number of adult visits per mesocosm decreased ($P = 0.001$), whereas **b** larval abundances per mesocosm were unaffected

Table 2 Statistical test results for the natural canopy experiments

Variables	Response	Estimate	Standard error	z value	P value
Canopy	Adult abundance	-0.03	0.008	-3	0.001
Canopy	Adult richness	-0.02	0.01	-2	0.03
Canopy	Larval abundance	-0.01	0.04	-0.3	0.8
Prey density	Larval abundance	-12	11	-1	0.3
Canopy	Larval presence	-0.03	0.03	-0.9	0.4

Each test was conducted using a GLMM, with 20 observations per test

Table 3 Statistical test results for the larval performance experiments, using Wilcoxon signed-rank tests (V), rank-sum tests (W), and two sample t tests

Species	N	Response	Mean ± standard error open/closed	Test statistic	P value
Leucorrhinia intacta	20	Growth	$-3 \pm 2 \times 10^{-3}$ mm day^{-1}	$V = 48$	1
Sympetrum hybrids	10	Growth	$8 \pm 2 \times 10^{-3}$ mm day^{-1}	$V = 55$	$P < 0.001$
		Differential growth	$10 \pm 3 \times 10^{-3}$ mm day^{-1}/ $6 \pm 2 \times 10^{-3}$ mm day^{-1}	$W = 17$	0.4
		Time to emergence	17 ± 2 days/21 ± 1 day	$t = -3$	0.03
Sympetrum vicinum	10	Growth	$0.3 \pm 0.1 \times 10^{-3}$ mm day^{-1}	$V = 28$	0.01
		Differential growth	$0.4 \pm 0.3 \times 10^{-3}$ mm day^{-1}/ $0.2 \pm 0.1 \times 10^{-3}$ mm day^{-1}	$W = 14$	0.8
		Time to emergence	18 ± 2 days/19 ± 3 days	$t = -0.3$	0.8

Means were taken across cages within each mesocosm. For *Leucorrhinia* individuals, responses were tested across four levels of canopy cover. For *Sympetrum* individuals, responses were tested under open (30–40%) and closed (90–100%) canopy cover

Discussion

Across all experiments, shading and natural canopy cover were associated with sharp decreases in the number of visits to mesocosms by adult dragonflies. In our first study, when light hitting the mesocosms was blocked by artificial shade (50% shade cloth), there were fewer adult visits to mesocosms than when mesocosms were exposed to full sun and covered with an open weave canopy (Fig. 3a). In the natural canopy experiment, both the number (Fig. 4a) and species richness of adult visitors decreased with increasing canopy cover. Canopy cover was not consistently a strong predictor of patterns of larval abundance or

diversity, nor did the number of adult visits seem to predict larval patterns. The small size of our mesocosms, which was necessary to accommodate mesocosms in our heating arrays and under higher canopy cover levels, may have limited reproduction at the mesocosms and/or the larval carrying capacity of our mesocosms, restricting our ability to detect the effects of these treatments on larval assemblages. However, small natural pond habitats (0–1 ha) can be very common across terrestrial landscapes (Semlitsch & Bodie, 1998), and the results from our mesocosms are likely to be predictive of patterns in these habitats which have lower abundances and species richness with higher levels of shading (McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data). Additionally, our experiments ran for one field season each and it is possible that larval patterns take longer to emerge. In a previous 2-year study with mesocosms situated under open and closed canopy conditions (22 and 7 mesocosms, respectively), adult dragonfly arrivals predicted larval dragonfly assemblages for open canopy mesocosms (McCauley, 2006, 2007). In that experiment, adults were not monitored at closed canopy mesocosms. However, larval insects following adult colonization were monitored the same way in both open and closed canopy mesocosms, and the probability of a closed canopy mesocosm having larvae was significantly lower than for mesocosms under open canopy (i.e. across 2 years, no larvae were found in closed canopy mesocosms versus the 11,270 dragonfly larvae collected from open canopy mesocosms; McCauley, 2005a). These results suggest that our own results based on adult visitors would likely translate into effects on larval assemblages over longer time periods. Indeed, adult visits are a pre-requisite for larval presence in ponds and occur before environmental filters affecting the persistence of colonists and/or species-sorting can act to structure larval assemblages (e.g. Fig. 1). But the sampling of both adult visitors and larval presence is imperative to understand dragonfly distributions, as the sampling of only one of these communities may not accurately reflect the presence or absence of the other (e.g. Luke et al., 2017). The observed patterns of adult habitat selection at these small experimental habitats likely play a role in structuring larval dragonfly assemblages at a larger scale (see Fig. S3).

Our performance trials, which assessed the effects of canopy cover on the larvae of 3 species, suggest that closed canopy habitats have conditions suitable for larval dragonflies. We found that larval survival and growth were equivalent across the canopy gradient in these species, suggesting that post-colonization processes are less important for determining previously observed patterns of decreased abundance and diversity with increasing canopy cover (McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data). One caveat here is that we explored these effects during summer and fall, which are critical periods for larval dragonfly survival and growth, but are not the only time periods during which environmental conditions could act as a filter to decrease abundances and diversity within larval assemblages. In particular, winter conditions may differ across the canopy gradient and result in differential survival of larvae in open versus closed canopy ponds.

Taken together, these results suggest that adult attraction to closed canopy habitats is limited, but if these habitats are located, adults can and do successfully breed, and their larvae perform well, in these environments. This provides support for the hypothesis that previously observed patterns of lower diversity and abundance of larval dragonflies in closed canopy ponds—specifically those in temperate regions which experience greater solar incidence and reflection than tropical regions—are related at least in part to limited attraction of adults to these environments. Canopy cover could obscure ponds and decrease their detection by the highly visual adults: directly, and by changing the availability of light cues from pond surfaces. Adult dragonflies can detect horizontally polarized light (Meyer & Labhart, 1993; Horváth, 1995), which they use as a visual cue to detect oviposition sites (Wildermuth, 1998; Bernáth et al., 2002; Kriska et al., 2009). Sunlight reflected from a water surface becomes horizontally polarized, but a lower incidence of sunlight reaching aquatic habitats under a closed canopy would result in less polarized light, potentially decreasing the detection of closed canopy habitats by adult dragonflies.

Adult habitat selection has been demonstrated in other taxa. For example, 8 species of migratory birds (Passeriformes) select nesting sites with no predators in order to improve offspring survival (Fontaine & Martin, 2006). Adult habitat selection decisions, however, do not always clearly relate to offspring performance. In the pine processionary moth, *Thaumetopoea pityocampa* (Thaumetopoeidae),

female adults that are expanding their ranges will oviposit on plants that do not improve larval performance (i.e. growth and survival), possibly due to an evolved specialization for a specific host plant in its native range (Stastny et al., 2006). Previous work in freshwater systems has found evidence of habitat selection across a canopy cover gradient in other taxa. At least one species of aquatic beetle selects habitat based on canopy cover, laying eggs in open but not closed canopy mesocosms (Binckley & Resetarits, 2009). However, other beetle species were either segregated across a canopy cover gradient, only colonizing mesocosms in open canopy or closed canopy conditions, or were generalists, occupying both (Binckley & Resetarits, 2009). This suggests that canopy cover can impact several members of aquatic communities. These choices can vary, however, among species, and without information on offspring performance, it is unclear how adult habitat selection drives larval distributions (e.g. beetles; Binckley & Resetarits, 2009).

In our study, adult habitat selection appeared to be a better predictor of previously documented natural patterns of larval dragonfly distributions across a canopy gradient (McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data) than species-sorting mechanisms, as larval performance remained consistent across increasing levels of canopy in our experiments. Adult habitat selection across the canopy gradient appeared to be unrelated to the quality of these habitats for larvae, at least within the levels of canopy cover examined. Instead, adults may avoid closed canopy habitats based on visual limitations (i.e. minimal amount of reflected polarized light; Wildermuth, 1998). Dragonflies detect surfaces that reflect horizontally polarized light through photoreceptors in their compound eyes (Meyer & Labhart, 1993; Horváth, 1995). Many taxa use polarized light as a visual cue to orient themselves towards potential habitats, as is the case for many insects with aquatic larval stages (Kriska et al., 2009), and possibly some amphibian and reptile species (Vitt & Caldwell, 2014). Different dragonfly species may also be attracted to aquatic habitats with varying levels of polarized light (Bernáth et al., 2002; Horváth et al., 2007). For our study, we generated rough estimates of reflected polarized light intensity off the mesocosms, which were collinear with canopy cover and thus not included in our analysis but which provided similar results (French & McCauley, unpublished data). Variation in the polarized light reflected from the surface of a pond may therefore be a key mechanism in structuring larval dragonfly assemblages, as species may colonize habitats across a gradient of polarized light, generated by differences in canopy cover. The selection of habitats by dragonflies may also be hierarchical in terms of choosing habitats in a landscape based on their perceptibility, and from making these large-scale decisions based on general polarized light cues to making site-level evaluations and microhabitat choices.

On a global scale, dragonflies have demonstrated species-specific responses to the presence of canopy cover over aquatic habitats. In tropical regions, the adults of some dragonfly species are very shade-tolerant (e.g. in Mayotte; Samways, 2003), whereas others thrive when [invasive] tree species are removed (e.g. in South Africa; Smith et al., 2007; Samways & Sharratt, 2010) or in urbanized habitats with little canopy cover (e.g. in Brazil; Monteiro-Júnior et al., 2014). Similarly, larval and adult dragonflies in Borneo have demonstrated species-specific distributions in response to gradients of forest, oil palm, and riparian cover (Dolný et al., 2012; Luke et al., 2017). In addition, lentic (standing waters) and lotic (moving waters) attract different assemblages of dragonflies, which may be influenced differently by surrounding tree cover (Balzan, 2012; Dolný et al., 2012; Ball-Damerow et al., 2014). As such, conservation initiatives centred around dragonfly and other invertebrate species should take careful consideration of species-specific tolerances to canopy cover across habitats and regions.

Forest regrowth is a valuable landscape change but can dramatically reshape communities. Secondary forests, which can dominate a landscape following agricultural abandonment (Bellemare et al., 2002), support structurally dissimilar terrestrial communities in comparison to primary forests (Foster et al., 1998), which could differentially impact aquatic communities. In the context of more temperate regions, less canopy cover at lentic habitats may be more favourable for the management or restoration of macroinvertebrate communities (e.g. Batzer et al., 2004). However, the complete removal of canopy cover in these areas is not necessarily warranted, as adult dragonflies still arrive and larvae still persist at habitats with low levels of canopy (e.g. McCauley,

2005a; Remsburg et al., 2008), and other taxa use shaded ponds (e.g. Skelly et al., 2002; Earl & Semlitsch, 2013). Instead, a mix of open and closed canopy cover over habitats in restored and/or managed landscapes may improve regional diversity. Understanding the impacts of both open and closed canopy conditions on communities is essential to inform management decisions about whether to maintain open or closed canopy at a habitat, including considerations of the type of habitat (e.g. lotic or lentic systems) and the history of local habitat conditions (e.g. persisting effects of historical land use; Bellemare et al., 2002). Other regional environmental factors, such as landscape type between habitats, may also play a role in maintaining connectivity among aquatic habitats, and therefore must be considered in conjunction with local factors.

Conclusion

Our results help to distinguish the mechanisms driving dragonfly distributions across an important environmental gradient, canopy cover. Habitat selection and species-sorting are difficult to separate, especially across aquatic and terrestrial environments (Vanschoenwinkel et al., 2010), and are generally inferred from patterns of species distributions (Binckley & Resetarits, 2005). Widespread forest regrowth across mid-latitudinal North America following agricultural abandonment is modifying both aquatic and terrestrial systems (Foster et al., 1998). Since forests may impact habitat colonization, understanding how habitat selection behaviour interacts with dispersal and spatial connectivity in patchy habitats can provide insight into how these processes determine community structure across aquatic habitats.

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Electronic Supplementary Material

Title: Canopy cover affects habitat selection by adult dragonflies

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Online Resource 1

Fig. S1

Mesocosms with closed and open canopy structure. The solid green material generated 50% canopy cover, whereas the more open green material was an open canopy structure, creating no shade on the mesocosms. The open canopy structures created similar structural barriers for flying dragonflies as the shade structures, and served as a sham treatment to control for the effects of the structures without the effects of shading. The mesocosms were covered with white netting pre-experiment to prevent colonization by dragonflies or other aquatic animals. This netting was removed when the experiment started
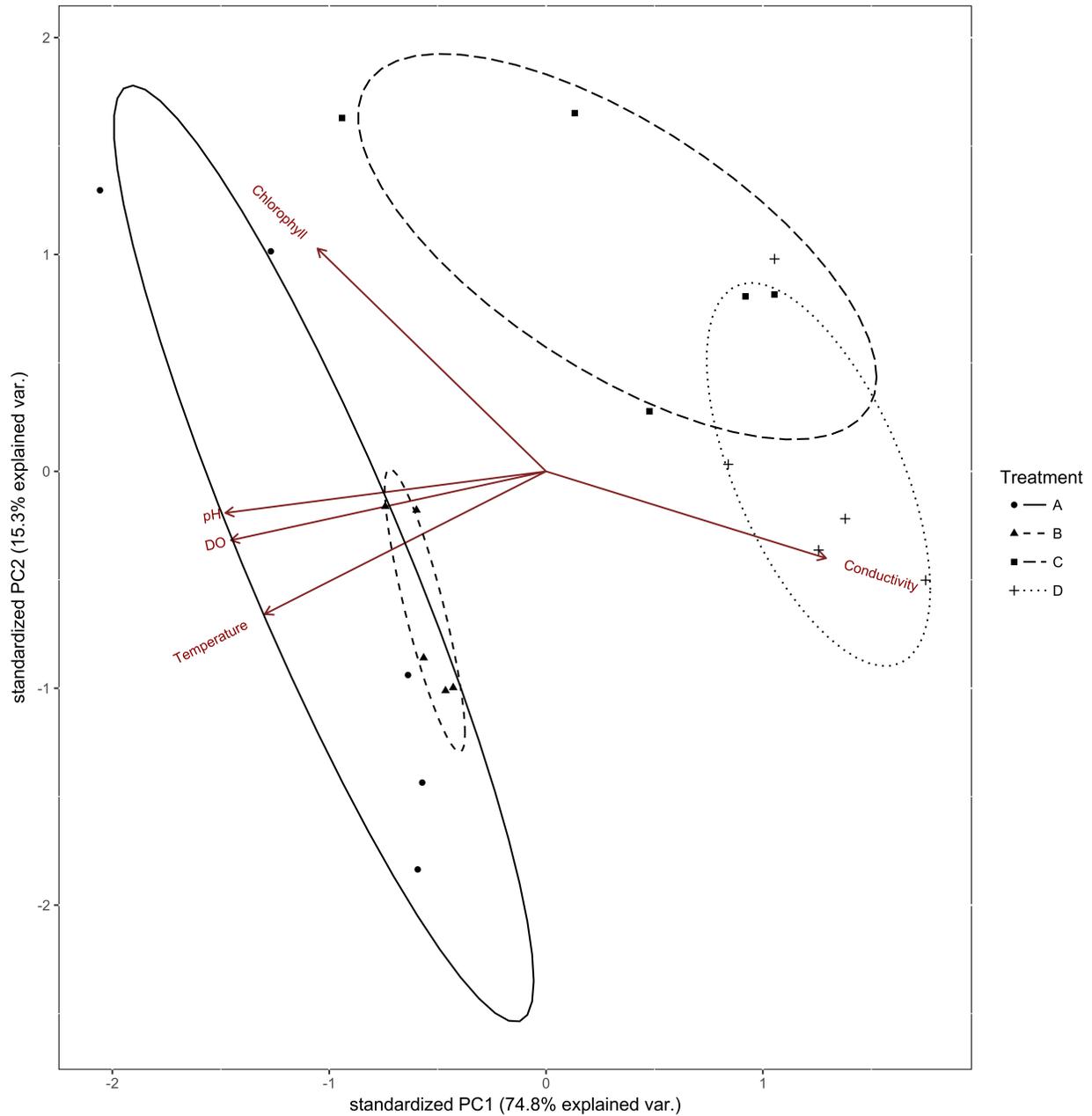
Fig. S2

Component scores of 20 mesocosms from a principal component analysis of water chemistry variables (dissolved oxygen, pH, conductivity, chlorophyll, and water temperature), grouped by canopy cover level (A: 30–40, B: 55–60, C: 70–75, and D: 90–100%). Only PC1 was retained for further analysis, however both PC1 and PC2 are shown for better visualization
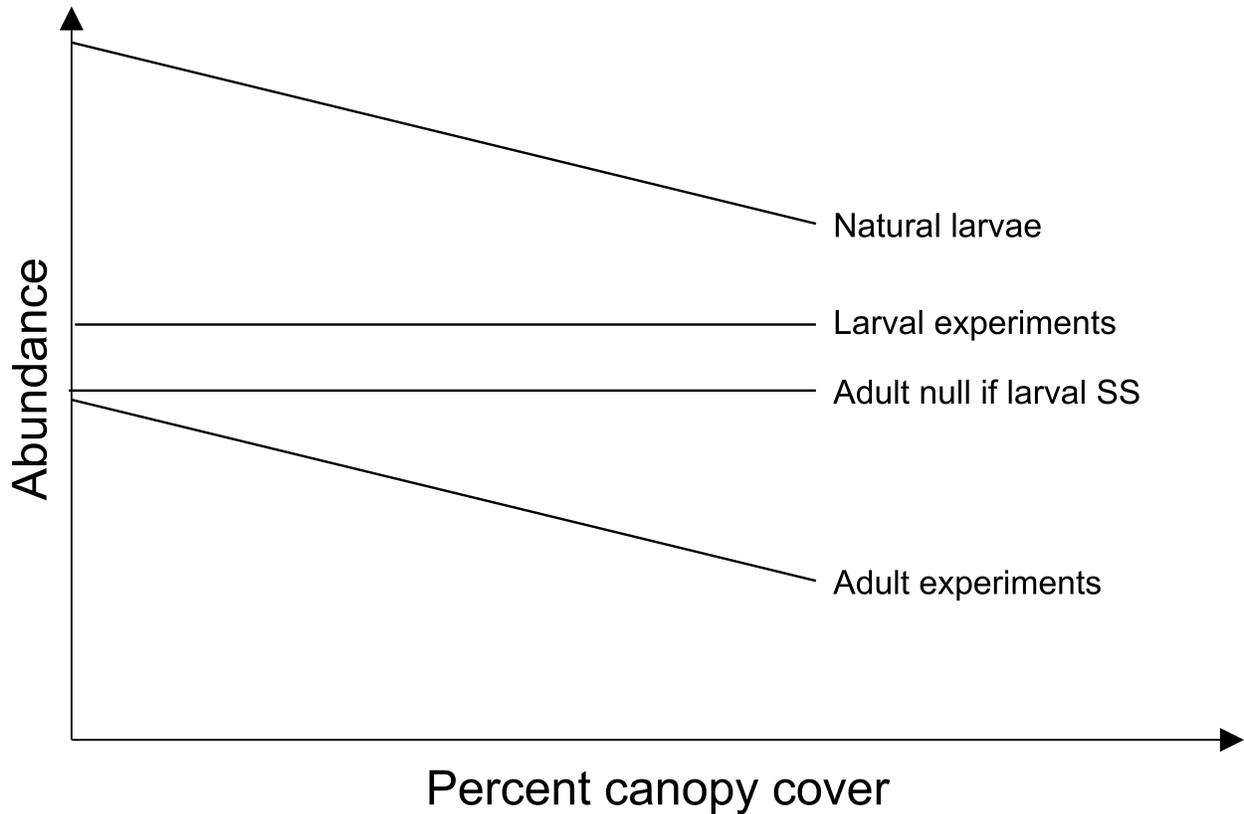
Fig. S3

Patterns of expected and observed larval and adult abundances, at the Edwin S. George Reserve and in our experiments at the Koffler Scientific Reserve. We see natural patterns of decreasing larval abundance at ESGR with an increase in percent canopy cover (Natural larvae; McCauley, 2005a; McCauley et al., 2008; Werner et al., unpublished data). If this decrease were due to species-sorting, we would expect a consistent number of adult visits across canopy conditions (Adult null if larval SS). Instead, we observed a decrease in adult visits to mesocosms across the canopy gradient (Adult experiments), and did not witness any changes in larval abundance or survival across this gradient (Larval experiments). Therefore, we expect that habitat selection is a strong driver of larval dragonfly distributions

Table S1

Loadings of the first principal component axis that explained 75% of the variance among mesocosms for the natural canopy experiments

Variable	Component 1
Dissolved oxygen	-0.491
pH	-0.500
Conductivity	0.436
Chlorophyll	-0.356
Temperature	-0.438

Table S2

Tukey's test results for all pairwise comparisons from a one-way ANOVA comparing water chemistry variables to canopy cover. The ANOVA was conducted on differences in PC1 scores of water chemistry variables (dissolved oxygen, pH, conductivity, chlorophyll, and water temperature) from a principal component analysis, among groupings of canopy cover (30–40, 55–60, 70–75, and 90–100%). The standard error in all cases was 0.7

Canopy cover grouping (%)	Canopy cover grouping (%)	Estimate	t value	P value
	55–60	0.9	1	0.5
30–40	70–75	3	4	0.006
	90–100	4	7	$P < 0.001$
	70–75	2	3	0.09
55–60	90–100	4	5	$P < 0.001$
70–75	90–100	2	3	0.07

Table S3

Species of adult dragonflies that visited the source pond, experimental area, and mesocosms during the colonizing experiments. Author information was obtained from the Michigan Odonata Survey (michodonata.org)

Experiment	Source pond	Experimental area	Mesocosms
Artificial shading	*Aeshna* sp. (Fabricius 1775)	*Aeshna* sp.	*L. luctuosa*
	Anax junius (Drury 1773)	*A. junius*	*L. pulchella*
	Celethemis elisa (Hagen 1861)	*C. elisa*	*P. longipennis*
	Erythemis simplicicollis (Say 1839)	*E. simplicicollis*	*P. lydia*
	Libellula luctuosa (Burmeister 1839)	*L. luctuosa*	*S. obtrusum*
	Libellula pulchella (Drury 1773)	*L. pulchella*	*S. vicinum*
	Pachydiplax longipennis (Burmeister 1839)	*P. longipennis*	
	Plathemis lydia (Drury 1773)	*P. lydia*	
	Sympetrum obtrusum (Hagen 1867)	*S. obtrusum*	
	Sympetrum vicinum (Hagen 1861)	*S. vicinum*	
	Tramea lacerata (Hagen 1861)	*T. lacerata*	
Natural canopy	*Aeshna* sp.	*Aeshna* sp.	*Aeshna* sp.
	Anax junius	*A. junius*	*L. luctuosa*
	Celethemis elisa	*Leucorrhinia intacta* (Hagen 1861)	*L. pulchella*
	Libellula luctuosa	*L. luctuosa*	*P. lydia*
	Libellula pulchella	*L. pulchella*	*S. obtrusum*
	Pachydiplax longipennis	*P. longipennis*	*S. vicinum*
	Sympetrum obtrusum	*P. lydia*	
	Sympetrum vicinum	*S. obtrusum*	
		S. vicinum	
		Tramea lacerata or *Pantala* sp. (Hagen 1861)	

Table S4

Mesocosm conditions during the artificial shading experiment. For the control treatment, shading and heating were not artificially manipulated. Values indicate means (± 1 SE) for each treatment

Treatment	Mesocosm temperature (°C)	Turbidity (% transmission)	Prey density (individuals mL^{-1})	Polarized light (μmol m^{-2} s^{-1})
Control	23.3 ± 0.2	99.7 ± 0.9	0.3 ± 0.1	1.3 ± 0.2
Heated	26.6 ± 0.1	96.7 ± 0.9	0.3 ± 0.1	1.3 ± 0.2
Shaded	22.7 ± 0.2	99.2 ± 0.6	0.2 ± 0.1	0.9 ± 0.1
Shaded plus heated	26.0 ± 0.1	97.7 ± 0.7	0.3 ± 0	0.9 ± 0.1

Table S5

Mesocosm conditions during the natural canopy experiment. Values indicate means (± 1 SE) for each treatment

Canopy cover (%)	Mesocosm temperature (°C)	Turbidity (NTU)	Prey density (individuals mL^{-1})	Chlorophyll ($\mu g\ L^{-1}$)	Distance (m)	Elevation (m)
34 ± 0.9	21.5 ± 0.1	1.1 ± 0.3	0.09 ± 0.03	20 ± 7	133 ± 7	281 ± 3
57 ± 0.6	20.5 ± 0.8	1 ± 0	0.06 ± 0.03	13 ± 2	135 ± 8	282 ± 2
72 ± 0.6	16.9 ± 0.4	0.9 ± 0.1	0.2 ± 0.1	17 ± 4	138 ± 7	283 ± 2
93 ± 1	15.9 ± 0.5	0.4 ± 0.1	0.3 ± 0.3	6 ± 3	137 ± 8	283 ± 2

Canopy cover (%)	pH	Polarized light ($\mu mol\ m^{-2}\ s^{-1}$)	Conductivity ($\mu S\ cm^{-1}$)	Dissolved oxygen ($mg\ L^{-1}$)	Adult abundance	Larval abundance
34 ± 0.9	8.4 ± 0.1	28 ± 1	265 ± 12	9.8 ± 0.3	3 ± 0.7	10 ± 8
57 ± 0.6	8.2 ± 0	23 ± 4	270 ± 10	9.2 ± 0.1	2 ± 0.6	20 ± 14
72 ± 0.6	7.9 ± 0.1	10 ± 3	275 ± 13	7.2 ± 0.8	2 ± 1.4	6 ± 6
93 ± 1	7.7 ± 0	3 ± 0.6	329 ± 12	6.3 ± 0.3	0.2 ± 0.2	7 ± 7