



Shifts in dragonfly community structure across aquatic ecotones

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Dragonflies (Odonata: Anisoptera) are often used as indicators of habitat type and quality due to their varied use of aquatic and terrestrial habitats. Species differ in their preferences for lotic and lentic waters, but community changes across ecotones, or transitional zones between distinct habitats (e.g. lotic and lentic), are not well understood. We quantified dragonfly species richness, abundance, and composition along a gradient of habitat types, including streams, stream mouths (ecotones), and open waters (lakes and ponds). We tested if dragonfly assemblages in aquatic ecotones differ from adjacent stream and open water habitats, and how species respond to riparian forest cover across these habitat types. Adult dragonflies were sampled in all habitat types at four sites in southwest Ohio during the summer of 2016. Riparian canopy cover and relative densities of algal mats and emergent vegetation were recorded. We sampled 157 individuals of 12 dragonfly species and found significant differences in community composition between stream and ecotone habitats, both forming subsets of the open water community. Canopy cover explained 55% and 75% of abundance and species richness variance across habitat types, respectively, but these relationships were strongest at ecotones. Finally, the Odonata Index of Wetland Integrity (OIWI), which uses sensitivities of adult odonates to habitat disturbances to evaluate wetland conditions, showed that species composition at ecotones uniquely represents the ecological integrity of the entire wetland system. Thus, transition zones may provide an effective and more efficient alternative to rapidly assess wetland quality for conservation monitoring than sampling the entire wetland.

Keywords: ecotone; Odonata; biotic index; canopy cover; riparian habitats

Introduction

Dragonflies (Odonata: Anisoptera) are often used as indicator taxa for rapid ecological assessments due to their unique life-history features and diverse habitat requirements (Chovanec, Waringer, Raab, & Laister, 2004; Córdoba-Aguilar, 2008; Golfieri, Hardersen, Maiolini, & Surian, 2016). Species use aquatic and terrestrial habitats differently based on the needs of larval and adult life stages. Moreover, terrestrial and aquatic resource requirements associated with life cycle stages dictate which dragonfly species can successfully inhabit a given body of water as larvae and the surrounding riparian zone as adults (Corbet & Brooks, 2008). For example, shade associated with canopy cover is a primary factor in structuring dragonfly assemblages (Clark & Samways, 1996; Clausnitzer, 2003). Too much shade reduces water temperatures and may delay dragonfly larval development (Corbet & Brooks, 2008; Samways, Sharratt, & Simaika, 2011). In addition, a lack of sunlight reduces algae and macrophytes that harbor prey, hide larvae, and are used for oviposition (Corbet & Brooks, 2008; Foote & Hornung, 2005; Kietzka, Pryke, Samways,

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Leather, & Sahlen, 2015; Richardson & Baker, 1997; Thornhill, Batty, Death, Friberg, & Ledger, 2017). As dragonflies are ectothermic, adults also require shade for thermoregulation, especially on hot days (Clausnitzer, 2003; Corbet & Brooks, 2008; Ball-Damerow, M'Gonigle, & Resh, 2014). In addition to their habitat tolerances, the ecological role of dragonflies as predators may reflect trophic responses to disturbance and water quality (Thornhill et al., 2017), making them useful for ecological and conservation monitoring (Foote & Hornung, 2005).

Dragonfly larvae and adults reflect different attributes of stream, lake, and riparian habitats. Immobile odonate larvae may more precisely indicate water quality of a specific location (Valente-Neto, Roque, Rodrigues, Juen, & Swan, 2016), but larvae often lack morphological features needed for field identification (Golfieri et al., 2016; Smith, Samways, & Taylor, 2007). Adult dragonflies are representative of both aquatic and terrestrial conditions, are easily identified in the field, and can be surveyed quickly along transects (Golfieri et al., 2016). Adults require a mixture of direct sunlight and shade within proximity of the water to perch and thermoregulate (Corbet & Brooks, 2008; Remsburg, Olson, & Samways, 2008). Terrestrial vegetation structure is also needed to support adequate prey populations for adult dragonflies (Córdoba-Aguilar, 2008). Therefore, it is not surprising that recently developed indices that assess wetland health (e.g. Dragonfly Biotic Index (Simaika & Samways, 2009), Odonata Index of Wetland Integrity (OIWI) (Kutcher & Bried, 2014), and Dragonfly Association Index (Chovanec, Schindler, Waringer, & Wimmer, 2015)) are in part or exclusively focused on adult dragonflies (Golfieri et al., 2016).

Despite the success of adult dragonflies serving as indicators of ecosystem structure and function, recent research suggests potential limitations of sampling scale. For example, dragonflies are often classified as shade or sun and lotic (moving-water) or lentic (still-water) species (Clausnitzer, 2003), but these environmental conditions vary along gradients of riparian forest, wetland, and stream habitats (Sparks, 1995). Due to individual species responses to small-scale environmental changes, dragonfly assemblages may differ among habitat types (Smith et al., 2007), including the transitional zones (i.e. ecotones) between them (Chessman, 1995; Batzer, 1996). Such differences may limit their value in management decisions if the sampled species composition is not representative of the larger wetland system. Research addressing adult dragonfly composition among water body types within forested floodplain systems is growing, and some indices incorporate variation along environmental gradients (i.e. Odonata Habitat Index) (Chovanec & Waringer, 2001). However, their general application to other regions is still limited (Golfieri et al., 2016) due to strong and variable responses of dragonfly communities to habitat structure adjacent to water bodies (Smith et al., 2007) and the inability to verify residential breeding populations without sampling larvae or exuviae (Kutcher & Bried, 2014; May, 2012). Studies comparing composition of adult dragonfly communities and their responses to environmental factors (i.e. canopy cover, oviposition substrate availability) among water body types will help to generalize patterns of dragonfly diversity and composition useful in monitoring and conservation assessments.

Here, we studied adult dragonfly communities associated with streams, lakes, and the ecotones between them. We hypothesized that dragonfly communities would shift along habitat gradients from streams to lakes due to changes in riparian forest cover and emergent vegetation. These aspects of vegetation structure reflect changes in water flow from fast-moving to slow-moving, to still water (Foote & Hornung, 2005). Since lotic and lentic bodies contain different dragonfly assemblages, we expected that ecotones would exhibit biotic and abiotic properties of both water body types and predicted ecotones to demonstrate the highest dragonfly species richness across habitat types. Furthermore, nutrients and other deposits from lotic waters (runoff) may increase the quantity of resources such as aquatic vegetation in shallow waters associated with ecotones (Blann, Anderson, Sands, & Vondracek, 2009). Therefore, we also predicted that dragonfly abundance would be higher in ecotones due to greater amounts of aquatic vegetation that dragonflies need for oviposition larval development. Finally, since we expected environmental and dragonfly

community complexity to be greatest at ecotones, we predicted that the conservation interpretation using the Odonata Index of Wetland Integrity (OIWI) at ecotones would be representative of the larger wetland system.

Materials and methods

Site selection and design

Four sites were established, each consisting of a feeder stream flowing into a large water body. Three sites were located on Acton Lake in Hueston Woods State Park: to the east (39.5074°N, –84.7389°W), northeast (39.5860°N, –84.7537°W) and northwest (39.5835°N, –84.7634°W) of the lake. A fourth site was located at Western Pond (39.5017°N, –84.7273°W) on the property of Miami University. Three habitat types (stream, ecotone, open water) were demarcated at each site based on observed water flow and change in water body diameter (Appendix Figure A1). Streams were variable in width, depth, and flow rate, but all were heavily shaded with intermittent areas of sun exposure in a riparian setting. Ecotone habitats were transition zones of shade and sun, marked by slow-moving shallow water over silty alluvial deposits with small vegetated islands and increased macrophytes. Open water habitats consisted of steeper embankments ending in deeper water with little current.

To reduce the likelihood of within-generation movement of adult dragonflies among sites, we chose open water habitats that ranged between 0.75 and 9.65 km apart, with the closest pair of sites located on opposing sides of Acton Lake. In general, all sites were in the regional landscape of second growth deciduous forest, urbanization, and agriculture of southwestern Ohio. Since not all ecotones were of the same length, one transect was established within each habitat type such that ecotone transects were 200 m from stream and open water transects, with the exception of Western Pond, where the distance between transects was reduced to 75 m due to the small size of the pond. All non-ecotone transects other than those at Western Pond were 100 m as suggested in Chovanec and Waringer (2001). Only one side of the water's edge was sampled at each site based on accessibility.

Sampling

Adult dragonflies were observed (on the wing) for 15 min and sampled for one hour between 10:00am and 14:00pm using hand nets along transects within each habitat type and site once a week for four weeks (20 July to 25 August 2016). Environmental variables were measured during the last week of the study and included categorical estimates of aquatic algal mat and emergent vegetation density (none, < 50% (less dense), > 50% (more dense)) and quantitative estimates of percent canopy cover in the riparian zone. All sampling was conducted by the same individual for consistency. For each transect, vegetation densities were estimated by walking the entire transect and evaluating aquatic vegetation within ~3 m of the water's edge. Canopy cover was calculated using a point–intercept method along transects recording a hit or miss of canopy cover every 10 m for 100 m or the total length of the habitat type, for a maximum of 11 recorded points per habitat type per site.

Analysis

Dragonflies observed on the wing and netted were pooled to represent the total species richness and abundance. Linear mixed effects models were fitted using the lme4 package (Bates,

Maechler, Bolker, & Walker, 2015) in R programming language (R Core Team, 2016) with species richness or abundance as fixed effects and site as a random variable. Likelihood ratio tests were then performed on models with and without a habitat variable using *anova* function to determine if species richness or abundance were different among habitat types. Post-hoc Tukey contrasts with Bonferroni–Holm corrections for multiple comparisons in the multcomp package (Hothorn, Bretz, & Westfall, 2008) were conducted to determine significance of response differences between ecotone and stream, and ecotone and open water habitats. Z-scores are reported for significant results. Species accumulation curves from *vegan* package (Oksanen et al., 2016) were developed with the *specpool* function to understand how variation in species richness among samples varied by habitat type.

To visualize dissimilarity relationships in species composition among habitat types we performed a non-metric multidimensional scaling (NMDS) ordination with two dimensions using the *metaMDS* function in the *vegan* package. The choice of the number of dimensions in NMDS was based on reductions in stress, which is a measure of the deviation of pairwise sample locations in ordination space from their observed pairwise species dissimilarities. NMDS uses an iterative procedure to minimize the stress, given the number of ordination axes, to arrive at an optimal solution that best represents species dissimilarities among samples (McCune & Grace, 2002). We applied Bray–Curtis dissimilarities to a fourth-root transformed species by sample matrix and overlaid 95% confidence ellipses on the ordination by habitat type. Differences in composition by habitat type were statistically determined by performing a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function and assigning site as a stratum. Statistics are reported as pseudo-F values obtained by comparing the observed F-statistic with those obtained from random permutations of the data. Response variables of abundance or richness, and aquatic vegetation density were modeled against environmental variables and habitat type, respectively, with site as a random effect. To acquire aquatic vegetation density, categories of vegetation were transformed (no veg = 0, < 50% cover = 0.5, > 50% cover = 1). Post-hoc Tukey contrasts with multiple comparison corrections were then used to identify significant relationships between habitat types as previously described.

To compare the interpretations of wetland integrity assessments among habitat types, we calculated estimates of the Odonata Index of Wetland Integrity (OIWI). The OIWI is based on mean Coefficient of Conservation (CoC) scores derived by Kutcher and Bried (2014) from the occurrence of 135 odonate species across 510 wetlands in relation to wetland degradation. Since the OIWI was developed on species in Rhode Island, we were only able to extract CoC scores for 11 of the 12 species sampled in this study. Therefore, one observation of *Dromogomphus spoliatus* Hagen in Selys, a common species listed as “Least Concern” by the IUCN (Paulson, 2017), was omitted from the analysis. We weighed a species occurrence at a site within a habitat type by its observation frequency across samples to estimate CoC contributions of each species. The resulting CoC scores at each site–habitat combination ($n = 12$) were averaged to obtain four OIWI values per habitat type, from which 95% CI were derived. OIWI values for the larger wetland were calculated using the same method, but considered species occurrences across habitat types within a site.

Results

Dragonfly communities across habitat types

We sampled 157 adult individuals and 12 species of dragonfly during the study (Table 1). All species were common habitat generalists (Paulson, 2011), consistent with previous dragonfly community descriptions of water bodies within agricultural landscapes (Davies, Biggs, Williams,

Table 1. Abundance of dragonfly species by habitat type. Number of individuals sampled by net in stream, ecotone, and open water habitats throughout the duration of the study. Species are ranked by total abundance across all habitat types.

Species	Stream	Ecotone	Open water	Total
<i>Erythemis simplicicollis</i> (Say)	3	43	7	53
<i>Pachydiplax longipennis</i> (Burmeister)	0	24	25	49
<i>Libellula luctuosa</i> Burmeister	3	10	10	23
<i>Plathemis lydia</i> (Drury)	5	7	1	13
<i>Perithemis tenera</i> (Say)	0	2	9	11
<i>Epitheca princeps</i> Hagen	0	1	2	3
<i>Dromogomphus spoliatus</i> (Hagen in Selys)	0	0	2	2
<i>Libellula pulchella</i> Drury	0	0	1	1
<i>Pantala flavescens</i> (Fabricius)	0	0	1	1
<i>Tramea lacerata</i> Hagen	0	0	1	1
<i>Anax longipes</i> Hagen	0	0	0	0
<i>Anax junius</i> (Drury)	0	0	0	0
Totals	11	87	59	157

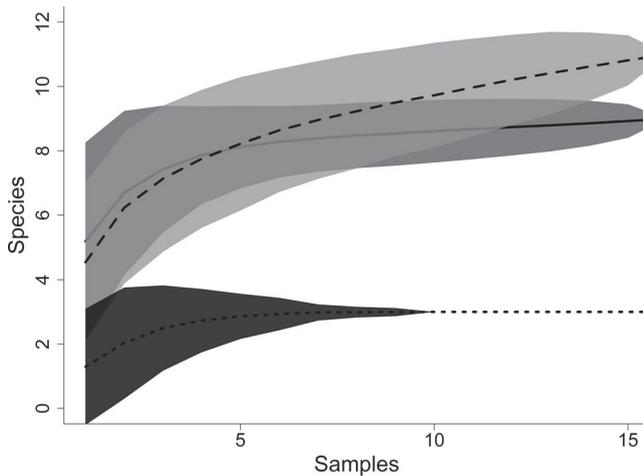


Figure 1. Species accumulation curves by habitat. Mean accumulation curves at stream (dotted), ecotone (solid), and open water (dashed) habitats are represented by lines and the accompanying 95% confidence intervals are depicted with black, dark gray, and light gray polygons around each habitat curve, respectively.

Lee, & Thompson, 2008; Simaika, Samways, & Frenzel, 2016). Although mean species richness within ecotones was greater than within streams ($Z = 9.34$, $P < 0.0001$), species richness between ecotones and open water habitats was similar ($Z = 0.92$, $P = 0.36$). Species accumulation curves showed similar patterns, with overlapping confidence intervals of total species richness between open water and ecotones, and lower total richness in streams (Figure 1). Dragonfly abundances were significantly different among habitat types ($\chi^2(2) = 29.96$; $P < 0.0001$), and our predictions that more dragonflies would be found in ecotones than streams ($Z = 6.39$, $P < 0.0001$) and open water habitats ($Z = 1.95$, $P = 0.05$) were supported (Figure 2). The species composition of dragonfly communities also differed among habitat types ($F = 2.58$, $P < 0.05$), which explained 39% of the variation in species dissimilarities (Figure 3). The 95% confidence ellipses within the NMDS ordination demonstrate a clear distinction between stream and ecotone communities and suggest both are subsets of open water communities.

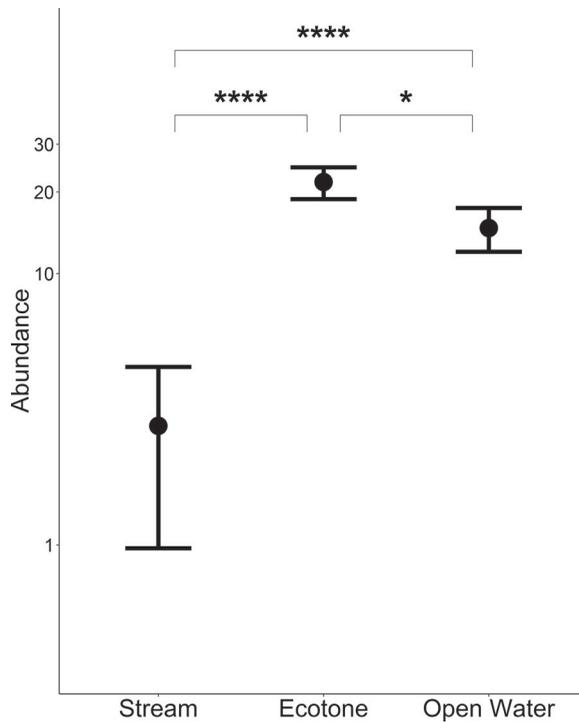


Figure 2. Mean dragonfly abundances across habitat types. Error bars are standard errors on raw abundances at sites ($n = 4$). P-values represent pairwise post-hoc analysis on mixed model * $P \leq 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

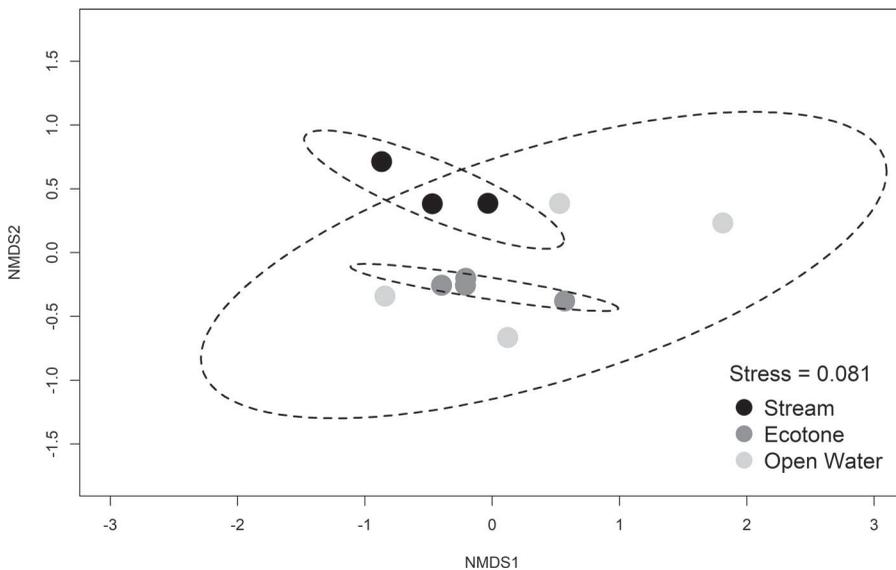


Figure 3. Non-metric multidimensional scaling (NMDS) of dragonfly communities separated by habitat type. Dashed ellipses represent 95% confidence intervals of dissimilarities between habitat types.

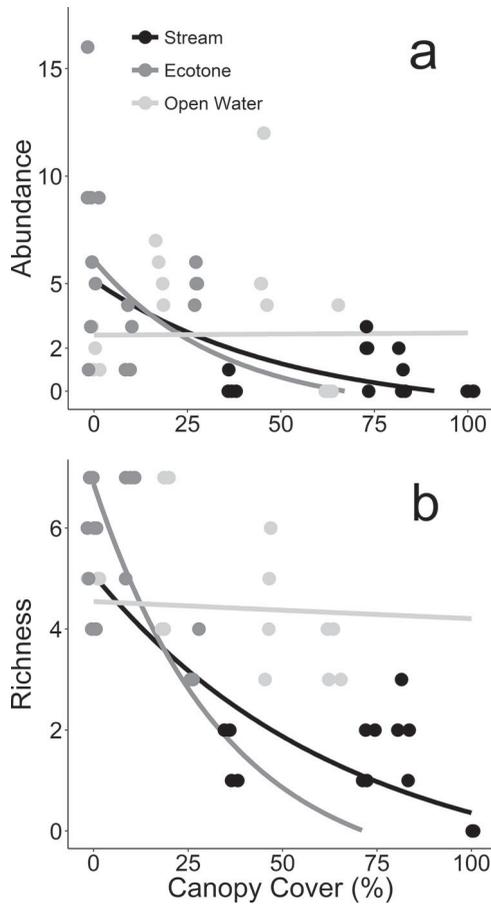


Figure 4. Dragonfly response to canopy cover by habitat. Predicted (lines) vs observed (points) effects of canopy cover on (a) abundance and (b) richness at stream (black), ecotone (dark gray), and open water habitats (light gray). Points are jittered along x-axis.

Environmental effects and wetland integrity

Dragonfly species richness was best explained by an interaction between habitat type and canopy cover ($X^2(5) = 82.1$; $P < 0.0001$), which was also a competing model to explain dragonfly abundance ($X^2(5) = 38.8$; $P < 0.0001$). Together with the interaction term, habitat type and canopy cover explained 79% of the variance in species richness (conditional $R^2 = 0.87$) and 46% of the variation in abundance (conditional $R^2 = 0.72$). However, the interaction between canopy cover and habitat type was significant for species richness ($X^2(2) = 12.0$; $P < 0.005$), but not abundance ($X^2(2) = 4.2$; $P = 0.12$). Dragonfly abundance (Figure 4a) and richness (Figure 4b) within ecotones were most sensitive to canopy cover, while those at open water habitats were least affected. The best model for dragonfly abundance included only canopy cover as a predictor and had a marginal (fixed effects) R^2 of 0.41. Other competing models ($\Delta AICc \leq 2$) for abundance responses included *canopy cover + algal mats* and *canopy cover + emergent vegetation* (Appendix Figure A2). Although not best fits, all models with aquatic vegetation predictors showed a positive association between dragonfly abundance and aquatic vegetation density. There was higher density of algal mats in ecotone habitats than open water ($Z = 3.3$; $P < 0.005$) and stream ($Z = 6.4$; $P < 0.0001$) habitats. Emergent vegetation density

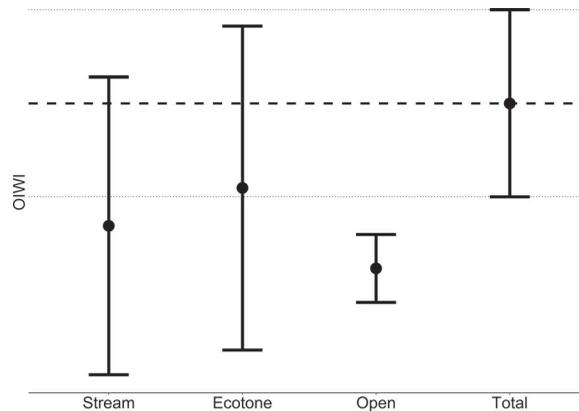


Figure 5. Mean OIWI values with 95% confidence limits of weighted mean CoC values at each habitat type (stream, ecotone, open), as well as each site where habitat types were pooled (total). Means of each habitat category are based on species CoC scores weighed by site observation frequencies. Dashed line represents the mean of total for comparison. Dotted lines represent upper and lower bounds of 95% CI of total.

in ecotones was also greater than streams ($Z = 4.4$; $P < 0.0001$), but not open water ($Z = 0.9$; $P = 0.36$). However, there was covariation between canopy cover and aquatic vegetation; canopy cover explained 35% and 22% of the observed algal mat and emergent vegetation density, respectively.

The weighted means approach to compare indicator values showed that mean OIWI values were highest in ecotones (3.36 ; $CI_{low} = 2.89$; $CI_{upp} = 3.83$) and lowest in open water habitat (3.13 ; $CI_{low} = 3.03$; $CI_{upp} = 3.22$). Only in ecotones was the mean OIWI value contained within the 95% CI of the larger wetland (3.61 ; $CI_{low} = 3.33$; $CI_{upp} = 3.88$) (Figure 5).

Discussion

The species richness, abundance, and composition of dragonfly communities differed along a gradient from stream to ecotone to open-water habitats. These shifts in dragonfly communities were predictable based on forest canopy cover and aquatic vegetation, which likely reflect differences in other factors important to dragonflies, such as thermal characteristics, breeding sites, and prey availability. Our findings suggest that canopy cover and relative amounts of aquatic vegetation can be useful in rapid assessments of dragonfly communities among riparian and aquatic habitats.

The dragonfly community of ecotones was a distinct subset of species from the larger species pool of dragonflies in our study areas. The species accumulation curve for ecotones rapidly reaching an asymptote, and the tight clustering of ecotone sites within the NMDS ordination, both indicate high similarity of species composition among ecotones. Although the species richness of ecotone and open-water habitats were not different, open-water habitats were more variable in species composition among sites. Each open-water site had a different set of less common species, leading to a continuous positive slope of the species accumulation curve and greater variability within the NMDS ordination. At least three of the four species sampled solely in open water habitats of this study are known migrants with large ranges (Table 1) (May, 2012; Paulson, 2011). Many species have residential and migrant populations with overlapping ranges; therefore, it is difficult to know if individuals of such infrequent species are representative of local conditions favorable for breeding success (Bried, D'Amico, & Samways, 2012; Golfieri et al., 2016; Kutcher & Bried, 2014; Raebel, Merckx, Riordan, Macdonald, & Thompson, 2010).

However, despite their ability to fly long distances, imagos of most resident species are unlikely to disperse far (Conrad, Willson, Harvey, Thomas, Sherratt, 1999) or may remain at their natal water body if conditions are favorable (Harms, Kinkead, & Dinsmore, 2014). This suggests that dragonflies were likely residents and adults of the same generation were unlikely to move among sites. We should further note that oviposition behavior was regularly observed in ecotone habitats by many individuals, but neither species identity nor oviposition frequency was recorded.

Dragonfly species abundances along streams differed from those in ecotones, yet all species within stream habitats were also found in ecotones, suggesting that minimal information would be lost in the absence of stream-specific data. However, this would assume that species breeding in stream habitats use the wider range of ecotone properties as adults. Furthermore, greater abundances in ecotone habitats than both stream and open water habitats is an indicative property of environmental conditions more favorable for breeding dragonflies (Kutcher & Bried, 2014); but studies of larvae composition would be needed to support this conclusion.

The results of this study support previous findings that canopy cover, or shade, is the primary driver of dragonfly assemblages (Clark & Samways, 1996; Clausnitzer, 2003; Samways & Sharratt, 2010; Smith et al., 2007; Thornhill et al., 2017). Canopy cover was present in all competing models and was associated with decreased dragonfly species richness and abundance for stream and ecotone habitats. However, dragonfly communities responded differentially to canopy cover according to habitat type (Figure 5). This finding supports the Clark and Samways (1996) analysis highlighting the interaction between shade and water body flow rate and adds a layer of complexity to the notion that most dragonflies can be categorized as either lotic/lentic and shade/sun species (Chovanec et al., 2015; Golferi et al., 2016; Samways & Sharratt, 2009). Dragonfly assemblages of open-water habitats did not demonstrate a strong response to canopy cover, and even showed a slight positive relationship between canopy cover and dragonfly abundance. One explanation is that individuals within locations of nearly full sun exposure, such as over open water, may need shade to assist thermoregulation or perching structures for foraging (Corbet & Brooks, 2008; Córdoba-Aguilar, 2008). Notably, our study demonstrated that ecotone assemblages were most sensitive to canopy cover and exhibited a strong negative response to increased cover compared with stream and open water assemblages. The mechanism governing this response is unclear but may involve the ecotone community responding to differences in aquatic vegetation complexity due to changes in light availability. Among other interactions, reduced light availability decreases photosynthetic ability of aquatic vegetation. In turn, aquatic vegetation structure is reduced and may support fewer dragonfly larvae (Remsburg & Turner, 2009) in addition to adult oviposition substrates. Therefore, a strong response to canopy cover may be representative of competition among species heavily dependent on aquatic vegetation, which would indicate that ecotones may be a preferred breeding habitat.

Established benthic and emergent vegetation provide resources required for prey, larvae, and breeding adults (Corbet & Brooks, 2008; Córdoba-Aguilar, 2008). Since algal mats and other aquatic vegetation shared relative importance within models and had similar coefficients (data not shown), our findings suggest that aquatic vegetation structure was important in predicting dragonfly abundance, but not species richness. In other studies, however, increased macrophytes are associated with increases in dragonfly species richness (Clark & Samways, 1996; Clausnitzer, 2003; Raebel et al., 2012; Sahlén & Ekestubbe, 2001). In our study, aquatic vegetation effects on species richness may have been masked by the relationship between canopy cover and aquatic vegetation. Other studies show that the increased availability of oviposition substrates, prey breeding grounds, and hiding locations associated with increased macrophyte density in ecotones better predicts dragonfly abundance (Clark & Samways, 1996; Clausnitzer, 2003; Foote & Hornung, 2005; Raebel et al., 2012).

Conservation monitoring and ecotones

Monitoring for conservation purposes often involves surveying taxa with diverse species-specific requirements, such as dragonflies. The time, effort, and expense required for such surveys underscores the need for a simpler and more accurate method. Adult dragonflies and other odonates show promise and provide the additional benefit of observers needing minimal training and time in the field, which reduces monitoring costs. Despite the potential for using adult dragonflies for rapid assessments, it is often difficult to (1) account for individuals that are not representative of the surrounding environmental conditions, such as migrants and founders, and (2) reliably sample locations representative of the larger waterbody system.

Ecotone habitats were defined by mosaics of slow moving shallow water, small islands, increased macrophytes, and a transition from the shaded streams to sun-exposed open water (Appendix Figure A1). These properties and their heterogeneous configurations may provide a focal area of dense and variable resources to resident and breeding populations (Chovanec et al., 2015). If true, assessing and monitoring the dragonfly community within the well-defined and limited area of an ecotone habitat may require less time than more expansive monitoring of stream and open-water habitats. Ecotone assemblages consisted of resident species in high abundances that collectively demonstrated a greater sensitivity to riparian and aquatic vegetation than stream or open-water communities. Since we did not sample larvae or exuviae, it remains unclear if the ecotone community is representative of successful breeding populations. However, the abundance of males and females of the same species, the observed oviposition behavior, and the high densities of oviposition substrates observed within ecotones suggest these habitats may be preferred by breeding individuals.

Derived OIWI values suggest that the interpretation of ecological integrity for these wetland systems would not be altered if only species composition at ecotones were considered (Figure 5). OIWI values suggest that stream species can exhibit high sensitivity to anthropogenic disturbances. However, it is not representative of the system and may be an artifact of a few species identities or the lack of detection (see Appendix Table A1). The lower OIWI values of open water habitats emphasize the inconsistent detection rates of species with moderate CoC values. Species tolerant of disturbed sites were driving these lower OIWI values despite the overall high species richness observed in open water habitats. The many species at ecotones were detected consistently across sites due to the similarity of environmental factors across ecotone habitats. Combined with the increased aquatic vegetation complexity, heightened shade sensitivities, and high species abundances and richness, the similarity in OIWI values between ecotones and the entire wetland system emphasize the potential importance of ecotones for conservation monitoring of wetland ecosystems.

Together, our results suggest dragonfly-focused assessments and monitoring schemes may require less time and expense without loss of interpretation if conducted at wetland ecotones. All details of our findings are largely in agreement with other studies conducted around the world. However, we emphasize that our findings, although consistent with others, was restricted to a single season. More importantly, studies verifying the presence of corresponding juvenile odonates of multiple life stages, as well as assessing the ranges of abiotic aquatic conditions at these transition zones are needed. Future research examining the conservation importance of ecotones would further benefit from the inclusion of other sensitive taxa, such as amphibians and other macroinvertebrates. Such studies may further support the effectiveness of applying an adult odonate conservation index exclusively to ecotones, or broaden the scope of our findings to better advise conservation management decisions to address multiple taxa. Nonetheless, we provide evidence of an approach to improve efficiency of riparian conservation monitoring through the focus of wetland ecotones.

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Appendix A



Figure A1. Examples of sampled habitat locations. Stream (*), ecotone (**), and open water (***) habitats were sampled for adult dragonflies along 100 m transects when available. One of three Acton Lake sites (left) and the Western Pond site (right) are depicted. Imagery from Google Earth Pro (2016). Google, Inc. Mountain View, CA, USA.

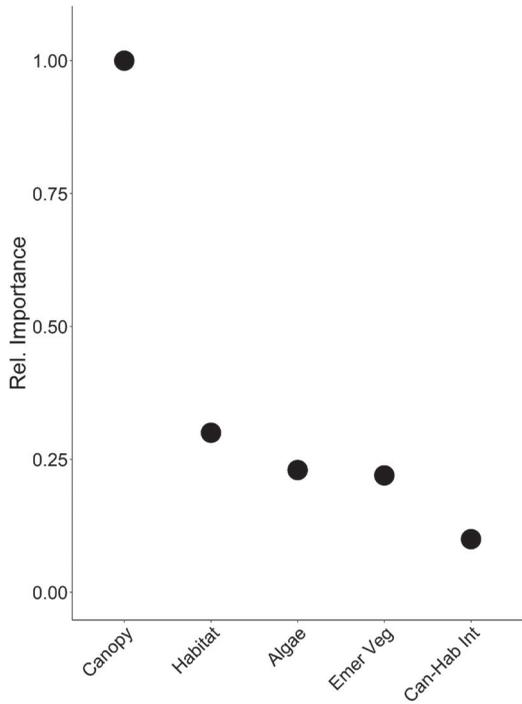


Figure A2. Relative importance of variables explaining dragonfly abundance. Values based on weights of averaged competing models (n = 5) and the appearance of canopy cover, habitat type, algal density, density of emergent vegetation, and interaction between canopy and habitat within models.

Table A1. Mean coefficient of conservatism (CoC) by habitat. Species occurrences during 1 hour (n = 4 samples) of observations along each transect (depicted by “X”) and the associated mean CoC scores used in OIWI analysis. CoC scores extracted from Kutcher and Bried (2014).

Habitat	Stream				Ecotone				Open				CoC
	1	2	3	4	1	2	3	4	1	2	3	4	
<i>Anax junius</i>	-	-	-	-	X	X	X	X	-	-	-	-	5.1
<i>Anax longipes</i>	-	-	-	-	-	-	-	-	X	-	-	-	8.3
<i>Dromogomphus spoliatus</i>	-	-	-	-	-	-	-	-	-	-	X	-	NA*
<i>Epitheca princeps</i>	-	-	-	-	X	X	X	-	X	X	X	X	5.8
<i>Erythemis simplicicollis</i>	-	X	X	X	X	X	X	X	X	X	X	X	5.3
<i>Libellula luctuosa</i>	-	X	X	X	X	X	X	X	X	X	X	X	4.0
<i>Libellula lydia</i>	-	X	-	X	X	X	X	X	-	X	X	X	6.0
<i>Libellula pulchella</i>	-	-	-	-	X	-	-	-	X	-	-	-	4.2
<i>Pachydiplax longipennis</i>	-	-	-	-	X	X	X	X	X	-	-	X	4.1
<i>Pantala flavescens</i>	-	-	-	-	-	-	-	-	-	X	-	-	3.1
<i>Perithemis tenera</i>	-	-	-	-	X	X	X	-	X	X	X	X	3.9
<i>Tramea lacerata</i>	-	-	-	-	X	X	X	-	X	X	-	X	5.0

* *Dromogomphus spoliatus* did not receive a CoC score in Kutcher and Bried (2014).