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ORIGINAL PAPER

Local and regional factors influencing assemblages of dragonflies and damselflies (Odonata) in California and Nevada

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Abstract Studies of landscape effects on assemblages and distribution of insects are relatively uncommon, largely because of the lack of occurrence data that span broad spatial or temporal scales. Here, we provide a multi-species analysis using generalized linear mixed models to examine the effects of local and regional variables on richness and occurrence rates of Odonata (dragonfly and damselfly) species at 81 sites throughout central California and northwestern Nevada, USA. These study sites were located across a range of ecoregions, including the Sierra Nevada Forests, California Mediterranean, Great Basin Shrub Steppe, and Northern Coastal California Forests. Dynamic regional variables in this study, degree-days and precipitation, influenced the richness of dragonflies, but not the less-mobile damselflies. In contrast, local habitat type influenced the richness of damselflies, but not dragonflies. Overall species occurrence was higher during site visits with higher degree-days, especially for highly mobile groups including dragonflies and migratory species. Dragonflies were also positively associated with total precipitation, but migratory species were not. Probability of presence across species was lower in highly urban sites, particularly for habitat specialists. Further, habitat specialists had lower rates of occurrence overall, suggesting that widespread generalist species may increasingly dominate Odonata assemblages. Our study indicates that Odonata in this semi-arid region are responsive to a combination of local and regional environmental variables.

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Introduction

The extinction rates of freshwater organisms are among the highest in the major ecosystem types (Ricciardi and Rasmussen 1999). However, the conservation status and effects of broad-scale land use on the diversity and distribution of many freshwater organisms remain poorly understood (e.g., Ball et al. 2013). Insects have likely experienced greater extinction than more well-studied groups, such as birds or plants (Thomas et al. 2004). However, only a small fraction (~10 %) of basic research on freshwater organisms has focused on invertebrates (Strayer 2006). Even for popular and charismatic groups such as Odonata (dragonflies and damselflies), their response to broad-scale environmental conditions in many regions of the world is largely unknown (Bried and Mazzacano 2010; Clausnitzer et al. 2009, 2012). Further assessment of the influence of local and regional environmental conditions on Odonata could provide an indication of conservation status for both species in this order and for aquatic insects in general (Sahlen and Ekestubbe 2001; Suhling et al. 2006), particularly in water-stressed regions like the western United States.

Odonata may serve as particularly good biological indicators of freshwater ecosystem conditions because they are widespread, experience a protracted nymphal phase, are conspicuous as adults (Clausnitzer et al. 2009; Smith et al. 2007; Sahlen and Ekestubbe 2001; Clark and Samways 1996), and are fairly easy to identify in the adult stage (e.g., Manolis 2003). Moreover, individual species and assemblages of odonates have been associated with a variety of local habitats (e.g., Silva et al. 2010; Smith et al. 2007; Buchwald 1992), climate (e.g., Hickling et al. 2005), and surrounding land-use conditions (e.g., Samways and Steytler 1996; Smith et al. 2007). For example, previous studies have demonstrated that the degree of shade and structural heterogeneity of emergent vegetation are particularly important habitat variables for odonates (Samways and Steytler 1996; Steytler and Samways 1995). Flowing (lotic) and still water (lentic) habitats are also essential factors that shape Odonata assemblages, as many species are primarily associated with one of these habitat types (e.g., Corbet 2004; Manolis 2003).

While temperature increases may generally facilitate the expansion of Odonata species ranges and lead to increases in regional biodiversity in northern latitudes (Hassall and Thompson 2008; Hickling et al. 2006), habitats in urban areas have often experienced declines in species richness (e.g., Samways and Steytler 1996). For example, studies in Africa and Germany have demonstrated that odonate diversity is lower in highly urban sites, and dominated by habitat generalist species (Suhling et al. 2006; Clausnitzer 2003; Samways and Steytler 1996). Overall, the greatest threats for many Odonata species are the intensification of human land use (Moore 1991; Samways and Steytler 1996; Corbet 2004; Clausnitzer et al. 2012), which fragments freshwater habitats, transforms water flow and distribution across the landscape, and degrades water quality through eutrophication and other forms of contamination (Paul and Meyer 2001).

Previous studies of Odonata distribution over broad spatial and temporal scales have largely focused on their responses to temperature and precipitation (United Kingdom: e.g., Hickling et al. 2005, 2006; South Africa: Finch et al. 2006; North America: Hassall 2012). To our knowledge, however, no previous studies have addressed the effects of broad-scale climate and land use parameters on odonates in the semi-arid western United States.

In the present study, we examine factors that influence species richness and the occurrence rates of Odonata species in central California and northwestern Nevada. In particular, we investigate the effects of local (canopy cover, emergent vegetation, and habitat type) and regional variables (degree-days, precipitation, elevation, agriculture, and urbanization) on species richness and the occurrence of species with certain biological traits (e.g., suborder, migratory species, and habitat specialists). In so doing, we evaluate the potential of Odonata communities to serve as indicators of land use and climate effects on freshwater systems of this region.

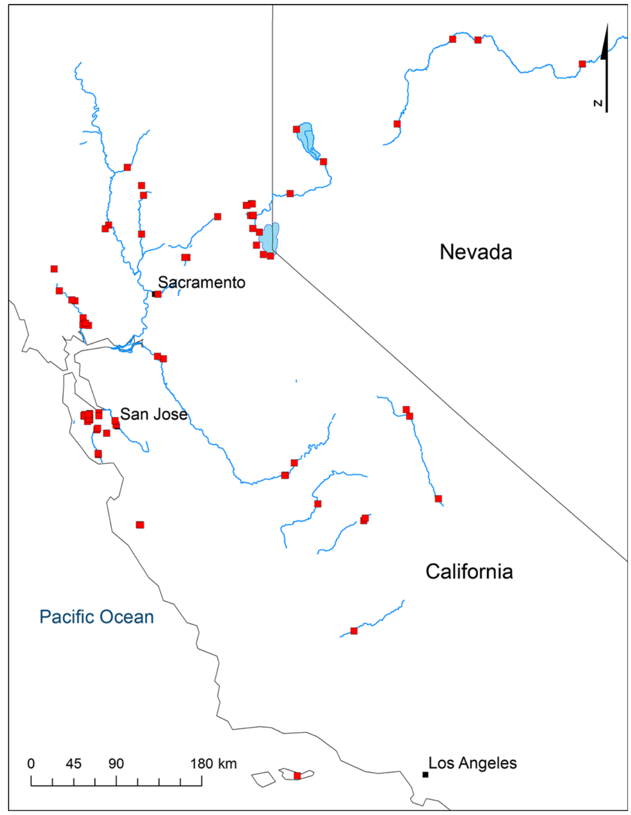

Fig. 1 Map of study sites and major rivers and lakes sampled throughout central California and north-western Nevada, USA

Methods

Study area

The study area encompassed 81 freshwater sites throughout central California and northwestern Nevada, ranging as far south as Santa Cruz Island near Santa Barbara, California, as far north as Chico, California, and as far east as Carlin, Nevada (Fig. 1). C.H. Kennedy surveyed the majority of these sites in 1914–1915, and was the first to characterize Odonata of this region (Kennedy 1917). We chose a majority of our sample locations to be the same or comparable to Kennedy's original locations, and we directly compare our surveys to his in a separate paper (Ball-Damerow et al. 2014). We also surveyed several additional locations for the present study.

Sites were located within four ecological regions, as delineated by the World Wildlife Fund Conservation Science Program (Olson et al. 2001), including the Sierra Nevada Forest (15 sites), California Mediterranean (39 sites), Great Basin Shrub Steppe (10 sites), and Northern Coastal California Forests regions (17 sites; Fig. 1). These four regions all have dry summers and wet winters, with precipitation occurring from October through April.

Table 1 Variables hypothesized to influence the occupancy rate and detection of Odonata species

Variable	Predicted effect							Data Source	Mean value (min–max)
	Species occurrence	Richness	Dragonfly/damselfly	Habitat specialist	Forest specialist	Lotic/lentic associated	Migrant		
Visit Effort (h)	+	+	+/+	n/a	n/a	n/a	n/a	Field	2.4 (0.25–7.8)
Lotic Habitat Type	0	0	n/a	n/a	n/a	+/0	n/a	n/a	Binary - 0/1
Lentic Habitat Type	0	+	n/a	n/a	n/a	0/+	n/a	n/a	Binary - 0/1
Canopy Cover (%)	–	–	n/a	n/a	+	n/a	n/a	Field	21 (0–80)
Emergent Vegetation	+	+	n/a	n/a	n/a	n/a	n/a	Field	Binary - 0/1
Degree-days	+	+	+/0	0/+	n/a	n/a	+	GHCN	959 °C (97–4,295)
Total Precip. (mm)	+	+	+/0	n/a	n/a	n/a	n/a	GHCN	540 mm (70–2,040)
Elevation (m)	–	–	n/a	+	n/a	n/a	n/a	NED	576 (1.7–2,535)
Agriculture (%)	0/+	0/+	n/a	–	n/a	n/a	n/a	NLCD	7 (0–45)
Highly Urban (%)	–	0/–	n/a	–	n/a	n/a	n/a	NLCD	11 (0–85)

Data sources are *GHCN* Global Historical Climate Network, with daily temperature records taken from nearest weather station; *NED* National Elevation Dataset, *NLCD* National Land Cover Dataset. Highly urban is the percent high and medium intensity development calculated within a 1-km buffer radius of the site. Agriculture is the percent agricultural land calculated within a 1-km buffer radius of the site

Habitat types sampled include both lotic (streams, rivers and canals) and lentic (wetlands, ponds, lakes and sloughs) sites (Table 1).

Odonata survey

We surveyed each site for adult Odonata from late-April through mid-September in 2011, 2012, and/or 2013. Surveys took place during peak periods of Odonata activity, usually from 10 am until 4 pm, when morning temperatures were above 17 °C and cloud cover was low. We found that lower morning temperatures near 17 °C resulted in more sluggish flight in fast-flying dragonflies, which facilitated capture and identification. Temperature then increased quickly by late morning when a wider range of species became active. The same primary collector (J.E. Ball-Damerow) was present at each survey, identified all species, and was accompanied by one or more additional collectors. In general, we captured voucher specimens of each species encountered with an aerial insect net, but in some cases (when certain of correct identification) we recorded species only by observation. We sampled each site from one to five times over the 3-year study period. For each individual site visit, we recorded the amount of time spent surveying (average 2.4 h ± 1.5; Table 1). We used hours spent collecting during individual site visits as a measure of visit sampling effort in analyses described below (Table 1).

We recognize that the presence of adult species does not necessarily indicate that the site is suitable for nymphal habitat and successful life-cycle completion, particularly for migratory species. However, adults do engage in habitat selection for reproduction and foraging (Corbet 2004), males defend territories that are attractive to females, and females oviposit in sites likely to be suitable nymphal habitat (e.g., Alcock 1990). Therefore, overall occurrence should generally indicate that the habitat is supportive for at least part of their life-cycle (Silva et al. 2010).

Biological traits

We collected 83 species in total. We predicted that several species traits would influence their environmental associations, including suborder (dragonflies vs. damselflies), migratory species, habitat specialists, forest specialists, lotic species, and lentic species. Migratory species include the five North American Odonata species that are known to migrate annually (*Anax junius*, *Tramea lacerata*, *Pantala flavescens*, *P. hymenaea*, and *Sympetrum corruptum*) (May 2013). Migratory species, and dragonflies in general, may become more successful when temperatures are warmer, as a result of high dispersal ability (e.g., Hickling et al. 2006; Table 1). These mobile migratory species may also occur more often in highly urban areas while habitat specialists likely occur less often in these areas (e.g., Goertzen and Suhling 2013).

Species were categorized as specialists if they require specific habitat types in order to complete their life cycle, such as flowing water or high elevation areas. A subset of habitat specialists only inhabits forested areas and we included this preference as a separate species-trait. This group of species should be positively associated with canopy cover while others are likely to be negatively associated. Species known to be associated with primarily lotic (flowing) or lentic (still) waters should occur more often in these respective habitat types. All habitat information was obtained from descriptions in a regional field guide for Odonata (Manolis 2003).

Local variables

We evaluated the importance of habitat type (presence or absence of lotic and/or lentic habitat), percent canopy cover, and presence of emergent vegetation as local variables. Emergent vegetation includes macrophytes that are rooted in the aquatic substrate and grow above or at the water line; many Odonata oviposit within this vegetation or use it as nymphal habitat (Corbet 2004). We recorded the presence or absence of emergent vegetation and estimated the average percent tree cover for each site in the field (Table 1). We also evaluated the importance of habitat type by classifying sites as lotic (flowing water, such as streams, canals and rivers) or lentic (still water, such as lakes, ponds, and river backwaters). Some sites had both lotic and lentic habitat types.

Regional variables

Because most Odonata have a tropical origin, their occurrence, richness, and abundance are often positively associated with increases in temperature and precipitation (Corbet 2004; Hassall and Thompson 2008). We therefore predicted that species richness and occurrence would be positively associated with degree-days and total precipitation (Table 1). We obtained daily maximum temperature, minimum temperature, and total precipitation data for the weather stations nearest to sampling sites from the National Climatic Data Center and the Global Historical Climatology Network (GHCN; NOAA 2012). Degree-days were calculated for each site over the time period starting October 1 through each collection date. This time period marks the water year in this Mediterranean-climate region, with October 1 being the approximate beginning of the wet season and includes the time over which most nymphs would develop. Accumulated degree-days for each site and collection date were calculated by subtracting the minimum temperature threshold for growth (10 °C for aquatic insects) from each daily average and summing these values (e.g., Corkum 1992). Because degree-days varied by site visit, and increased each day as the season progressed, they can be considered as a proxy for both temperature and time of year during a particular site visit. We also used total precipitation over the water year for each site visit. Unlike degree-days, precipitation usually did not vary between sample dates within a given year, because collections occurred in the dry season when precipitation had largely ceased. Precipitation did, however, vary between visits if they occurred in different years.

The study area included sites with a range of elevations, from near sea-level (1.7 m) to high-elevation, mountainous sites (2,535 m). Because many species occur at specific elevations and because these are well-documented for dragonflies (e.g., Manolis 2003), we also investigated the effect of elevation on occurrence. We expected elevation would be negatively associated with species richness and occurrence for many warm-adapted Odonata species; however, high-elevation specialists should occur more often in high elevation regions (Table 1). In addition, many species may be moving to higher elevation areas with increasing annual temperatures (e.g., Forister et al. 2010). Elevation for each site was obtained using the National Elevation Dataset (NED) (Gesch 2007; Gesch et al. 2002).

Finally, we predicted that highly urban and agricultural areas would negatively influence the occurrence rates of habitat specialist species, while highly mobile and generalist migratory species may occur frequently in these habitats (Goertzen and Suhling 2013; Table 1). At the highest levels of urbanization, we expected species richness to decline (Goertzen and Suhling 2013). Species richness within agricultural areas of California, however, may actually increase or not be affected because irrigation canals often create more aquatic habitat, particularly for habitat generalists (R. Garrison, *personal communication*). We used ArcGIS Desktop, release 10.1 (ESRI 2012) and the National Land Cover Dataset (NLCD), at 30-m resolution (Fry et al. 2011), to calculate the proportion of high and medium intensity development and agriculture within a one-km buffer area surrounding each site (Table 1).

Data analysis

Our primary goal was to investigate the occurrence rates of multiple Odonata species in relation to local and regional environmental variables. Recently, ecologists have adopted methods for estimating occupancy that account for uncertainty in the detection process (MacKenzie et al. 2003; Kery and Royle 2008). However, because of the generally low rates of detection associated with insect collection, we did not have enough repeat visits at enough sites to accurately estimate both detection and occupancy probabilities using a multi-species occupancy approach. Instead, to account for differences in sample effort on each site visit, we include a measure of time spent collecting during that visit.

To determine which local and regional variables most strongly impact Odonata communities, we ran generalized linear mixed models (GLMMs) based on predictions described above and in Table 1. Models were implemented using the linear mixed-effects models lme4 package (Bates et al. 2013) of the statistical program R, version 3.1.1 (R Development Core Team 2014). These models can accommodate non-normal error distributions and incorporate random effects to control for correlations brought about by groups of observations. We first standardized all continuous variables by subtracting the mean and dividing by the standard deviation to facilitate interpretation of effect sizes. We also tested for collinearity of all variables using Spearman rank correlation coefficients. None of the variables presented here were strongly correlated ($r \leq 0.50$). We first examined the effects of the local and regional variables described above on overall species richness for individual site visits. We then analyzed the effects of these covariates on the probability of occurrence at each site-visit across all species in a multi-species analysis. Although some variables do not change between survey visits, effort, degree-days, and total precipitation often varied between site visits. It is important to note here that our response variables in both of these models are modeled at the visit level and, thus, the fact that we did not visit all sites the same number of times is not a concern.

We used a GLMM that assumes a log link function and Poisson error distribution to model the observed species richness for each site visit. To determine whether there were differences in response for the two suborders, we ran the richness model separately for dragonflies and damselflies. Both site and year were treated as random effects, and the full model is defined as follows:

$$
\begin{aligned}
&\text{Visit - level species richness} \sim \text{intercept} + \text{visit effort} \\
&\quad + \text{lotic habitat type} + \text{lentic habitat type} + \text{canopy cover} \\
&\quad + \text{emergent vegetation} + \text{visit degree - days} \\
&\quad + \text{visit total precipitation} + \text{site elevation} \\
&\quad + \text{site agriculture} + \text{site urbanization} \\
&\quad + \text{random effects (site, year).}
\end{aligned}
$$

We next modeled species' probabilities of presence during individual site-visits using a logistic regression with a binomial error distribution and logit link function. Genus was included in the model as a random effect to, at least partially, account for the fact that related species might exhibit similar trait values through common ancestry. This is necessary, because we do not have a full species-level phylogeny and thus are unable to fully account for phylogenetic non-independence. A recent study using bees showed that nesting species within a genus as random effects produced essentially the same results as a more sophisticated analysis that removed phylogenetic non-independence using phylogenetic trees created using genetic data (Bartomeus et al. 2013). Species identity, site, and year were also treated as random effects. The final model was built using backward deletion of non-significant explanatory variables starting with the full model. Our full multi-species model is given by:

$$
\begin{aligned}
&\text{Visit - level species occurrence} \sim \text{intercept} + \text{visit effort} \\
&\quad + \text{lotic habitat} \times \text{lotic species} + \text{lentic habitat} \\
&\quad \times \text{lentic species} + \text{site canopy cover} \times \text{forest specialist} \\
&\quad + \text{emergent vegetation} + \text{visit degree - days} \times \text{dragonfly} \\
&\quad + \text{visit degree - days} \times \text{migratory species} \\
&\quad + \text{visit degree - days} \times \text{habitat specialist} \\
&\quad + \text{visit total precipitation} \times \text{dragonfly} \\
&\quad + \text{visit total precipitation} \times \text{migratory species} \\
&\quad + \text{site elevation} \times \text{habitat specialist} \\
&\quad + \text{site agriculture} \times \text{habitat specialist} + \text{site urbanization} \\
&\quad \times \text{habitat specialist} + \text{site urbanization} \times \text{migrant} \\
&\quad + \text{random effects (genus, species, site, year).}
\end{aligned}
$$

Numeric covariates were standardized and we present coefficient estimates for each on the logarithmic scale. Because the covariates were standardized, the regression coefficient values provide a measure of effect size for individual variables.

Results

Odonata species richness estimated for individual site visits showed several statistically significant relationships with local and regional variables measured. Dragonfly species richness was influenced by regional variables, while damselflies appeared more influenced by local attributes of the site. Visit-level richness for dragonflies was positively related to precipitation and degree-days, and was negatively associated with canopy cover (Table 2). Canopy cover had the highest effect size for dragonflies (regression coefficient = −0.47). In contrast, lotic habitats had much higher damselfly richness (regression coefficient = 0.51). Similar to dragonflies, damselflies were negatively associated with canopy cover, but to a lesser degree (regression coefficient = −0.32; Table 2).

The multispecies GLMM assessing relationships between probability of presence during site visits and environmental covariates showed several relatively strong and significant relationships. Lotic habitat type had a strong positive effect on overall probability of presence (regression coefficient = 0.47; Table 3). The probability of presence was also higher in areas of higher precipitation (regression coefficient = 0.34; Table 3). In contrast, the probability of occurrence was lower with high canopy cover (regression coefficient = −0.44) and urbanization (regression coefficient = −0.37; Table 3). Finally, habitat specialists were much less likely to occur overall (regression coefficient = −1.19; Table 3). Emergent vegetation was not statistically significant, and was therefore removed

Table 2 Regression coefficient estimates for GLMs that examined visit-level species richness for dragonflies and damselflies as a function of local and regional variables per site visit

Parameter	Dragonflies				Damselflies			
	Estimate	Std. error	Z-Value	*P* value	Estimate	Std. error	Z-Value	*P* value
(Intercept)	0.55	0.38	1.46	0.14	0.36	0.35	1.01	0.31
Survey								
Visit effort (h)	**0.34**	**0.05**	**6.94**	**<0.001**	**0.26**	**0.05**	**5.05**	**<0.001**
Local								
Lotic habitat type	0.33	0.24	1.36	0.17	**0.51**	**0.24**	**2.15**	**0.03**
Lentic habitat type	0.32	0.23	1.36	0.17	0.20	0.23	0.91	0.37
Canopy cover (%)	**−0.47**	**0.09**	**−5.40**	**<0.001**	**−0.32**	**0.08**	**−3.89**	**<0.001**
Emergent vegetation	0.11	0.25	0.44	0.66	0.14	0.26	0.52	0.60
Regional								
Degree-days	**0.23**	**0.06**	**3.67**	**<0.001**	0.01	0.07	0.13	0.89
Total Precipitation	**0.31**	**0.09**	**3.57**	**<0.001**	0.08	0.10	0.80	0.42
Elevation (m)	−0.12	0.07	−1.66	0.10	−0.07	0.07	−1.06	0.29
Agriculture (%)	−0.01	0.06	−0.15	0.88	−0.09	0.07	−1.38	0.17
Highly Urban (%)	−0.05	0.07	−0.76	0.45	−0.06	0.07	−0.93	0.35

Significant values are bolded

from the final model. Other variables and traits did not significantly influence occurrence probability overall, but were significant in their interactions and therefore remain in the model output.

Many interactions between odonate traits and both local and regional environmental variables were significant in the multi-species model. Some of the most dramatic effect sizes were, not surprisingly, the positive interactions between lotic habitat type and lotic associated species (regression coefficient = 0.38), canopy cover and forest specialists (regression coefficient = 0.35), and lentic habitat and lentic species (regression coefficient = 0.33). Habitat specialists occurred more often in high elevation sites (regression coefficient = 0.29) and less often in areas of high urbanization (regression coefficient = −0.34; Table 3). Furthermore, the average percentage of specialists found at sites was ~20 % lower at sites surrounded by >15 % high and medium intensity urban development than at sites with lower levels of urbanization (Fig. 2). Both migratory species (regression coefficient = 0.14) and dragonflies (regression coefficient = 0.11) had higher probabilities of occurrence with higher degree-day values, and dragonflies had higher probabilities of occurrence with higher total precipitation (regression coefficient = 0.08; Table 3). Several covariates were removed from the final model during backwards deletion because they were not significant, including the interaction between damselflies and lotic habitat, that between total precipitation and migratory species, and those between habitat specialists and both degree-days and agriculture.

Discussion

Local variables

Odonate species are known to engage in habitat selection in relation to local factors, particularly those associated with visual cues (Corbet 2004). Emergent vegetation is well-documented as a primary habitat feature because it provides nymphs with foraging habitat and predation cover, and provides adults with perching structures for thermoregulation, foraging, territorial defense, mate attraction, and protection from adverse weather (Remsburg and Turner 2009; Corbet 2004; Buchwald 1992). However, we did not find a significant relationship between species richness or species occurrence and emergent vegetation in the present study. The lack of a significant relationship may be because we assessed the presence of emergent vegetation, and not specific vegetation types or the degree of structural heterogeneity. Previous research has shown that odonate richness can depend on heterogeneity of plant structure in both natural and urban settings (Goertzen and Suhling 2013; Schindler et al. 2003; Remsburg and Turner 2009).

Several studies have also highlighted the importance of sunlight compared to shade in habitats for various Odonata species (Steytler and Samways 1995; Samways and Steytler 1996; Clausnitzer 2003). For example, following the creation of a conservation pond in South Africa, Steytler and Samways (1995) found that eight Odonata species that colonized the pond were negatively correlated with shade whereas others were positively associated. As expected, we

Table 3 Regression coefficients estimates for the GLMM that best explained the presence of Odonata species in relation to survey, habitat, landscape, and species traits variables per site visit

Parameter	Estimate	Std. error	Z Value	*P* value
(Intercept)	−3.77	0.29	−13.24	<0.001
Survey				
Visit effort (h)	**0.41**	**0.05**	**8.80**	**<0.001**
Local				
Lotic habitat type	**0.47**	**0.13**	**3.60**	**<0.001**
Lentic habitat type	0.15	0.12	1.21	0.23
Canopy cover (%)	**−0.44**	**0.08**	**−5.31**	**<0.001**
Regional				
Degree-days	**0.16**	**0.07**	**2.33**	**0.02**
Total precipitation	**0.34**	**0.08**	**4.00**	**<0.001**
Elevation	0.08	0.08	1.07	0.29
Urbanization	**−0.37**	**0.10**	**−3.80**	**<0.001**
Traits				
Dragonfly	−0.26	0.17	−1.56	0.12
Habitat specialist	**−1.19**	**0.17**	**−6.99**	**<0.001**
Migrant	−0.02	0.15	−0.13	0.90
Forest specialist	−0.06	0.16	−0.41	0.68
Lotic species	0.02	0.18	0.13	0.90
Interactions				
Lotic habitat × lotic species	**0.38**	**0.09**	**4.31**	**<0.001**
Lentic habitat × lentic species	**0.33**	**0.08**	**4.28**	**<0.001**
Canopy cover × forest specialist	**0.35**	**0.05**	**6.86**	**<0.001**
Degree-days × dragonfly	**0.11**	**0.04**	**2.57**	**0.01**
Degree-days × migrant	**0.14**	**0.03**	**5.10**	**<0.001**
Total precipitation × dragonfly	**0.08**	**0.04**	**2.04**	**0.04**
Elevation × habitat specialist	**0.29**	**0.04**	**7.11**	**<0.001**
Urbanization × habitat specialist	**−0.34**	**0.06**	**−5.37**	**<0.001**

The difference in probability of presence is the difference in probability of presence per standardized unit increase of the respective covariate. Significant values are bolded

found that most odonates in our sites generally occurred less often and richness was lower in sites with high canopy cover. Forest specialists, however, occurred more often in sites with high canopy cover. Other habitat factors, such as water temperature, substrate, and water flow have been documented to influence Odonata distribution (Samways and Steytler 1996; Corbet 2004; Steytler and Samways 1995), but such data were not collected in this study.

Regional variables

Odonata are known to be particularly sensitive to temperature because they are mostly warm-adapted, highly mobile, and shift their ranges readily (Hassall and Thompson 2008). Hassall (2012) found that the highest species richness of Odonata in North America existed in the southeastern USA, where the combination of temperatures and precipitation are highest. We found that dragonfly species richness was higher in areas of higher degree-days, which is a cumulative measure of both temperature and time of year and influences insect growth. The overall occurrence of odonate species was also higher in areas with higher degree-days. Further, in looking at interactions with specific traits, occurrence rates for highly mobile groups, migratory species and dragonflies, was greater in sites with higher degree-days. Previous studies have demonstrated that vagile insect species are more likely to track their climatic niche and expand with climate warming (Pöyry et al. 2009). Highly mobile species are known to be expanding for warm-adapted groups, such as Odonata (Ball-Damerow et al. 2014; Hickling et al. 2006). These groups may become more successful with warmer temperatures that could extend their reproductive period and increase growth rates (Hassall and Thompson 2008).

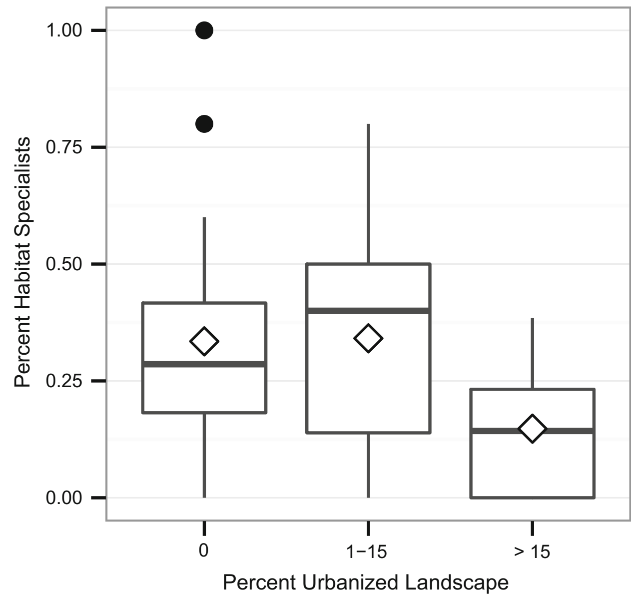

Fig. 2 Percentage of habitat specialists at sites with 0, 1–15, and >15 % high and medium intensity development within a surrounding 1-km buffer radius

Although our study region in California and Nevada is relatively arid, sites had significant variation in precipitation during the wet season (70–2,040 mm with an average of 540 mm), and range from desert regions to mountainous and coastal areas with higher total precipitation. Our study found that dragonfly species richness and odonate species occurrence were positively related to total precipitation. Precipitation is particularly important for aquatic insects, because water availability and precipitation influence the permanence of freshwater habitats.

The western United States has been experiencing extended drought, and climate models predict that future warming will lead to increasingly arid conditions in the region (Cook et al. 2004). Continued and potentially more severe droughts are, therefore, likely to cause future declines in species richness for aquatic taxa, such as Odonata, and particularly for taxa that require perennial water habitat (Boulton 2003). Future taxonomic assemblages in some areas may shift to drought-tolerant specialists with adaptations for ephemeral habitats, such as species with high mobility, desiccation resistant stages, or short life-cycles (Bêche et al. 2006, 2009; Boulton 2003). Specialists for drought conditions often have high conservation value, and currently are relatively rare (Manolis 2003). Increases in these species are less likely to take place in intensively altered landscapes, such as highly urban or agricultural areas where increases in artificial flow from water treatment and irrigation often occurs (e.g., Helms et al. 2009).

Freshwater habitats are often highly degraded in developed regions, partly because humans live disproportionately near waterways (Sala et al. 2000). Rivers and streams in urban areas tend to have high water temperature, exotic vegetation, highly variable flow rate, and poor water quality (Samways and Steytler 1996; Paul and Meyer 2001). As a result, extinction rates of freshwater organisms are among the highest of the major ecosystem types (Ricciardi and Rasmussen 1999).

We found that odonates in general, and particularly habitat specialists, had significantly lower occurrence in highly urban landscapes. Studies of odonates in Europe and Africa have shown that changes in landscape or habitat conditions have resulted in significant declines of habitat specialists, while generalists have increased (Korkeamaki and Suhonen 2002; Clausnitzer 2003). This pattern of decline for habitat specialists and expansion of generalists has been observed for a wide variety of organisms (e.g., McKinney 2002, 2006, 2008). Conservation efforts should therefore seek to promote a diversity of aquatic habitats that support a variety of specialist species in order to protect the widest range of species (e.g., Korkeamaki and Suhonen 2002).

In contrast, there was no significant relationship between highly urbanized areas and site visit species richness in our study. Urban ponds can support relatively large numbers of mostly generalist species when diverse types of aquatic and semi-aquatic vegetation are present (Ball-Damerow et al. 2014; Goertzen and Suhling 2013). Our results also suggest that ponds and streams surrounded by urban landscapes may still provide viable habitat for many generalist species, as long as local habitat features are suitable. At our Coyote Creek site in San Jose, California, for example, we observed 15 species in a sunny section of the river with abundant vegetation, even though the site is surrounded by 74–83 % high and medium intensity development. Other reaches of this stream that were heavily polluted with trash, had very high canopy cover, and little emergent vegetation had much lower species richness (e.g., only four species). Similarly, the Truckee River in Reno, Nevada (58 % highly urban) and Mormon Slough in Stockton, California (73 % highly urban) had moderate species richness, at 10 and 13 species, respectively. At the same time, two of our most urban sites, Stevens Creek in Mountain View (68 % highly urban) and Kern River in Bakersfield (63 % highly urban) had low species richness (five and three total species), which was likely a result of high canopy cover and lack of water, respectively.

Finally, we found that while species richness was not significantly associated with elevation, habitat specialists were more likely to occur in high elevation areas. Low elevation sites are generally associated with greater habitat destruction, which are more likely to negatively influence habitat specialists (Forister et al. 2010). Furthermore, high elevation sites support specialists to montane conditions. These high elevation specialists are adapted to colder conditions and may decline as high-elevation areas become warmer; they may simply have nowhere else to go and are less likely to disperse to new regions (e.g., Angert et al. 2011; Forister et al. 2010).

Conclusions

The relative lack of landscape-scale studies concerning odonates and other aquatic insects in part reflects the limited temporal and spatial scope of occurrence records that are available for large-scale investigations. Exceptions include one study of odonates in North America (Hassall 2012), a few studies in Africa (Clausnitzer 2003, 2012; Finch et al. 2006), and several in Europe (Hassall et al. 2007; van Strien et al. 2010, 2013; Hickling et al. 2005, 2006). Progress in making insect museum specimens and other occurrence data accessible for broader-scale studies lags behind that for other groups, such as vertebrates (e.g., Guralnick and Constable 2010). However, museum specimens of insects are becoming increasingly available in online databases, and may provide a valuable source of data for future landscape-scale studies (Schuh et al. 2010). Moreover, charismatic insects that have been well-collected, such as dragonflies and butterflies, are more likely to have the best available data for future landscape and global change analyses.

While our study identified significant effects of urbanization on the occurrence rates of habitat specialists, the suitability of climate and local habitat may be more important than land use in promoting overall Odonata species richness at individual sites. We found that neither urbanization nor agriculture was significantly related to species richness, indicating that canopy cover and climate may be more important for Odonata diversity in the California-Nevada region studied. This may result from the high vagility and relatively low total-space requirements of most generalist odonates and other insects. In contrast to vertebrate species, the quality of patches rather than the extent of urbanization often determines the diversity of insects (Goertzen and Suhling 2013; Kearns and Oliveras 2009). However, the single most important cause of insect extinction for habitat specialists is the destruction of diverse natural habitats (Pyle et al. 1981). Homogenization of the landscape with urbanization and agriculture has translated into a parallel homogenization of aquatic fauna, with the expansion of habitat generalists and the decline of specialists across large regions (Rahel 2002). This phenomenon is a fundamental driver of biodiversity decline in both terrestrial and aquatic ecosystems throughout the world (McKinney 2006).

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