

Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century

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Received: 9 March 2014 / Revised: 8 April 2014 / Accepted: 15 April 2014 /
Published online: 13 May 2014
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Abstract Increases in water demand, urbanization, and severity of drought threaten freshwater ecosystems of the arid western United States. Historical assessments of change in assemblages over time can help determine the effects of these stressors but, to date, are rare. In the present study, we resurveyed 45 sites originally sampled in 1914–1915 for Odonata (dragonflies and damselflies) adults throughout central California and north-western Nevada, USA. We examined changes in species occurrence rates, taxonomic richness, and biological trait composition in relation to climate changes and human population increases. While species richness at individual sites did not change significantly, we found that odonate assemblages have become more similar across sites. Homogenization is a result of the expansion of highly mobile habitat generalists, and the decline of both habitat specialists and species with an overwintering diapause stage. Using a multi-species mixed-effects model, we found that overall occurrences of Odonata increased with higher minimum temperatures. Habitat specialists and species with a diapause stage, however, occurred less often in warmer regions and more often in areas with higher precipitation. Habitat specialists occurred less often in highly populated sites. Life history traits of Odonata, such as dispersal ability, habitat specialization, and diapause, are useful predictors of species-specific responses to urbanization and climate change in this region.

Keywords Climate change · Urbanization · Long-term change · Life-history traits · Resurvey · Overwintering diapause · Migrant species · Habitat specialization

Communicated by B.D. Hoffmann.

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Introduction

Biodiversity is declining globally in response to widespread habitat degradation and climate change, and rates of decline exceed those of historical periods (Butchart et al. 2010; Dupont et al. 2011; Pimm et al. 1995). Historical resurveys of organisms over time provide particularly useful assessments of biological change, and have revealed significant reductions in biodiversity and pronounced shifts in distribution for a variety of plants (e.g. Lavergne et al. 2006), mammals (Moritz et al. 2008; Rowe et al. 2010; Rubidge et al. 2011), birds (Julliard et al. 2004), fish (Patton et al. 1998), and insects (Bojkova et al. 2012; Cameron et al. 2011; Warren et al. 2001). Such studies, however, are inherently limited by the accessibility and quality of historical records. As a result, relatively few comparisons exist between historic and current surveys, and most comparisons tend to focus on terrestrial habitats (Bojkova et al. 2012). With the exception of butterflies (e.g. Menendez et al. 2006; Poyry et al. 2009; Warren et al. 2001) and bees (e.g. Burkle et al. 2013; Cameron et al. 2011; Dupont et al. 2011), historical studies are particularly rare for insects.

Freshwater ecosystems are one of the most degraded habitat types (Dudgeon et al. 2006). Consequently, freshwater species extinctions are occurring more rapidly than for most terrestrial groups (Ricciardi and Rasmussen 1999). Freshwater insects may be particularly good candidates for historical comparisons that assess the impacts of freshwater habitat degradation over broad spatial and temporal scales. They and other aquatic macroinvertebrates are well-established as biological indicators of ecosystem condition and have a range of tolerances to pollution, different types of stressors, and environmental impairment (Chang et al. 2014; Resh 2008). For example, previous analyses comparing historical museum records with more recent field studies indicate that Plecoptera (stoneflies), which are known to be one of the most sensitive freshwater insect orders, have become extirpated or extinct at alarming rates over the past century in the USA state of Illinois, (DeWalt et al. 2005, 2009; Favret and Dewalt 2002) and in Europe (Fochetti and De Figueroa 2006; Bojkova et al. 2012). Similarly, studies of historical Trichoptera (caddisfly) collections in the midwestern USA suggest high degrees of imperilment (as high as 30–44 %; Houghton and Holzenthal 2010; Resh and Unzicker 1975).

Odonata (dragonflies and damselflies), as a whole, are more tolerant to pollution than taxa in the aquatic insect orders Plecoptera and Trichoptera, but are still significantly less tolerant than other macroinvertebrate groups (Chang et al. 2014). Individual odonate species have a wide range of environmental tolerances, and are good indicators of ecosystem health (e.g. Clausnitzer 2003; Smith et al. 2007), particularly for wetlands (Lunde and Resh 2012). Odonata are also known to be highly responsive to ecosystem conditions in relation to broad-scale factors such as climate (Hickling et al. 2006) and urbanization (Samways and Steytler 1996; Smith et al. 2007; Suhling et al. 2006).

Trends of increasing minimum temperatures over the past several decades have likely enabled many Odonata species to complete development faster, have a longer reproductive period, and expand into higher latitudes or elevations (Hassall and Thompson 2008). However, certain biological traits or other environmental factors may counter potential benefits of higher temperatures for some species. For example, those species with an overwintering diapause stage may not benefit from higher minimum temperatures or could even be negatively impacted (Harrington et al. 2001; Hassall and Thompson 2008). Likewise, lower precipitation and increased drought severity (which has occurred in the western USA over the past century) are both likely to negatively influence Odonata species in general, as species richness tends to be higher in warm and wet regions (e.g. Hassall and Thompson 2010). In addition, habitat specialists are known to have higher local extinction

in areas with increased urbanization, while generalists often do not (Goertzen and Suhling 2013; Warren et al. 2001). Overall, global predictions of future biodiversity indicate that the California Mediterranean is one of the world's ecoregions likely to experience the most change over the next 100 years due to continued land use change and introduced species (Sala et al. 2000).

The earliest comprehensive assessment of freshwater insects in the western USA was C.H. Kennedy's surveys of Odonata in central California and northwestern Nevada in 1914–1915 (Kennedy 1917). Here, we compare Odonata assemblages from C.H. Kennedy's historical survey to resurveys conducted at the same sites in 2011–2013. We investigate the impact of several environmental factors on odonate occurrence. To our knowledge, there have been no studies that assessed historical resurveys of Odonata at large spatial or temporal scales. In this study, we determine whether there have been changes in species richness and community similarity among sites across the study area and within individual ecoregions. We then identify individual species and biological traits that have increased or declined in prevalence over time, and assess the effects of temperature, precipitation, and urbanization on species richness and occurrence.

Methods

Study area

The study area encompassed 45 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). Sites were located within four of the ecological regions delineated by the World Wildlife Fund Conservation Science Program (Olson et al. 2001), including the Sierra Nevada Forest, California Mediterranean, Great Basin Shrub Steppe, and Northern Coastal California Forests regions (Fig. 1). These four regions all have dry summers and wet winters, with precipitation generally from October through April.

C.H. Kennedy first surveyed these sites in 1914–1915 in an effort to characterize Odonata species distributions and identify any new species within the region (Kennedy 1917). We chose our sample locations to be the same or comparable to his original locations. Kennedy collected extensively around Palo Alto, CA, and his site descriptions for this area are general (e.g. streams and ponds). Therefore, for this region, we also surveyed numerous ponds and streams to represent habitats within the vicinity. Habitat types included both lotic (streams, rivers, and canals) and lentic (wetlands, ponds, lakes, and sloughs) habitats. However, some habitats, such as sloughs of large and urban rivers (e.g. those of the Yuba River and Sacramento River) and hot springs (e.g. Golconda hot springs and Calistoga hot springs), that he sampled were now inaccessible or no longer present as a result of development, and consequently were excluded from the analysis.

Since the early 1900s, urbanization has greatly expanded throughout the western USA; the total human population in California has increased from around 2.7 million to over 37 million (California Department of Finance 2010), and from 80,000 to 2.7 million in Nevada (US Census Bureau 1913, 1922, 2002, 2013). Coastal and valley regions of California, in particular, have been covered in impervious surfaces and crops (Mount 1995). Irrigation canals and channelized urban streams now provide water sources throughout regions that were previously dry in summer, while also draining water from other natural streams and lakes (Mount 1995). As a consequence, freshwater habitats in the western



Fig. 1 Map of study sites and ecoregions

USA now exhibit altered water quality, stream flow, and habitat structure compared to their original state (Mount 1995).

Odonata survey

We designed the field surveys for this study to be as similar as possible to the original surveys of C.H. Kennedy (Kennedy 1917). Survey dates were determined using collection dates for Kennedy's specimens in the Essig Museum of Entomology, the California Academy of Sciences, Florida State Collection of Arthropods, the Museum of Zoology at the University of Michigan, the National Museum of Natural History, and, in some cases, from Kennedy's description in his survey (Kennedy 1917). Lists of species for the historical survey were compiled from Kennedy's study. We updated old species names and, in a few cases, added species that were present in the collections for certain sites but were missing from his 1917 article. We visited Kennedy's sample locations the same number of times (or more) and within one or 2 weeks of the original calendar dates of his collections. Kennedy's notes indicate that he generally visited individual sites for more than 3 h during each visit. Therefore, we also visited each site for more than 3 h, unless the habitat was

highly degraded and there was little to no Odonata activity. The total time spent surveying averaged 4.6 ± 3.3 h (Table 1) per site.

We surveyed each site for adult Odonata from late-April through mid-September in 2011 and 2012, and re-visited or added a few sites in 2013. Surveys took place during peak periods of Odonata activity, usually from 10 am until 4 pm, when temperatures were above 17 °C and cloud cover was low. We visited each site from one to five times over the study period. The same primary collector (J.E. B-D.) was present at each survey, identified all species, and was accompanied by one or more additional collectors. We typically 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. Specimens collected are now in the Essig Museum of Entomology Collection at the University of California, Berkeley.

Change in species occurrence

To compare the number of occurrences in the two surveys, we first summed the number of sites where each species was observed. The absolute difference in number of occurrences could be influenced by the degree of effort in the surveys, which we accounted for by calculating change in relative occurrence rates. We obtained relative occurrence values by dividing the absolute number of occurrences by the total number of occurrences within each respective survey.

Change in species richness

We calculated species richness across different scales by separately summing the total number of species encountered over the course of the historical survey and of the resurvey. We also calculated the total and average species richness within each ecoregion and at each site for the two time periods. To assess whether significant changes in species richness have occurred across individual sites, across ecoregions, and across sites within each ecoregion, we conducted paired t-tests to compare means for the two time periods.

To determine whether climate and human population increases have impacted Odonata species richness over time, we used a generalized linear mixed model (GLMM) with a log link function and Poisson error distribution. These models can accommodate non-normal error distributions and incorporate random effects to control for correlations brought about by groups of observations. GLMMs were implemented using the linear mixed-effects models lme4 package (Bates et al. 2013) in the statistical program R, version 3.0.1

Table 1 Summary of effort and environmental variables in the 1914–1915 surveys and 2011–2013 resurveys

Variable	1914–1915 avg. value (min–max)	2011–2013 avg. value (min–max)	Change
Effort (# visits)	2.3 (1–5)	2.4 (1–5)	N/A
Min. monthly temp over water year (°C)	−0.85 (−10.7 – 6.1)	−1.9 (−12.4 – 4.1)	−1.05
Avg. min. annual temp for calendar year (°C)	5.25 (−3 – 9.6)	6.32 (−1.5 – 12.2)	1.07
Total precipitation (mm)	785 (133 – 2,082)	585 (64 – 1,926)	−200
Human population	6,069 (0 – 53,181)	88,889 (0 – 956,142)	82,820

(R Development Core Team 2013). Site and an era indicator (i.e. 1914–1915 survey or 2011–2013 resurveys) were both included as random effects. The model is defined as follows:

$$\begin{aligned} \text{Species richness} = & \text{intercept} + \text{minimum temperature} + \text{total precipitation} \\ & + \text{human population} + \text{random effects (site, era)}. \end{aligned}$$

Change in community similarity

In order to determine whether Odonata assemblages have become more similar across sites since the 1914–1915 surveys by Kennedy, we first calculated pairwise Jaccard Similarity Indices among sites within each ecoregion and survey-wide for each time period. This widely-used similarity index is a measure of percent similarity: $[a/(a + b + c)]$, where a is the number of species present in both assemblages, b is the number of species present only in the first assemblage, and c is the number of species present only in the second assemblage. These values range from 0, where no species are shared, to 1, where assemblages are exactly the same (Rahel 2002). We then subtracted each pairwise Jaccard Index of Kennedy's survey from the same pairwise comparison of resurveys (Marchetti et al. 2001). Finally, we determined the proportion of pairwise comparisons that increased or decreased in community similarity since 1914–1915, and conducted binomial tests to determine if there were significantly more increases in similarity than decreases.

Change in biological traits

We predicted that the prevalence of several biological traits within Odonata assemblages would have changed over time in response to climate or habitat alterations, as summarized in Table 2. It should be noted that two traits, tolerance value and the presence of an overwintering egg/larval diapause stage, were often only available at the genus-level. To determine whether species with certain biological traits have changed in occurrence rates over time, we used a GLMM with a logit link function and binomial error distribution.

Model parameters included interactions between all species traits and era. Both family and genus were included in the model as random effects to, at least partially, account for the related species being more likely to exhibit similar trait values. 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 genus within family 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 and site were also included as random effects. The model is defined as follows:

$$\begin{aligned} \text{Species detection} = & \text{intercept} + \text{era} \times \text{low dispersal} + \text{era} \times \text{migrant} \\ & + \text{era} \times \text{habitat specialist} + \text{era} \times \text{forest specialist} \\ & + \text{era} \times \text{lotic specialist} + \text{era} \times \text{tolerance value} \\ & + \text{era} \times \text{generation time} + \text{era} \times \text{diapause} \\ & + \text{era} \times \text{elevation preference} \\ & + \text{random effects (family, genus, species, site)}. \end{aligned}$$

Table 2 Predicted increase or decline in biological traits over time

Trait	Explanation	Predicted change	References
Low dispersal (0/1)	Limited distribution, not known to move far from natal habitat	(–)	Corbet (2004)
Migrant (0/1)	Migrate annually, includes 5 species in CA	(+)	May (2013)
Habitat specialist (0/1)	Require certain habitat types to complete life cycle, such as flowing water or high elevation	(–)	Habitat descriptions in Manolis (2003)
Forest specialist (0/1)	Specialized to occur within forested regions	(–)	Habitat descriptions in Manolis (2003)
Lotic specialist (0/1)	Specialized to occur within streams or rivers	(–)	Habitat descriptions in Manolis (2003)
Tolerance value (1–10)	Sensitivity to poor water quality, usually organic pollution	(–)	Barbour et al. (1999)
Generation time (long, short)	Long-lived species generation times >1 year, short-lived species ≤1 year	(–)	Bêche et al. (2006) (genus-level), Corbet (2006)
Overwintering (egg/larval) diapause (0/1)	Presence of overwintering diapause to resist desiccation and/or cold temperatures	(–)	Bêche et al. (2006) (genus-level), Corbet 2004
Elevation preference (low, low-mid, high)	Estimates of elevation preferences, including low: 0–900 m, low-mid: 0–2,000 m, high: only known from higher elevations	(–)	Habitat descriptions in Manolis (2003)

Effects of climate and urbanization

We obtained monthly minimum temperature and total precipitation data from the PRISM Climate Group (2013). These variables were calculated over the duration of the water year before the sample date (i.e. from October 1 through the month before each site visit), which is the period over which most species would be developing as aquatic larvae. For sites that were visited more than once, we took the average minimum temperature and precipitation values over the site visits. To put temperature values in context of trends occurring over time within the region, we calculated average annual minimum temperatures across California and Nevada using the raster package (Hijmans 2013) in the statistical program R, version 3.0.1 (R Development Core Team 2013). We also averaged annual minimum temperatures across the study sites over the respective calendar years of the 1914–1915 and 2011–2013 surveys.

To assess the impact of urbanization over time, we used human population as the best available measure of both historical and current urbanization. We obtained population data for the nearest town to sampling site for each time period, including 1910, 1920, 2000, and 2010 (California Department of Finance 2010; US Census Bureau 1913, 1922, 2002, 2013). We then calculated the average annual population increase over 1910–1920 and 2000–2010 to obtain population values for 1914 and 2012.

We used results of the first GLMM (described above) to identify traits to then include in a second, more complex model. The purpose of this second GLMM was to assess, in finer detail, potential mechanisms responsible for changes in biological trait composition over time. We first normalized all continuous variables by subtracting the mean and dividing it

by the standard deviation to facilitate interpretation of effect sizes. We tested for collinearity using Spearman rank correlation coefficients and found that none of the variables were strongly correlated with one another ($r \leq 0.50$).

We again modeled multi-species occurrence as a logistic regression, assuming a binomial error distribution and logit link function. In this case, family, genus, species, site, and era were all treated as random effects. Instead of using era as a fixed effect in the model, we included the three variables described above (minimum temperature, total precipitation, and human population). Our full model is given by:

$$\begin{aligned} \text{Species occurrence} = & \text{intercept} + \text{minimum temperature} \times \text{migrant} \\ & + \text{minimum temperature} \times \text{habitat specialist} \\ & + \text{minimum temperature} \times \text{diapause} + \text{total precipitation} \\ & \times \text{migrant} + \text{total precipitation} \times \text{habitat specialist} \\ & + \text{total precipitation} \times \text{diapause} + \text{human population} \\ & \times \text{migrant} + \text{human population} \times \text{habitat specialist} \\ & + \text{human population} \times \text{diapause} \\ & + \text{random effects (family, genus, species, site, era)}. \end{aligned}$$

Regression estimates from these models were given in the logarithmic scale for standardized covariate values. We therefore converted the estimates from the logarithmic scale to obtain differences in the probability of presence per standardized unit increase for the respective covariate.

Results

Change in species occurrence

Over the course of the 2011–2013 resurveys, we collected and observed a total of 69 species, while Kennedy observed a total of 80 species across the 45 sites. We collected 67 of the same species that Kennedy found (Table 3). *Libellula luctuosa* and *Enallagma civile* were both completely absent from Kennedy's surveys, but were common in 2011–2013 with nine and 18 site occurrences, respectively. Kennedy observed *Sympetrum danae* (6 occurrences), *Ophiogomphus occidentis* (5 occurrences), *Sympetrum costiferum* (3 occurrences), and *Libellula nodisticta* (3 occurrences), which we did not observe in our surveys. During 2011–2013 resurveys, we did not observe nine additional species that were rare in Kennedy's survey (one or two occurrences; Table 3).

Overall, a total of 52 species declined (65 %) in relative frequency of sites when compared to the 1914–1915 surveys, while 29 species increased (36 %). Fifty-two species were considered habitat specialists, and 34 (65 %) of them declined since 1914–1915. Out of the 16 species with the largest declines since 1914–1915, all but three (*Lestes congener*, *Sympetrum pallipes* and *S. semicinctum*) were habitat specialists. Conversely, there were a total of 29 habitat generalists, and 18 (62 %) of them increased since 1914–1915. The average percentage of generalists at each site increased from about 55 % in 1914–1915 to 73 % in 2011–2013 ($t = 5.28$, $P < 0.0001$). Out of the 14 species with the largest increases since 1914–1915, all but three (*Argia vivida*, *Argia emma* and *Enallagma clausum*) were habitat generalists.

Table 3 Comparison of species occupancy from 1914–1915 surveys and 2011–2013 resurveys at 45 sites throughout California and Nevada

Species name	1914–1915	2011–2013	Occurrence change	Relative change	Specialization
<i>Lestes congener</i>	14	3	–11	–0.0217	G
<i>Sympetrum pallipes</i>	18	7	–11	–0.0220	G
<i>Sympetrum obtrusum</i>	9	2	–7	–0.0138	S
<i>Sympetrum danae</i>	6	0	–6	–0.0117	S
<i>Macromia magnifica</i>	9	3	–6	–0.0119	S
<i>Ophiogomphus occidentis</i>	5	0	–5	–0.0097	S
<i>Progomphus borealis</i>	7	2	–5	–0.0099	S
<i>Ophiogomphus morrisoni</i>	8	3	–5	–0.0100	S
<i>Aeshna interrupta</i>	6	2	–4	–0.0080	S
<i>Stylurus olivaceus</i>	6	2	–4	–0.0080	S
<i>Hetaerina americana</i>	11	7	–4	–0.0084	S
<i>Libellula nodisticta</i>	3	0	–3	–0.0058	S
<i>Sympetrum costiferum</i>	3	0	–3	–0.0058	S
<i>Coenagrion resolutum</i>	4	1	–3	–0.0059	S
<i>Ophiogomphus bison</i>	4	1	–3	–0.0059	S
<i>Sympetrum semicinctum</i>	9	6	–3	–0.0063	G
<i>Archilestes californicus</i>	2	0	–2	–0.0039	S
<i>Ischnura gemina</i>	2	0	–2	–0.0039	S
<i>Lestes unguiculatus</i>	2	0	–2	–0.0039	S
<i>Leucorrhinia glacialis</i>	2	0	–2	–0.0039	S
<i>Ophiogomphus severus</i>	1	0	–1	–0.0019	S
<i>Sympetrum internum</i>	2	0	–2	–0.0039	G
<i>Aeshna umbrosa</i>	1	0	–1	–0.0019	S
<i>Epitheca spinigera</i>	1	0	–1	–0.0019	S
<i>Plathemis subornata</i>	1	0	–1	–0.0019	S
<i>Enallagma praevarum</i>	5	9	4	0.0071	G
<i>Argia vivida</i>	14	18	4	0.0064	G
<i>Argia emma</i>	15	19	4	0.0063	S
<i>Enallagma clausum</i>	1	6	5	0.0093	S
<i>Sympetrum corruptum</i>	21	27	6	0.0095	G
<i>Ischnura cervula</i>	19	26	7	0.0116	G
<i>Pachydiplax longipennis</i>	5	13	8	0.0146	G
<i>Rhionaeschna multicolor</i>	23	31	8	0.0131	G
<i>Libellula luctuosa</i>	0	9	9	0.0168	G
<i>Libellula saturata</i>	12	21	9	0.0159	G
<i>Tramea lacerata</i>	7	21	14	0.0256	G
<i>Pantala hymenaea</i>	4	19	15	0.0277	G

Table 3 continued

Species name	1914–1915	2011–2013	Occurrence change	Relative change	Specialization
<i>Anax junius</i>	13	28	15	0.0270	G
<i>Enallagma civile</i>	0	18	18	0.0336	G
Total occurrences	275	304			

Species with no change or with change of only one or two occurrences are not included, unless they were not observed in resurveys. Relative change is the number of species occurrences divided by the total occurrences among all species during the respective surveys

S habitat specialist, G habitat generalist

Change in species richness

Species richness showed no statistically significant changes across individual sites, either survey-wide or within individual ecoregions (Table 4). The average species richness within individual ecoregions was 42 in 1914–1915 and 37 in 2011–2013 ($P = 0.22$). Total species richness within the California Mediterranean declined from 51 in 1914–1915 to 45 in 2011–2013, declined within the Great Basin shrub steppe from 44 in 1914–1915 to 32 in 2011–2013, and remained similar in the Northern California coastal forests (37 in 1914–1915 and 38 in 2011–2013) and the Sierra Nevada forests (34 in 1914–1915 and 34 in 2011–2013; Table 4).

The species richness GLMM demonstrated only weak or insignificant relationships with environmental covariates. Species richness, however, was significantly lower in areas with increased human population over the past century (Table 5).

Change in community similarity

Community similarity across all sites significantly increased between 1914–1915 and 2011–2013 (Table 6). When comparing Jaccard indices for all sites pairs between the two time periods, there were 638 increases in Jaccard similarity indices out of 989 site comparisons (probability of increase = 65 %, $P < 0.001$, Table 6). There were also significantly more increases in Jaccard similarity indices than decreases within sites of the California Mediterranean, with 144 increases out of 231 comparisons (62 %, $P < 0.001$) and the Northern California Coastal Forests, with 13 increases out of 15 comparisons (87 %, $P = 0.007$). The number of increases was not significantly greater than decreases for the Great Basin Shrub Steppe, the Sierra Nevada Forests, or for total species within each ecoregion.

Change in biological traits

The results of our GLMM model for interactions between biological traits and era indicate that only three traits changed significantly from the 1914–1915 surveys to 2011–2013 resurveys. Migratory species increased significantly, whereas habitat specialists and species with an overwintering diapause declined significantly over time (Table 7, Fig. 2).

Effects of climate and urbanization

The average minimum temperature for the study sites decreased from -0.85 °C (± 5.1) in 1914–1915 to -1.9 °C (± 5.3) in 2011–2013 during the water year, and average total

Table 4 Total and average species richness for 1914–1915 and 2011–2013 at different scales: for individual sites, sites within each ecoregion, total species of each ecoregion, and total species survey-wide

Scale	1914–1915	2011–2013	Change	t	df	P value	Confidence interval	
Site	12.1 ± 7.5	11.9 ± 5.7	−0.2	0.28	44	0.78	−1.37	1.82
Ecoregion	42 ± 7.3	37 ± 5.7	−4.5	1.55	3	0.22	−4.73	13.73
Avg. California Mediterranean	14 ± 7.6	13 ± 5.8	−0.9	−0.22	41	0.83	−4.64	3.73
Avg. Great Basin shrub steppe	15 ± 9	11 ± 4.1	−3.7	0.91	12	0.38	−3.57	8.68
Avg. Northern California coastal forests	17 ± 8.6	19 ± 7.9	1.9	−0.39	9	0.71	−12.59	8.93
Avg. Sierra Nevada forests	13 ± 5.7	12 ± 4.1	−1.1	0.35	13	0.73	−5.20	7.20
Total California Mediterranean	51	45	−6.0	–	–	–	–	–
Total Great Basin shrub steppe	44	32	−12.0	–	–	–	–	–
Total Northern California coastal forests	37	38	1.0	–	–	–	–	–
Total Sierra Nevada forests	34	34	0.0	–	–	–	–	–
Total survey-wide	80	69	−11.0	–	–	–	–	–

Table 5 Model estimates for effects of minimum temperature, total precipitation and human population on Odonata species richness for 1914–1915 surveys and 2011–2013 resurveys

	Estimate	SE	Z value	P value
(Intercept)	2.33	0.10	24.41	<0.001
Minimum temperature	−0.09	0.06	−1.532	0.125
Total precipitation	−0.05	0.04	−1.346	0.178
Human population	−0.07	0.02	−4.002	<0.001

Significant relationships are bolded

precipitation across sites decreased from 785 mm (±492) in 1914–1915 to 585 mm (±421) in 2011–2013 (Table 1). Minimum temperature averaged across California and Nevada over calendar years, however, have shown consistent increases over time (Fig. 3a, b). Annual average minimum temperature over calendar years at the study sites also increased from 5.25 (±4.0) in 1914–1915 to 6.32 (±3.9) in resurveys (Table 1). The average human population across sites increased from 6,069 (±10,802) to 88,889 (±178,224), with considerable variation among sites (Table 1).

The multispecies GLMM that we used to assess interactions between traits and environmental covariates showed several relatively strong and significant relationships. The following values represent differences in the probability of occurrence per standardized unit increase in the respective environmental covariate. The probability of species occurrence was 29 % higher with higher minimum temperature, but 13 % lower with higher human population (Table 8). For habitat specialists and species with overwintering diapause, the probability of occurrence was lower with increasing minimum temperature

Table 6 Number of increases and decreases in Jaccard Similarity Index Scores for site comparisons, from 1914–1915 surveys to 2011–2013 resurveys

	# Sites	Total comparisons	Increases	Decreases	Sign test <i>P</i> value	Prob. of change	Confidence interval	
All sites	45	989	638	263	<0.001	0.65	0.61	0.67
California Mediterranean	22	231	144	56	<0.001	0.62	0.56	0.69
Great Basin shrub steppe	9	36	18	18	1	0.50	0.33	0.67
Northern California coastal forests	6	15	13	2	0.007	0.87	0.60	0.98
Sierra Nevada forests	8	28	10	17	0.345	0.61	0.41	0.78
Ecoregions	4	6	5	1	0.219	0.83	0.36	1.00

Significant differences in number of increases over decreases in similarity are bolded

Table 7 Multi-species model estimates for the effects of time period (era, from 1914–1915 to 2011–2013), biological traits, and interactions on Odonata species detection

Parameter	Estimate	SE	Z value	<i>P</i> value	Diff. in prob. of presence
(Intercept)	−1.46	1.24	−1.18	0.239	−0.77
Era	0.07	0.62	0.11	0.916	0.07
Low dispersal	−0.05	0.80	−0.07	0.946	−0.05
Migrant	−2.73	0.65	−4.23	0.000	−0.93
Habitat specialist	−1.03	0.35	−2.92	0.004	−0.64
Forest specialist	−0.41	0.45	−0.90	0.370	−0.33
Lotic specialist	−0.19	0.43	−0.45	0.649	−0.18
Tolerance value	−0.04	0.08	−0.52	0.600	−0.04
Generation time (long or short)	0.71	0.76	0.93	0.351	1.03
Diapause	0.49	0.35	1.41	0.159	0.63
Elevation preference (low, mid, high)	−0.12	0.30	−0.39	0.697	−0.11
Low dispersal × era	−0.44	0.41	−1.07	0.284	−0.36
Migrant × era	1.49	0.26	5.71	0.000	3.42
Habitat specialist × era	−0.37	0.17	−2.18	0.029	−0.31
Forest specialist × era	0.07	0.23	0.31	0.754	0.07
Lotic specialist × era	0.18	0.21	0.87	0.385	0.20
Tolerance value × era	−0.01	0.04	−0.24	0.809	−0.01
Generation time × era	−0.11	0.39	−0.28	0.778	−0.10
Diapause × era	−0.45	0.17	−2.74	0.006	−0.36
Elevation preference × era	−0.01	0.16	−0.09	0.929	−0.01

Difference in probability of presence values correspond to the difference in probability of presence per standardized unit increase of the respective covariate. Significant values are bolded

(−38 and −42 %, respectively), but higher with increasing precipitation (21 and 53 %, respectively; Table 8). In contrast, migratory species had a lower probability of presence (−48 %) in areas of higher precipitation (Table 8). Finally, habitat specialists had a lower probability of occurrence (−24 %) in areas of higher human population (Table 8).

Fig. 2 Proportional change in occurrences of migrant species, species with overwintering diapause, and habitat specialists from the 1914–1915 surveys to 2011–2013 resurveys

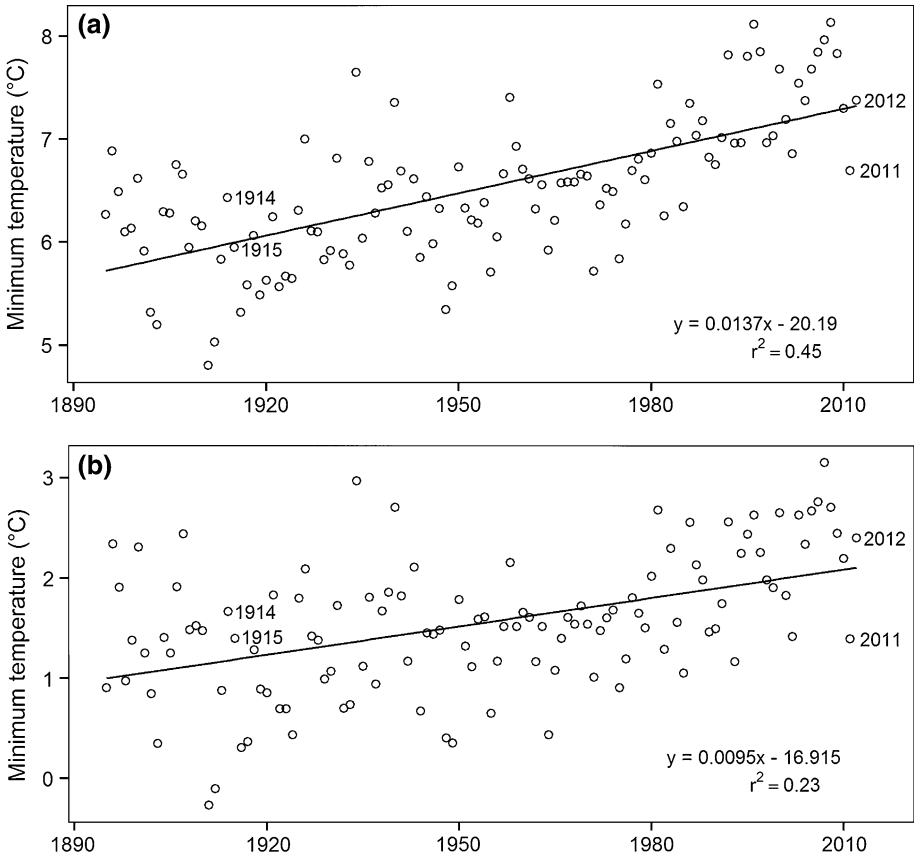
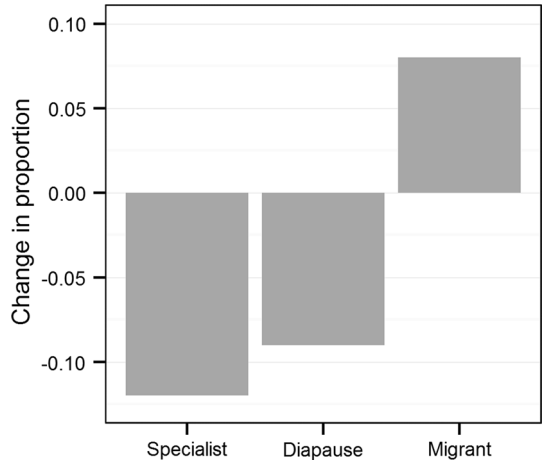


Fig. 3 Average annual minimum temperature, over the calendar year, from 1895 to 2012 across (a) California and (b) Nevada

Table 8 Multi-species model estimates for the effects of temperature, precipitation, human population, species traits, and interactions on Odonata species detection for 1914–1915 surveys and 2011–2013 resurveys

Parameter	Estimate	SE	Z value	P value	Diff. in prob. of presence
(Intercept)	−1.50	0.28	−5.43	<0.001	−0.78
Migrant	−0.63	0.49	−1.27	0.204	−0.47
Habitat specialist	−1.65	0.22	−7.45	<0.001	−0.81
Diapause	−0.30	0.25	−1.21	0.226	−0.26
Minimum temperature	0.25	0.12	2.15	0.032	0.29
Total precipitation	−0.11	0.09	−1.25	0.212	−0.11
Human population	−0.14	0.05	−2.73	0.006	−0.13
Minimum temperature × migrant	−0.04	0.14	−0.29	0.775	−0.04
Minimum temperature × habitat specialist	−0.47	0.06	−7.44	<0.001	−0.38
Minimum temperature × diapause	−0.54	0.07	−8.04	<0.001	−0.41
Total precipitation × migrant	−0.64	0.17	−3.72	<0.001	−0.47
Total precipitation × habitat specialist	0.20	0.07	3.06	0.002	0.22
Total precipitation × diapause	0.44	0.07	6.50	<0.001	0.55
Human population × migrant	0.00	0.11	−0.03	0.977	0.00
Human population × habitat specialist	−0.28	0.10	−2.72	0.007	−0.24
Human Population × diapause	−0.12	0.09	−1.23	0.218	−0.11

Difference in probability of presence values correspond to the difference in probability of presence per standardized unit increase of the respective covariate. Significant values are bolded

Discussion

Change in occurrence

Two currently common species, *Enallagma civile* and *Libellula luctuosa*, were not present at all during Kennedy's 1914–1915 surveys (Table 3). *Enallagma civile* and *L. luctuosa* did not show up in California collection records until 1926 and 1936, respectively, and both have steadily increased in distribution and prevalence since that time (Manolis 2003). These species have expanded with human alteration of landscapes and waterways, and are often abundant where they occur, especially *E. civile* (Manolis 2003). The expansion of irrigation throughout the Central Valley has created perennial freshwater habitat where it previously did not exist during the dry summer season, and this may allow generalists such as these species to expand in distribution and abundance (Rosser Garrison, *personal communication*).

Changes in species detection may be the result of increased or decreased abundance brought about by climate or land-use (Gaston 2011). Local abundance and regional occupancy tend to be correlated, so that abundant species are often more widely distributed (Gaston 2011). In contrast, populations of some species that decline in abundance may become increasingly localized, but not eliminated from a region or site (Beketov et al. 2013), and therefore have lower detection probabilities. It is likely that at least some of the species from Kennedy's survey that we did not find have declined in abundance and become more difficult to detect.

Shifts in phenology (e.g. Dingemanse and Kalkman 2008), changes in predators (e.g. McPeck 1998), competition with introduced species, and other specific interactions undoubtedly also contribute to rates of occurrence of Odonata (Corbet 2004). We note that such factors are likely to be at least partially responsible for changes in Odonata occurrence rates that we observed. For example, the reduction that we observed in occurrences for species with synchronous emergence (e.g. *L. congener* and *S. pallipes*; Table 3) could, in some cases, be from a mismatch between their emergence time and the time of site visits.

We also recognize that the presence of adult species does not necessarily indicate that the site is suitable for larval habitat and successful life-cycle completion, particularly for migrant species. However, adults do engage in habitat selection for reproduction and foraging (Corbet 2004). Adult males defend territories that are attractive to females, and females oviposit in sites likely to be suitable larval 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).

Change in species richness and community similarity

While species richness of Odonata in our study declined survey-wide, richness did not change significantly at the site-level (Table 4). This is because site-level colonization of more generalized species compensated for loss of specialized species, leading to the increased similarity of Odonata assemblages across sites. Similar homogenization has occurred in numerous studies of other organisms, such as fish across California (Marchetti et al. 2001), multiple freshwater organisms in North America (Rahel 2002), plant communities across metropolitan areas of the USA (McKinney 2006), and butterfly species across Canada (White and Kerr 2007).

Urbanization and development have resulted in increased homogenization of odonate assemblages. We found that the most highly developed ecoregions of California, including the California Mediterranean and Northern California Coastal Forests have become significantly more similar, while the least developed regions (Great Basin Shrub Steppe and Sierra Nevada Forests) did not. Studies of Odonata in Africa also demonstrated that the most highly disturbed and urbanized regions had lower β -diversity (Clausnitzer 2003). Increasing community similarity reflects homogenization of the landscape, which has occurred largely as a result of urbanization and agriculture, and is a leading cause of global biodiversity decline (Marchetti et al. 2001; McKinney 2002, 2006).

Change in biological traits

We found that most species that declined in relative occurrence were habitat specialists and most that increased were generalists. Numerous studies have shown that ecological generalization often promotes rates of colonization in a variety of organisms, while specialization has the opposite effect (Dupont et al. 2011; Ruesink 2005; Vall-Ilosera and Sol 2009; Warren et al. 2001). A study in Finland comparing odonate communities present in 1930–75 to those in 1995–96 found that generalist species were much less likely to become locally extinct (Korkeamaki and Suhonen 2002). We found that although habitat specialists have declined, certain types of specialists (i.e., forest or lotic specialists) have not changed significantly. This finding mirrors those of Julliard et al. (2004) who demonstrated that bird species with the highest degrees of specialization showed the steepest declines, but that specialization itself (rather than affinity for any one type of habitat) was associated with

decline. Habitat generalization may thus increase the likelihood that species will be able to find suitable resources in new location (Hill et al. 2002; Poyry et al. 2009).

Four out of the five Odonata species in California that are known to migrate annually (*Anax junius*, *Tramea lacerata*, *Pantala hymenaea*, and *Sympetrum corruptum*) were among the species that expanded most in their occurrence. Our multispecies model also demonstrated that migrant species greatly increased in prevalence since the 1914–1915 survey (Table 7). Previous work in Namibia has shown that highly mobile Odonata species have become increasingly common in areas affected by anthropogenic disturbance (Suhling et al. 2006). Reduced area and connectivity of natural habitats limit colonization to highly mobile and widespread species, which are known to have larger foraging ranges (Warren et al. 2001). Therefore, these species may respond to environmental change on a larger spatial scale and may be less vulnerable to habitat fragmentation (Dupont et al. 2011).

We found that species with overwintering egg or larval diapause declined significantly in the resurvey. Overwintering diapause is considered to be an adaptation for some tropical species that has enabled them to survive the winters in temperate regions (Corbet 2004). Winter mortality from cold temperature is a primary concern for many temperate insects, and thus increases in winter temperatures may improve survival and growth rates of species lacking a dormant stage (Harrington et al. 2001). In contrast, species with diapause are highly resistant to cold temperatures, but may not benefit to the same extent from a warming climate, because they are less likely to experience higher growth rates from slight increases in warmth (Harrington et al. 2001). Cold spells that occur soon after eggs hatch can also be detrimental to such species, as their early instar larvae are highly susceptible to cold (Sawchyn and Gillott 1974). Warmer temperatures could place species with diapause at risk as temperature thresholds that cue the onset of diapause or the egg hatching may occur at inopportune times (Hassall and Thompson 2008).

Effects of climate and urbanization

As a generally warm-adapted group, we would expect most Odonata species to benefit from rising temperatures and precipitation (Hassall and Thompson 2008). Hickling et al. (2006) demonstrated that, among a range of taxa in Britain, odonates expanded the most into higher latitudes and altitudes as warming increased. Similarly, Rosset and Oertli (2011) found that dragonflies were more successful in responding to climate warming than snails, beetles, amphibians, and plants in small ponds in Switzerland. These authors predicted that 61 % of dragonfly species would expand their ranges as climates warmed.

Although average annual minimum temperature has increased steadily over the past century in the study region, our resurvey was conducted in years with unusually low temperatures during the water year period (i.e. October through the sampling month). Overall, we found that significantly more Odonata occurred at sites with higher minimum (water year) temperatures, but a higher proportion (65 %) of species declined in occurrence. Some of the apparent declines observed here may then have resulted from the cooler winter temperatures that occurred during the years of our resurveys.

A subset of species are more adapted to cooler temperatures and may not benefit from warming temperatures, and many are likely to suffer from lower annual precipitation (Hassall and Thompson 2008). In our study, habitat specialization and diapause traits were both negatively associated with higher minimum temperatures and positively associated with precipitation. Many habitat specialists occur in high elevation areas or forested regions with cooler temperatures and higher precipitation (Corbet 2004; Manolis 2003).

Species with an overwintering diapause stage may occur more often in areas with colder minimum temperatures, because diapause is largely an adaptation to survive cold winters (Corbet 2004; Harrington et al. 2001). However, they also tend to occur in highly variable intermittent or ephemeral habitats, and may therefore be more susceptible to “boom” or “bust” years associated with precipitation (Bêche et al. 2006).

Freshwater ecosystems are particularly threatened by land use, in part because people live disproportionately near waterways, even in regions where surrounding areas are sparsely populated (Sala et al. 2000). As a result, freshwater biomes are experiencing much greater rates of extinction (Ricciardi and Rasmussen 1999). We found that areas of high human population supported the occurrence of fewer specialist odonates. Likewise, other more localized studies have demonstrated that urban areas supported lower odonate species richness, and were dominated by tolerant, generalist species (Goertzen and Suhling 2013; Samways and Steytler 1996).

Overall, habitat loss through anthropogenic land use is a major cause of both extinctions and declines in species richness in modern landscapes (Sala et al. 2000), and it is the leading cause of biotic homogenization (Marchetti et al. 2001; McKinney 2002, 2006, 2008). In revisiting sites sampled by an Odonata specialist nearly a century ago, our study has demonstrated significant homogenization of Odonata communities in central California and northwestern Nevada. However, many urban sites with suitable habitat can still support relatively species rich communities with high abundance, albeit dominated by widespread species. This finding may prove hopeful for urban restoration projects that aim to support diverse communities of charismatic insects, such as dragonflies. Generalist species are likely to continue expanding with urbanization, at the expense of specialists and of regional and global biodiversity (Marchetti et al. 2001; McKinney 2006; White and Kerr 2007).

Acknowledgments This research was supported in part by the National Science Foundation under Grant No. DBI 0956389, and the Margaret C. Walker Fund for teaching and research in systematic entomology. LKM was supported by a Natural Sciences and Engineering Research Council of Canada Postdoctoral Fellowship. We thank Dennis Paulson, Rosser Garrison, Timothy Manolis, and Giovanni Rapaciuolo for their advice on aspects of the work. We also thank Norm Penny and Mark O'Brien for their assistance with C. H. Kennedy's original Odonata specimens at the California Academy of Sciences and the University of Michigan Museum of Zoology, respectively.

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