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Diversity and Distribution of California Dragonflies and Other Aquatic Taxa Over the Past Century

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Diversity and Distribution of California Dragonflies and Other Aquatic Taxa Over the Past Century

By

Joan Elizabeth Damerow

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Abstract

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Climate and land-use change have altered and continue to affect the diversity, composition, and distribution of freshwater organisms throughout the world. This is particularly true in arid and semi-arid regions, where aquatic organisms may experience more pronounced reductions in available habitat with declines in precipitation, increases in water demand, and habitat degradation through human land-use. However, documentation of changes in taxonomic assemblages over long-time periods has been rare because of the difficulty in obtaining historical occurrence data. This dissertation used data from previously published literature, a resurvey study, museum specimens, and enthusiast sightings to document changes in the occurrence rates and distribution of freshwater organisms throughout California over the past century.

Summary information regarding freshwater taxa known to occur in California did not previously exist in a central publication. I therefore conducted a review of several primary groups of stream organisms found in the Mediterranean region of California and statewide. For this work, I gathered data from a variety of literature sources and museum specimens to summarize species composition and endemism in the region, and to identify data gaps and conservation priorities for the examined groups. The remainder of this dissertation focuses largely on changes in Odonata species diversity, composition, and occurrence rates over time in California. This charismatic group was ideal for study of change over time because of their relatively low diversity, well-known taxonomy, and the existence of sufficient historical and current specimen records and more recent enthusiast sightings of odonates.

I conducted a resurvey of sites originally sampled for Odonata by Clarence H. Kennedy 1914-1915. This work involved surveys of odonates at 81 sites throughout central California and northwestern Nevada, 45 of which were directly comparable to Kennedy's original sites. I found that while site-level species richness has not changed significantly, assemblages have become more homogeneous across sites. Habitat generalists have generally expanded in the extent of their distribution while habitat specialists have declined. In examining current local and regional factors influencing the occurrence of Odonata species in this region, I found that species occurrence was higher during site visits with higher degree-days, especially for highly mobile groups, including dragonflies and migratory species. The probability of presence across species was lower in highly urban sites, particularly for habitat specialists. Overall, both regional and local factors influenced the occurrence of odonates in the study with implications for conservation.

A large component of this dissertation included development and analysis of a database of over 33,000 Odonata occurrence records throughout California over the past century. This database included specimen records from museums in California and large odonate collections elsewhere, as well as statewide enthusiast sightings from recent years. I noted that these unstandardized data contain biases with regards to uneven sampling effort, which must be addressed in analysis. Subsequent analyses of occurrence records before and after 1975 indicated that Odonata distribution may have generally shifted northwards with temperature warming and to lower minimum elevations in response to increased summer water-availability in low-elevation agricultural regions. Similar to results from the resurvey study, the museum specimen data indicated that highly mobile migratory species have increased while habitat specialists have declined. I concluded that a combination of sampling biases, species traits, and climate that have influenced the probability of detection of Odonata species over the last century.

DEDICATION

This dissertation is dedicated to my brother, Jerry Garnica, for inspiring and guiding me early on, to my parents Ronald Ball and Laura Killen, and to my husband, Carl Damerow, for his loving support during the process of this work.

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INTRODUCTION

Diversity and Distribution of California Dragonflies and Other Aquatic Taxa

Diversity and Distribution of California Dragonflies and Other Aquatic Taxa

INTRODUCTION

Increases in water demand, urbanization, and severity of drought threaten freshwater biodiversity in the arid western United States. Since the early 1900s, urbanization has greatly expanded throughout this region. For example, 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, during this period (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). In contrast, irrigation canals and channelized urban streams now provide new 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 now exhibit altered water quality, stream flow, and habitat structure compared to their original state (Mount 1995). Evaluating the effects of these changes on biological communities is necessary in order to effectively manage freshwater ecosystems and conserve biodiversity moving forward.

Broad-scale, historical assessments of change in assemblages over time can help determine the biological effects of these stressors but, to date, are rare. However, the time and resources required to obtain sufficient species occurrence records for large regions or groups of organisms has often proven to be prohibitive (e.g., Favret & Dewalt 2002; Schuh et al. 2010). Such records are usually scattered throughout numerous museum collections, literature sources, independent field studies, and (for more charismatic groups) enthusiast observation lists (Guralnick & Van Cleve 2005; Pyke & Ehrlich 2010). While many vertebrate specimen databases have been largely completed (e.g., Guralnick & Constable 2010), databases of the most diverse animal group, the insects, has lagged behind (Schuh et al. 2010). However, in response to a growing need for specimen data in research, more insect and other large natural history collections are in the process of undergoing or beginning digitization (Abbott 2005; Favret & Dewalt 2002; Graham et al. 2004; Hill et al. 2012; Schuh et al. 2010). With large databases of insect occurrence records, we have begun to assess conservation status of organisms, and broad-scale impacts of climate and land use on species richness and occurrence rates.

Aquatic insects are the most widely used biological indicators of freshwater ecosystem health (Resh 2008), and are of economic importance as disease vectors (e.g., Chaves et al. 2012) and food for fishes (e.g., Wallace & Webster 1996). For a majority of this dissertation, I focus on the aquatic insect order Odonata, the dragonflies and damselflies, which provided a useful starting point for a statewide database of insect specimens. This group contains fewer species than most insect orders, is well-known taxonomically (Clausnitzer et al. 2009), is charismatic to the general public, and has naturalist sightings that are available to supplement recent occurrence records (Abbott 2005). Odonata are also known to be useful indicators of freshwater ecosystem health, and are thus likely to contribute to our understanding of general response to changes in aquatic habitat and water quality (e.g., Clausnitzer 2003; Smith et al. 2007).

For this doctoral dissertation, I brought together many existing sources of data to create a master list of known freshwater species, and a large database of species occurrence records of Odonata throughout the state of California. These combined resources have filled a data gap that previously existed. The databases have enabled us to review current known biodiversity in California streams and conduct historical assessments of change in Odonata communities over time in California in relation habitat, climate, and land use variables. The complete dataset is now available for future use in California diversity and distribution studies.

Chapter Overviews

This dissertation begins with a review of biodiversity and distribution of freshwater fauna and flora in California, and proceeds to focus on Odonata (dragonfly and damselfly) assemblage composition and species occurrence in the region. A majority of the work relies on a historical resurvey and museum records of Odonata species occurrence over the past century. These valuable historical datasets enabled assessment of broad-scale changes in species occurrence and community composition in relation to climate and land use change.

In Chapter 1, I reviewed current knowledge of biodiversity for several groups of flora and fauna in California Mediterranean streams. Major groups explored in the review include diatoms, macrophytes, molluscs, crustaceans, aquatic insects (the orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, and Hemiptera), fish, and amphibians. In this chapter, I quantified and summarized species richness information, and compared richness within the Mediterranean ecoregion to that statewide. I then summarized knowledge of conservation status of all lotic groups in the study. Finally, the chapter identified knowledge gaps and conservation priorities to better protect stream biodiversity in California and the Mediterranean climate region in particular.

Chapter 2 compared Odonata assemblages from the first comprehensive Odonata survey in California and Nevada, conducted by C.H. Kennedy in 1914-1915, to surveys that I conducted at the same sites in 2011-13. In this chapter, I investigated the impact of several environmental factors on odonate assemblages and species occurrence. I determined whether species richness and community similarity among sites have changed across the study area and within individual ecoregions. I then identified individual species and biological traits that have increased or declined in prevalence over time, and assessed the effects of temperature, precipitation, and urbanization on species richness and occurrence.

In Chapter 3, I examined environmental factors that influenced species richness and the probability of presence of Odonata species at 81 sites throughout central California and northwestern Nevada. Specifically, I investigated the effects of survey effort, local variables, and regional variables on species richness and the occurrence of certain types of species, such as migrants and habitat specialists. My assessment then highlighted the potential of Odonata communities to serve as efficient and effective indicators of land use and climate effects on freshwater systems of this region.

Chapter 4 summarized a recently completed database of California Odonata records, including both museum specimens and observation-based species lists. I outlined the methods used in the California Odonata database development, which was part of a larger project (known as Calbug) to digitize over one million California arthropod specimens. I then presented the taxonomic, spatial, and temporal distribution of records to identify data gaps and biases in the database. In this study, I determined contributions of different collection types to total number of records and unique county records. Finally, I assessed the prevalence of records for each Odonata species before 1976 and after 1979 to determine both potential taxonomic biases and changes in species prevalence, altitude, and elevation ranges over time.

Chapter 5 examined changes in Odonata richness, community similarity, and species occurrence rates from 1900-2013, using data from the Odonata database outlined in Chapter 4. I presented average site-level changes in species richness and community similarity before and after 1975. I then compared observed and estimated region-level (statewide and for individual ecoregions) species richness for these time periods. Using a method known as list-length analysis to account for variation in survey effort, I determined changes in species occurrence rates in relation to list-length, year, Julian date, and climate. Finally, I explored whether particular species attributes, such as habitat specialization, overwintering diapause, and tolerance value, were associated with increases or declines in detection rates over time.

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CHAPTER 1

Biodiversity in Mediterranean-Climate Streams of California

Joan E. Ball, Leah A. Bêche, Patina K. Mendez, and Vincent H. Resh

Biodiversity in Mediterranean-Climate Streams of California

Abstract

Although the California Mediterranean (med) climate region is widely considered a biodiversity hotspot for terrestrial plants and vertebrates, freshwater biodiversity in this region is generally not well known. Using information from museum specimen databases, published literature, biological assessment surveys, and specialist's knowledge, we developed species lists for several groups of stream organisms in the med-climate region of California, which includes 2,838 species in 322 families. The groups with the highest diversity of lotic species are aquatic insects and diatoms, which comprise 39% and 36% of species in our lists, respectively. Sequential floods and drying periods limit the overall biodiversity of many stream organisms in California med-rivers, and continued climate and land-use change may cause disproportionate biodiversity declines in the region. However, only 4% of lotic species have been evaluated in the IUCN Red List of Threatened Species, and many assessments are outdated. Future development of online databases for botanical and zoological collections will significantly enhance biodiversity and distribution knowledge. This information will enable us to more accurately and efficiently assess the effects of global change on biodiversity of freshwater organisms, to evaluate conservation status of individual taxa, and to set conservation priorities for stream ecosystems.

Introduction

Over 1,200 kilometers long and 400 kilometers wide, California is the most environmentally diverse state or province within North America. Its distinctive flora and fauna are unusually species-rich for its latitudinal location in the temperate zone, which is the result of its highly varied topography, large size, and a long coastline (Caterino, 2006; Moyle, 1995). The California floristic province is a biodiversity hotspot because the state as a whole supports large numbers of endemic species and it has experienced intensive habitat modification (Myers et al., 2000). California contains numerous large urban and suburban areas, and provides year-round growing conditions for agriculture in the fertile Central Valley (Mount, 1995). These altered landscapes have resulted in acute biodiversity loss, and continue to threaten the endemic flora and fauna of the region.

Knowledge of terrestrial plants and vertebrates has largely shaped the current understanding of California as a biodiversity hotspot. Previous estimates indicate that there are around 4,400 - 5,000 plant species in the California Floristic Province, of which over 40% are endemic (Keeley & Swift, 1995; Myers et al. 2000). Terrestrial vertebrates are the best known organisms, but this group is the least numerically diverse, containing only 450 species of birds, 210 mammals (mostly rodents), and fewer than 150 species of amphibians and reptiles (Keeley & Swift, 1995). Insects are one of the least well-known but the most diverse animal group, with estimates of around 37,500 species in the state (Jerry Powell, personal communication, September 19, 2012), including about 1,600 bees (Thorp, 2012) that provide pollination services for 90% of California plants (Keeley & Swift, 1995). Within California, there are approximately 0.7% of global plant species within a land area of approximately 324,000 km^2; the other the top 25 biodiversity hotspots contain 0.5% to 6.7% of total known plant diversity in areas ranging from 18,000 km^2 to 2,362,000 km^2 (Myers et al., 2000).

Relatively little information exists on the biodiversity of freshwater habitats throughout the world (Allan & Flecker, 1993; Ricciardi & Rasmussen, 1999). Although fishes are one of the best known groups of freshwater organisms, richness estimates and ranges are generally less complete than for terrestrial vertebrates. This lack of information is largely because fish species are more diverse and their taxonomy is less well-known than that of terrestrial vertebrate species (Ricciardi & Rasmussen, 1999). Biodiversity knowledge in California lotic environments varies considerably among taxonomic groups. Although studies have reviewed the biodiversity of certain freshwater groups in California, such as amphibians (Fisher & Shaffer, 1996; Shaffer et al., 1998), mayflies (Meyer & McCafferty, 2008), and fish (Moyle, 1995; Moyle, 2002; Moyle et al., 2011; Moyle & Williams, 1990), the species richness of many groups has not been summarized, and no reviews to date have compiled species diversity information from the major orders of freshwater species in California.

A majority of California falls within a Mediterranean (hereafter referred to as med) climate, where higher stream flows occur in winter and spring followed by low flows during the summer (Gasith & Resh, 1999). In California, freshwater organisms with limited dispersal abilities frequently become confined as portions of intermittent streams dry out in the summer; this seasonal stream-fragmentation often prevents colonization of new waterbodies, possibly resulting in high endemism and speciation (Marchetti et al., 2001; Moyle, 1995). The sequential flooding and drying of the California med-climate also creates harsh conditions for freshwater organisms, and generally limits long-term survival to organisms with adaptations to survive highly variable, yet seasonally-predictable extremes in river flows (Gasith & Resh, 1999). Moreover, high water demand for agriculture and flashy hydrographs of urban areas often exacerbate the natural flow extremes of California's med-climate streams (Grantham et al., 2010).

California generally suffers from an inadequate water supply to meet demands of both its human population and the environment, adding to the many threats that already exist for freshwater species (Grantham et al., 2010; Moyle et al., 1995). The state has over 320,000 kilometers of streams and rivers, which is more than any other U.S. state except Alaska (Barbour, 2003). However, all major streams and many smaller streams have one or more dams regulating water flow, altering sediment and vegetation regimes of streams, and obstructing migration of lotic species, such as salmon (Kondolf, 1998; Mount 1995; Moyle, 2002; Hobbs & Mooney, 2001). Numerous other factors alter stream ecosystems throughout the state, including large amounts of impervious land surfaces that cause flashy hydrographs, pollution from agriculture and urban landscapes, removal of native riparian vegetation, the presence of invasive species, and mining and logging activities (Mount, 1995; Marchetti et al., 2011; Moyle et al., 2011). Moreover, intensive agricultural production uses approximately 80% of the available freshwater in California (Mooney et al., 2001). In fact, nearly all riparian and wetland habitats in the state are highly altered or are completely destroyed (Mooney et al., 2001). Besides causing reductions in abundances of many species, these impacts may eventually result in significant biodiversity loss. Consequently, homogenization of freshwater biota is becoming an increasing threat in California (as in other med-climate areas throughout the world) as conditions become less suitable for endemic native species and more amenable to cosmopolitan, and often invasive species that thrive in highly altered habitats (Rahel, 2002; Marchetti et al., 2001; Olden, 2006).

The purpose of this review is to summarize current knowledge of stream biodiversity in the med-climate region of California. We consider several groups of aquatic insects (the orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, and Hemiptera), non-insect invertebrates (crustaceans and molluscs), vertebrates (fish and amphibians), diatoms, and macrophytes. Our objectives in this review are to: (i) quantify and summarize species richness information for major groups of lotic vertebrates, invertebrates, diatoms, and macrophytes within the region; (ii) compare California med-region biodiversity to overall California biodiversity, including analyses of taxonomic richness at the species level and life history traits at the genus level; (iii) summarize knowledge of conservation status of these lotic groups; and (iv) identify knowledge gaps and conservation priorities to better understand and protect stream biodiversity in the California med-region.

Biogeography

The California med-ecoregion extends from southern Oregon through California to northern Baja California, Mexico, on the Pacific Coast of North America, and east to the foothills of the Sierra Nevada (Aschmann, 1973). This review uses the delineations of ecoregions provided by the World Wildlife Fund Conservation Science Program (Olson et al., 2001) to identify the boundaries of the California med-region (Fig. 1). We focus on the med-region within the state of California because it comprises a majority of the region and the existing biodiversity information is currently the most readily available and complete. Within California, the med-region largely includes the California Pacific coastal area, the Central Valley, Sierra Nevada foothills, the Transverse Ranges, and the Peninsular Ranges (Fig. 1). The Sierra Nevada mountain range, the Mojave desert, and the Klamath mountains are not considered part of the California med-region.

Geologically recent tectonic-activity has greatly influenced both the physical aspects of California rivers and their biota. The highly varied topography in the region has been a primary factor shaping climate, hydrology, geomorphology, and the present day biology of lotic organisms (Carter & Resh, 2005). Diverse physical barriers, such as the Coast Ranges, have periodically blocked the migration of fish and other organisms. Isolation has in general resulted in well-recognized unique floristic and faunal regions, and high endemism in the California ecoregions (Minckley et al., 1986; Marchetti et al., 2001).

California shares more geomorphological and climatic characteristics with Chile than any other med-climate region (di Castri, 1981). Both regions are north-south in orientation and have a longitudinal central valley with fertile soils bordered by coastal and interior mountain ranges. They have both been highly influenced by similar tectonic activity and glaciations events (di Castri, 1981; di Castri, 1991). The California Coast Ranges lie to the west of California’s Central Valley (see Fig. 1). These mountains were formed in the north by faulting and active subduction of the Pacific plate beneath the continental plate, which began after their collision around 29 million years ago (mya). Tectonic activity of the San Andreas Fault zone formed the southern Coast Ranges (Minckley et al., 1986, Carter & Resh, 2005). To the east of the Central Valley are the Sierra Nevada Mountains, which rose through uplift to their current elevation (more than 4,300 meters [m]), beginning around 18 mya (Minckley et al., 1986). The basin of the Central Valley contains alluvial sediments originating from both continental and marine sources throughout the Pliocene (5.3 - 2.8 mya) (Minckley et al., 1986). Recent glaciations occurred in the region as a result of rapid uplift and global cooling during the Pleistocene (2.5 mya - 11.7 thousand years ago), and altered the profiles of many rivers (Carter & Resh, 2005).

The California med-region is typical of other med-climate regions in being characterized by cold, wet winters and hot, dry summers. The system is influenced by the cold California current, but is buffered by coastal fogs that are frequent and intense (di Castri, 1981; di Castri, 1991). However, compared to Chile, it has a warmer and drier coastal climate; Southern California is influenced by the hot, dry Santa Anna winds, and the region as a whole lacks the moderating marine air of Chile (Cody & Mooney, 1978). The average annual temperature in the basin of the Central Valley is approximately 12.9°C-15.7 °C, and summer temperatures may exceed 40 °C (Carter & Resh, 2005).

The topography of the region is largely responsible for its climatic extremes. There is a north-south and an east-west gradient in rainfall, which also varies significantly based on altitude. Approximately 75% of rainfall occurs in northern California, which has average annual rainfall of 900 millimeters (mm) (Carter & Resh, 2005). The average precipitation in the Coastal Mountains ranges from 250 mm/year to over 500 mm/year. In the Sierra Nevada Mountains, precipitation increases as moist air rises over the mountains and drops an average of 500 mm/year in the foothills within the med-climate, and up to 2,000 mm/year in the highest elevations – outside of the med-climate (Carter & Resh, 2005). In the Central Valley, precipitation ranges from 380 mm/year in the north to 120 mm/year in the south. Over the past 25 years, the California med-region as a whole received a mean annual rainfall of 490 mm ± 260 mm, ranging from 290-1,380 mm (Cowling et al., 2005).

Of the med-regions, California has the lowest fraction of rainfall during the summer and has a more intense summer drying period. Approximately 95% of med California rainfall is concentrated in winter (Oct-Mar), while other med-regions have closer to 75% of their rainfall during that time (Cowling et al., 2005). Med California also has the lowest number of winter rainfall events. The onset date of winter rainfall occurs one month sooner than in other regions (Oct-Nov) and is the most unpredictable of the world's med-regions (Cowling et al., 2005).

The diversity of ecosystem types that occur in the med California contributes to its characterization as a biodiversity hotspot for terrestrial plants. Ecosystem types range from comparably moist forests characterized by evergreen *Quercus* species to drier regions with chaparral and scrubland; deciduous *Quercus* species reside on coastal hills and inland valleys (Mooney et al., 2001). Redwood forests exist in relict coastal forests restricted by the coastal fog belt, but less than 5% of the old growth forest remains (Mooney et al., 2001). Coniferous forests can be found in foothills of the Sierra Nevada Mountains (Arroyo et al., 1995).

Riparian zones are often dominated by species such as alder (*Alnus* spp.), oaks (*Quercus* spp.), California Bay Laurel (*Umbellaria californica*), Douglas fir (*Pseudotsuga menziesii* (Marib.) sycamores (*Platanus* spp.), hazels (*Corylus* spp.), walnuts (*Juglans* spp.), cottonwoods (*Populus* spp.), and willows (*Salix* spp.) (e.g. Bonada et al., 2006). A number of species pairs in *Platanus*, olives (*Fraxinus*), *Alnus, Juglans*, *Populus*, and buckeyes (*Aesculus)* exist between California med and other med-regions, such as Israel (Shmida, 1981).

Current status of freshwater biodiversity knowledge

Knowledge of the biodiversity, distribution, and conservation status of freshwater organisms in California varies significantly for the major groups. Although vertebrates, such as fish and amphibians, are relatively well-studied, they are relatively species-poor groups, contributing only 5% of the species in our list for California as a whole, that do not provide an adequate representation of the state's biodiversity. Macrophytes are relatively well-studied, and previous studies address the evolution (e.g. Ackerly, 2009), distribution (e.g., Loarie et al., 2008), and invasive species in the state (Schwartz et al., 2006). However, these studies do not address biodiversity of lotic macrophyte species in med California. As in most regions of the world, we know the least about highly diverse benthic macroinvertebrates and algae in med California streams. Improvements in our understanding of the taxonomy, distribution, and ecology of these hyper-diverse groups, in particular, would provide a much more complete representation of California's overall biodiversity, and may enable detection of finer-scale effects of climate change and habitat modification on these organisms.

Distribution and taxonomic richness

We compiled existing information on species richness and distribution for several major taxonomic groups that occur in California streams, including aquatic insects, crustaceans, molluscs, fish, amphibians, diatoms, and macrophytes. First, we reviewed existing literature on the topic of biodiversity for each of the groups of taxa examined (e.g. Ephemeroptera). We then compiled species lists for California streams using records currently available in museum-specimen databases, information provided by specialists, and accounts from published literature.

In this review, we evaluate species distribution in the California med ecoregion as delineated by the World Wildlife Fund Conservation Science Program (Olson et al., 2001) (Fig. 1); however, for fish we use the Sacramento-San Joaquin and Central Coast ichthyological provinces described by Moyle (2002), which fall into the same med-region of California. Using GIS layers from the Terrestrial Ecosystems Database (Olson et al., 2001) and ArcGIS v10.0 (ESRI, 2011), we calculated the proportion of each California county's area falling within the California med or non-med-region. We designated a county as within med California if at least 50% of the county area fell within the California med GIS layer. Using this procedure, we identified 35 counties as California med and the remaining 23 counties as non-med (Fig. 1). For this study, we only included counties within the state of California and do not include southern Oregon or northern Baja California, Mexico.

We summarized species distribution by ecoregion and determined whether taxa are known to occur in the med-region exclusively, in the med-region plus other areas, or only in areas of California outside of the med-region. In most cases, distribution information for individual species was given by county, so we considered presence within one med county to qualify a species as occurring in California med-climate. We generally used the same information to infer whether species may be endemic to the med-region (e.g. specimens or occurrences reported in the literature covering a given species only exist from the med-region and nowhere else), unless more conclusive information on endemism was available in the literature, which was most often the case for fish, amphibians, mayflies, and dragonflies.

Species that inhabit streams and rivers for at least a portion of their life cycle are included in this review, even those that are also found in terrestrial, lentic, or marine habitats during some life stage. Distribution information for some species in high-diversity groups that are generally less well-known (e.g. aquatic insects) may sometimes be based on limited information, such as a few specimen records or even a single record. Like other recent reviews of biodiversity (e.g. Caterino, 2006) we also do not distinguish between historical and current records when developing species lists, and it is possible that some species included in our lists are no longer present in California.

We include information on non-native species only for groups where information about whether species are native or non-native is available, which include crustaceans, molluscs, amphibians, fish, and macrophytes. Non-native species may increase the overall biodiversity at local scales in some cases (e.g. fish), but they are often associated with declines in biodiversity of native species (Moyle, 2002; Marchetti et al., 2001).

Aquatic insects

Community-level studies have addressed taxonomic richness of aquatic insects in med streams of California, although some have mostly evaluated generic-level richness. For example, a large body of research has involved seasonal and annual changes in assemblage structure for specific streams (e.g., Bêche & Resh, 2007; Gasith & Resh, 1999; Resh et al., 2013). These studies identify strong correlations between community structure and annual precipitation (e.g., Bêche & Resh, 2007), seasonal biodiversity peaks in spring during moderate flow periods, and biodiversity reductions during summer and early fall (Bêche et al. 2006; Bonada et al., 2006).

Much of the information on aquatic insects and other macroinvertebrate fauna comes from biological assessment studies. Regional biological assessment efforts in California began in the early 1990's, and include data on taxonomic composition for over 3,000 sites across the state (e.g., Barbour, 2003; Stoddard et al., 2005a,b; USGS, 2011). Most agencies and universities that conduct biological assessments use benthic macroinvertebrates as indicators of ecological health, because of their ubiquity, large numbers of species with a spectrum of responses to environmental stressors, long life-cycles, and the relative ease of sampling and identifying them (Resh, 2008; Rosenberg & Resh, 1993). These surveys generally provide detailed site information that can be used to determine genus level distribution and richness for different regions of the state.

Usinger's *Aquatic Insects of California* (1956) is the only comprehensive taxonomic treatment of aquatic insect species and their distribution throughout California (Resh, 2011). Although now outdated, this book was the starting point for developing most of the species lists for aquatic insects and determining species richness for the region. The Southwest Association of Freshwater Invertebrate Taxonomists (SAFIT) provides more recent checklists of freshwater macroinvertebrates in California, but the checklists do not provide distribution information within the state and sometimes include only genus- and family-level taxonomic information (Richards & Rogers, 2011). Recent, more detailed treatments of taxonomic diversity of stream insects in California exist for the insect orders Odonata (Biggs, 2011; Manolis, 2003) and Ephemeroptera (Meyer & McCafferty, 2008). For the orders Trichoptera, Plecoptera, Coleoptera, and Hemiptera, we compiled information using museum specimen records that are currently in databases [including the Essig Museum of Entomology at University of California Berkeley (2011), California Academy of Sciences (2011), Santa Barbara Museum of Natural History (2011), Illinois Natural History Survey (2011), and the Smithsonian Institution National Museum of Natural History (2011)], and information provided by experts and published literature. We used Merritt et al. (2008), Richards & Rogers (2011), Manolis (2003), and specialist knowledge to determine whether species occur in lotic habitats or if they are exclusively lentic. We excluded Diptera, which is by far the most diverse aquatic insect order, from this review because distribution information is not usually available and identifications are often to generic-level or higher levels, especially for groups as diverse as Chrironomidae. Because insects are the most diverse animal group, and many taxa remain both undescribed and likely uncollected, the true biodiversity for med California is not known and the numbers we present are certainly underestimates.

The combined species richness for the aquatic insect orders Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, and Hemiptera in California streams is at least 1,117 species. Approximately 79% of these species exist in the med-region of California for at least part of their range, and 5% may be endemic to the region (Table 1).

Ephemeroptera

We obtained species and distribution information for Ephemeroptera primarily from previous reviews of this order in California (Day, 1956; Meyer & McCafferty, 2008), 624 museum specimen records from the Essig Museum of Entomology, and the United States Geological Service (USGS) "Mayflies of the United States" website (Kondratieff, 2000).

As one of the three orders of pollution-sensitive aquatic insects (Ephemeroptera, Plecoptera, Trichoptera, or EPT) often used in biological assessments, the Ephemeroptera of California are relatively well-known among the insects in the state. Meyer & McCafferty (2008) summarize species richness and endemism, and provide detailed information on individual species of mayflies in the far western United States. Their work describes distribution and museum-specimen data, and provides references to existing scientific literature for 155 species (comprising 44 genera and 15 families) in both lotic and lentic systems of California, four species of which are exclusively lentic. Meyer & McCafferty (2008) found that 14 of these species are endemic to California. We found two additional lotic species in our review to total 153 lotic species from 14 families in California. Based on these records and Meyer & McCafferty (2008), 131 species occur in the med-region (11 families), and 4 species are likely to be endemic to med California (Tables 1 and 2).

Plecoptera

Species accounts and distribution information for Plecoptera were compiled from online resources, museum records, published literature, and specialist knowledge. The "Plecoptera Species File Online" website (DeWalt et al., 2011) provided an extensive faunal list of species for California. We also used specimen records, the USGS "Stoneflies of the United States" website (Kondratieff & Baumann, 2000), Jewett (1956), and additional scientific literature for individual species (reference list available upon request). Dr. Richard Baumann provided distribution information for species with little published information available; this information came from undatabased specimens at the Brigham Young University Life Science Museum. For California, we developed a list of 188 lotic species from 9 families (Table 1). We found that 127 species occur in the med-region, and 14 may be endemic to the region (Tables 1 and 2).

Trichoptera

For Trichoptera species and distribution information, we used 1,904 records currently available in specimen databases for the Essig Museum of Entomology, the California Academy of Sciences and the Illinois Natural History Survey, Denning (1956), and additional published literature. We then confirmed current taxonomic status for all species using the "Trichoptera World Checklist" website (Morse, 2011).

Of the EPT taxa, Trichoptera had the most specimen records from online databases, but few other resources were available with information on California biodiversity. We compiled a list of 350 lotic species from 19 families in California. Of the lotic species, 278 occur in the med-region, and 20 may be endemic to the region (Tables 1 and 2).

Odonata

We compiled information on Odonata species and distribution using museum records, observation records, and published field guides. Also, in the late 1990s, Biggs (2009) organized a formal enthusiast group for California, known as CalOdes, that now includes both amateur enthusiasts and odonatologists who specialize in the distribution and occurrence of this group in California and the western U.S. Members of CalOdes, many of whom have been identifying and observing dragonflies for years or even decades, have been actively recording county records and exchanging information about dragonflies since 2000. They continually update county records using CalOdes photo or specimen-vouchered observations, and databases of over 20,000 museum specimens with county-level distribution information (Biggs, 2011). We developed our species list using these databases and the two existing field guides for California dragonflies, which include basic habitat and distribution information for each species (Biggs, 2009; Manolis, 2003).

The Odonata are the least diverse, but the best known of the aquatic insects in California, and likely elsewhere. These "birdwatcher's insects" attract a significant following of amateur naturalists, primarily because they are highly aesthetic and conspicuous insects that are relatively easy to identify in the field. There are 80 lotic Odonata species from 8 families known to occur in California, of which 68 occur in the med-region and one is endemic (Tables 1 and 2).

Coleoptera

Previous work on Coleoptera of California includes reviews of the order that summarize both terrestrial and aquatic species (Caterino, 2006; Leech & Chandler, 1956), and information from a large digitization effort for beetles at the Santa Barbara Museum of Natural History (2011). There are over 10,000 species of terrestrial and aquatic beetles known to occur in California, and hundreds to thousands of yet undescribed species (Caterino, 2006). We found a total of 263 lotic Coleoptera species from 14 families. According to the above-listed sources, there are 216 lotic species in the med-region, of which 19 species may be endemic (Tables 1 and 2).

Hemiptera

Although Menke (1979) provides a review of Hemiptera species and distribution, little other published research exists on this order of aquatic insects. Using Menke (1979) and Richards & Rogers (2011), we developed a list of 83 lotic species from 11 families, 61 of which occur in the med-region (Table 1). Three species may be endemic to the region (Resh & Barnby, 1987; Resh & Sorg, 1983) (Table 2).

Biological Traits of EPT genera

Using the biological trait database developed by Bêche et al. (2006), Bêche & Statzner (2009), and Mendez (2007), we examined potential differences in key life history, morphological, and behavioral traits among Ephemeroptera, Plecoptera and Trichoptera genera occurring in California med-climate areas (taxa lists were obtained as described above) and in non-med occurring genera. We used traits and trait categories defined by Statzner et al. (2007). Individual traits in the databases were coded using the fuzzy coding approach of Chevenet et al. (1994). Bonada et al. (2007) and Bonada & Dolédec (2011) made predictions of differences expected among med and temperate (non-med) taxa from Europe (see Table 3). In this study, we tested these predictions using California med and non-med genera. A total of 251 genera were included in the analysis (172 CA med genera, 79 non-med genera), including 60 genera of Ephemeroptera (32 med, 28 non-med), 83 Plecoptera (62 med, 21 non-med) and 108 Trichoptera (78 med, 30 non-med), which represent the majority of the EPT genera described in the above section. Of the 49 trait categories (Table 3) included in the EPT database, we tested hypotheses for 24 trait categories falling into one of 8 traits: maximum body size; life cycle duration; voltinism; reproduction; resistance to adverse conditions; locomotion and substrate relation; food eaten, and feeding habits. We compared each of the 24 traits categories between California med and non-med genera using Wilcoxon non-parametric U-tests.

A preliminary multivariate analysis (i.e. between-class analysis) showed that the three EPT orders had distinct trait profiles. These results combined with the unequal number of genera in each of the three orders led us to conduct additional comparisons of each order separately to better account for potential phylogenetic influences on the results. We used permutational multivariate analysis of variance using distance matrices (non-parametric MANOVA, model: traits ~ region, where region = med or non-med) to compare overall trait profiles among med and non-med genera within each order (i.e. separate tests for Ephemeroptera, Plectopera and Trichoptera). We used the “adonis” function in the vegan package (Oksanen et al., 2011) in R v2.13.2 (R Development Core Team, 2010) with Bray-Curtis distance and 999 permutations. These results were confirmed using fuzzy correspondence analysis (FCA) followed by a between factor analysis (in the R “ade4” package; Dray & Dufour, 2007).

When considering all EPT genera together, the EPT biological traits data did not support *a priori* predictions that med-climate seasonal-discharge patterns, habitat availability, and other stream ecosystem characteristics should affect several (not all) biological traits, particularly those conferring resilience or resistance to flooding and droughts (see Table 3). In fact, three trait categories significantly contradicted our hypotheses (i.e. that med-occurring genera were more likely to feed on CPOM and be crawlers than non-med genera, and that non-med genera were more likely to have asexual reproduction); all other results were not significant (Table 3).

However, when we considered the orders separately our results did support some *a priori* predictions. Analyses conducted separately for Ephemeroptera showed that med genera were more likely to feed on CPOM and to be scrapers than non-med genera, results that both contradict and support the *a priori* hypotheses, respectively. For Trichoptera, med genera were more likely to have a life cycle duration less than or equal to 1 year, and feed on periphyton, and non-med genera were more likely to be semivoltine. These three results support the *a priori* hypotheses. None of the analyses for Plecoptera genera were significant (Table 3).

None of the genera, however, exhibited a statistically significant difference in trait profiles between med and non-med genera using multivariate analyses (non-parametric MANOVA, $p > 0.05$). These results were confirmed by a failure to discriminate between med and non-med genera using FCA followed by between factor analysis.

Crustaceans and molluscs

Rogers (2005) provides the most comprehensive summary of lotic crustacean biodiversity in med California in an identification manual to freshwater Crustacea occurring in the western United States. The arthropod class Crustacea is considered to be the most morphologically diverse group of animals living today, and taxonomy within this group is extremely difficult to resolve (Martin & Davis, 2001). Most biodiversity and distribution studies on crustaceans are therefore limited to a particular family, genus, or species (e.g. Hill et al., 1997; Witt et al., 2006). Some studies focus on freshwater lentic taxa such as branchiopods in vernal pool habitats of California, which have a high level of endemism and many threatened or endangered species (e.g., Helm, 1998). Numerous studies of Crustacea in California treat certain invasive species, such as the signal crayfish, *Pacifastacus leniusculus*, and the Louisiana or red swamp crayfish, *Procambarus clarkii*, which have caused declines in or have eliminated native freshwater species (e.g., Gamradt & Kats, 1996; Kerby et al., 2005; Light, 2003).

To obtain crustacean species information within California, we used Rogers (2005) and Richards & Rogers (2011). We found records of 46 lotic crustacean species from 17 families in California, 38 of which occur in the med-region and 8 of which are likely to be endemic to this region (Tables 1 and 2). Seventeen, or 45%, of the 38 med California species are non-native.

Similar to Crustacea, there is little published research on the biodiversity of freshwater Mollusca in California, and we found only one distributional checklist for the state (Taylor, 1981). We compiled a mollusc species list with distribution information using this review of California Mollusca species (Taylor, 1981), Richards & Rogers (2011), and various literature sources for individual taxa (available upon request).

There are 98 lotic species of molluscs from 19 families (including bivalves and gastropods) known to occur in California. Of these species, 54 occur within the med-region, and 2 are endemic (Tables 1 and 2). There are currently 10 introduced Mollusca species known from California med streams. The two most widespread invasive mussels are the Asian clam, *Corbicula fluminea* and zebra mussel *Dreissena polymorpha,* both of which threaten native species (Williams et al., 1993). The most successful gastropod invaders have been pulmonate snails (Physidae, Lymnaedae, and Planorbidae) and the parthenogenic species *Melanoides tuburculata* and *Potamopyrgus antipodarum* that can establish a population with just one individual (Strong et al., 2008).

Fish and amphibians

Fish are the most diverse vertebrates in the world, and the biodiversity of this commercially and recreationally valuable group is relatively well-known in California. Moyle et al. (2011) recently reviewed biodiversity and evaluated the conservation status of native fishes throughout California today, which include 129 native taxa in California (7 of which are presumed to be extinct) when incorporating species, subspecies, and distinct populations (Moyle, 2002; Moyle et al., 2011). Moyle (2002) divides the state into six ichthyological provinces, and both the Sacramento-San Joaquin and South Coast provinces fall within the med-region. Extreme conditions of winter flooding and summer drought in the region have produced a large percentage of anadromous fishes (24%) and fish adapted to intermittent streams (Moyle et al., 2011). Most fish live in rivers of the Central Valley and North Coast, which are areas with the most water and diversity of freshwater habitats. The med-region of California also supports an unusually high number of endemic species (63%), which generally occur in geographically confined areas or ecologically harsh habitats (Moyle 2002; Moyle et al. 2011).

There are several recent reviews of fish biodiversity in California that specifically address the med-region of the state (Moyle, 1995; Moyle, 2002; Moyle et al., 2011). We used information from these sources, and the "California Fish Website" (UC Davis, 2011) to develop a list of lotic species. There are 110 lotic fish species in the state, including non-native fishes, and 71 lotic species in the two med provinces (Table 1). Of these, 9 fishes are endemic to the region (Table 2). Non-native species are increasing at a rate where one new species is established every six years, presenting the greatest threat to native fishes (Moyle et al., 2011). There are 35 non-native fishes currently established in med streams of California, and 36 species that are native.

To develop a list of lotic amphibians in California, we used the "California Herps" website (Nafis, 2011), "Amphibia Web" (UC Berkeley, 2011), and the Amphibian field guide for the Western U.S. (Stebbins, 2003). Information on amphibian biodiversity in California is both relatively current and comprehensive. These resources provide distribution information for 38 lotic species of amphibians in California, 22 of which occur in the med-region and one of which is endemic (Tables 1 and 2). Three lotic amphibian species in this region are non-native and invasive.

Diatoms

Diatom research has largely focused on community-level studies demonstrating their importance in river foodwebs (e.g., Power, 1990) and, like macroinvertebrates, on biological assessments of streams and rivers (Porter et al., 1993). In California, Pan et al. (2006) assessed the relationships between environmental variables and benthic diatom assemblages in the Central Valley, which comprises the majority of the med-region of the state. This study used data collected by the California Department of Fish and Game (CDFG) for the Regional Environmental Monitoring and Assessment Program (EMAP) to document 249 species throughout 53 stream sites in the Central Valley. CDFG and the USGS have conducted statewide algal surveys as part of their biological monitoring programs. CDFG's western EMAP program surveyed 1,200 streams in 12 western states from 2000-2004, including 263 sites throughout California (100 of which are in the med-region) (Stoddard et al. 2005a; Stoddard et al. 2005b; USEPA, 2011). USGS's National Water Quality Assessment (NWQA) includes 89 sites in California (Porter et al., 1993; USGS, 2011).

Using the EMAP and NWQA bioassessment data, we developed a list of 1,011 lotic species in California from 85 families. Of the total lotic species, 835 occur in the med-region and 367 may be endemic. It is important to note that information on individual diatom species was too limited to gather detailed information on distribution, so that many species we list as occurring exclusively in the med-region are likely to occur in other areas as well. This limitation is potentially a problem for all taxa covered, but especially so for microscopic and easily dispersed organisms. Globally, studies show that diatom distribution ranges from narrow endemics to cosmopolitan species (Vanormelingen et al., 2008).

Macrophytes

Previous studies of macrophyte biodiversity in California have generally addressed all flora in the state, which includes over 5,500 native plant taxa, including species, subspecies, or varieties (Loarie et al., 2008). The California med-region is considered to be a biodiversity hotspot largely because of the high endemism rate in the California med flora that is over 40% (Loarie et al., 2008; Myers et al., 2000).

Riparian habitats are known to increase the number of available microclimates in a landscape and generally support the highest plant biodiversity, particularly in arid regions such as med California (Ward, 1998; Welsh et al., 2005). The vegetation regime in many of these habitats has changed rapidly as a result of human alterations to the watershed landscape, such logging, agriculture, urbanization, and the construction of dams and canals (e.g. Welsh et al., 2005). For example, Welsh et al. (2005) found that the vegetation across the Mattole River watershed, located in a seemingly "natural" area of northwestern med California, has changed dramatically from late seral forests in the mid 1900's to early succession forests and mixed grasslands today. This change has contributed to the warming of stream temperature regimes in the watershed.

We compiled a list of species associated with lotic habitats of California using the "Jepson Online Interchange of California Floristics" (Jepson Herbaria, 2009). Our list does not include species that may also occur in dry land habitats (e.g., grassland), but does include species that may also be found in other types of wetlands (e.g., ponds, lakes, and wet meadows). The total number of lotic-associated species in our list for California is 418 species from 95 families, of which 319 species from 83 families occur in the med-region, and 13 species from 10 families are endemic to the region (Tables 1 and 2).

Species summary

The flora and fauna that occur in med-climate streams make up the majority of lotic organisms in California. About 78% of lotic species occur in the med-region, which is slightly higher than the percentage of California's land area that is within the med-region (74%). Approximately 3% of lotic taxa that we examined are only known to occur in the California med-region (Tables 1 and 2).

Conservation

We examined the conservation status of the above taxa using information from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2011), and the CDFG (state) and U.S. Fish and Wildlife Service (federal) lists of threatened and endangered species (CDFG, 2011). We list all lotic taxa in the med-region of California that the IUCN has categorized as in decline (i.e. vulnerable, near threatened, threatened, or endangered) or extinct, and those that the state and federal government lists as threatened or endangered (Table 4). We also include taxa that the IUCN has evaluated and are not considered to be threatened or endangered (i.e. least concern).

State and federal lists of threatened and endangered species include some species of crustaceans, molluscs, fish, and amphibians, whereas the IUCN Red List includes these groups and also some dragonflies that occur in the med-region of California. In total, 6% of species within these groups are listed as threatened or endangered by the state and federal government and 3% are listed as in decline by the IUCN (Table 4, Fig. 2). Only 15% of species within these groups have been assessed by the IUCN. There are no species of Ephemeroptera, Plecoptera, Trichoptera, Hemiptera, Coleoptera, or diatoms from California included in federal lists or in the IUCN Red List. Conservation status for aquatic insects and diatoms as a whole is largely unknown, as these groups are hyper diverse, not as well-known taxonomically or in the extent of their distribution, and generally attract little public attention. The IUCN has evaluated the conservation status of only 4% of all the lotic species in our lists and the state and federal government has assessed only 2% of species in our lists. We also note that assessments of threat are often outdated.

Aquatic insects

Although none of the generally pollution-sensitive aquatic insects, Ephemeroptera, Plecoptera and Trichoptera, which are the most common indicators of freshwater ecosystem integrity, are listed on the ICUN Red List, it is likely that many of these species are threatened, endangered, or even locally extinct. In an analysis of museum records of Plecoptera in Illinois over the past century, Dewalt et al. (2005) found that there have been 22 extirpations out of 77 stonefly species in the state, and close to 25% of Plecoptera species are imperiled, as they have been found in fewer than 5 locations recently.

The IUCN Red List includes assessments for 25 out of 68 Odonata species (37%) that occur in streams of med California, of which only the damselfly *Ischnura gemina* is listed as vulnerable (Table 4). The remaining 24 species are listed under the category of least concern, meaning that their populations were not declining according to the best available evidence presented at the time of assessment, and none were listed on the state or federal lists. However, two lotic dragonfly species, *Erpetogomphus lampropeltis* and *Calopteryx aequabilis*, have been observed in only 2 and 7 sites in California, respectively, over the past ten years (Biggs, 2009) but were listed as least concern, having stable populations, and are not in the state and federal lists.

A particular problem with establishing the conservation status of aquatic insects is the difficulty in identifying larval and nymphal stages to the species level for most groups, and even less is known about the taxonomy of the egg and pupal stages. Aquatic insect larvae and nymphs are most commonly collected in biological assessments. Although there is currently a great deal of information available from regional and national bioassessment programs, it is difficult to exploit this information for biodiversity conservation purposes because identifications are generally not made below the genus level.

Crustaceans and molluscs

The crustaceans of med California are one of the least diverse groups with only 38 species (along with amphibians, 22 species), but the status of a few problematic invasive species and endangered species are well-documented relative to aquatic insects (Gamradt & Kats, 1996; Kerby et al., 2005; Light, 2003). The California Freshwater Shrimp, *Syncaris pacifica* is listed as an Endangered species by the state and federal governments and the IUCN, and is located exclusively within the med-region of California, in Napa, Sonoma, and Marin counties (Richards & Rogers, 2011). Two crustacean species in this region have gone extinct, the crayfish

Pacifastacus nigrescens and the shrimp *S. pasadenae*. Eight out of 38 crustaceans (21%) in California med streams have been evaluated for the IUCN Red List (Table 4). Although not covered in this review, the conservation status of lentic, vernal pool crustaceans in med CA is of great concern for conservation, in that 5 species are federally listed as threatened or endangered in California and Oregon (Rogers, 2005).

Molluscs are arguably one of the most highly threatened groups of animals (Gamradt & Kats, 1996; Kerby et al., 2005; Light, 2003). Previous studies have found that 71% of mussels in the United States and Canada (Williams et al., 1993) and 13% of gastropods worldwide are endangered, threatened, or of special concern (Strong et al., 2008). Yet, there is generally a lack of baseline information on mollusc distribution and abundance, and only 16 mollusc species (30%) from med California have been assessed by the IUCN (four of which were data deficient). Only two (4%) are listed as vulnerable, and no mollusc species are classified as threatened or endangered on state and federal lists (Fig. 2).

Fish and amphibians

The conservation status for fish taxa throughout the state is much better known than for the invertebrates. Moyle et al. (2011) determined that 30 fish taxa are threatened and 70 are in decline, while only 31 taxa are formally listed as threatened or endangered under the Endangered Species Act. The conservation status of fish has been assessed using not only species, but also subspecies and distinct populations. Seven species are now extinct or extirpated from California, including those that inhabit lotic, lentic, and marine habitats. The overall proportion of native taxa that are threatened or extinct is 83%, representing a 16% increase in these listings since 1995 (Moyle, 1995; Moyle et al., 2011). Moyle et al. (2011) noted that some of this increase has resulted from improved information, but also represents increased endangerment of many species. In our analysis, 16 out of 99 fish taxa (16%) were listed as threatened or endangered on state and federal lists, and 6 (6%) were listed as Vulnerable, Near Threatened, or Critically Endangered on the IUCN Red List.

The conservation status of amphibians is also relatively well-known, as global declines of amphibians were first documented in the late 1980s. Since that time, numerous studies in California and elsewhere have attempted to understand mechanisms of both regional biodiversity-loss and drops in local abundances (Davidson, 2004; Fisher & Shaffer, 1996; Mendelson et al., 2006; Pounds et al., 1999; Skelly et al., 2003; Sparling et al., 2001; Wake & Vredenburg, 2008). Some of the most well-known studies of amphibian decline were conducted in the Sierra Nevada Mountains of California, and research in the med-region has also documented widespread decline of native California species (Davidson, 2004; Fisher & Shaffer, 1996; Jennings & Hayes, 1994; Sparling et al., 2001). Pond-breeding species in the Central Valley of California, which is the majority of the med-region, are declining in association with the introduction of non-native predators into the med-climate Sacramento Valley (Fisher & Shaffer, 1996). Widespread habitat alterations often allow invasive-type species to thrive and force indigenous species into more pristine, high-elevation areas. In the med-climate San Joaquin Valley, intensive agriculture dominates the landscape, so that neither indigenous nor introduced species occur there (Fisher & Shaffer, 1996).

At least two species of amphibians in the state, the Lowland Leopard Frog, *Lithobates yavapaiensis,* and the Sonoran Desert Toad, *Incilius alvarius*, have become extinct (Stebbins, 2003) but neither are listed on the IUCN Red List. A statewide evaluation by the CDFG concluded that 11 amphibians were threatened as of 1994, which was 28% of total amphibian biodiversity in the state (Jennings & Hayes, 1994). This number is similar to the percentage of med-region species currently listed as in decline on the IUCN Red List, which is 27%. Globally, more than one-third of 6,300 described species are reported to be threatened with extinction, and 43% have declining populations (Wake & Vredenburg, 2008). In our analysis of lotic med amphibian species in California, 6 species (27%) were listed as Vulnerable, Near Threatened or Endangered on the IUCN Red List and 3 were listed as threatened or endangered on state and federal lists (Table 3, Fig. 2). Amphibians had the highest proportion of taxa (68%) that have been evaluated in the IUCN Red List.

Macrophytes

Although California flora as a whole has gained conservation attention because of the high degree of endemism in the state and the decline of many endemic species, the conservation status of stream-associated macrophytes is not well-known. Schwartz et al. (2006) found that California flora in urban and urbanizing regions are becoming more homogenized as a result of the expansion in distribution of many non-native species and declines in distribution or extinction of many endemic and/or rare species. Loarie et al. (2008) used species distribution models to predict that up to 66% of all endemic plant taxa in California will experience over 80% reductions in range size within the next 100 years as a result of climate change. However, species distribution information is often scarce and of variable quality, which limits the ability to accurately make future predictions of species distributions (Loarie et al., 2008). We found that only 2% of the med lotic macrophytes in our lists have been identified by state and federal lists as rare, threatened, or endangered (Table 4, Fig 2). The IUCN has identified 0.3% as being in decline (Fig 2), and has assessed 6% of med lotic macrophytes in our lists.

Future challenges

Each species contributes to the array of phenologies, physiologies, and recruitment strategies that enable ecological communities to remain resilient through changes in climate and land-use (Keeley & Swift, 1995; Vaughn, 2010). Knowledge of the biodiversity of any given taxonomic group generally comes from the detailed studies of many researchers over periods of years, decades, or even generations. The species lists and distribution information that we compiled for organisms summarizes this extensive work and can be used to set informed priorities for conservation of endemism, biodiversity, and ecosystem function.

Museum specimens are essential for studies that explore biodiversity over relatively broad spatial and temporal scales (Pyke & Ehrlich, 2010; Shaffer et al., 1998). In most cases, these specimens are the primary source of our taxonomic and distribution knowledge of any group of organisms (e.g., Meyer & McCafferty, 2008). Specimens are often the only resource for determining past distribution, making them useful in documenting species decline and environmental change (DeWalt et al., 2009; DeWalt et al., 2005; Fisher & Shaffer, 1996; Hall & Ide, 1987; Resh & Unzicker, 1975), and evaluating conservation status (Harding et al., 1998; Moyle et al., 2011; Ricciardi & Rasmussen, 1999; Taylor et al., 1996). However, studies that incorporate museum-specimen data are necessarily limited in taxonomic and geographic scope, because of the difficulty in obtaining information on individual taxa for many groups. This difficulty is particularly true for invertebrates and plants. For example, because specimen collections often lack online databases, researchers usually have to visit individual museums or arrange loans to determine where individual specimens of a given taxa have occurred. Finally, many ecological studies collect species diversity and abundance data across multiple seasons and timescales, but do not voucher collected material so that potentially rich biodiversity and distribution information is often lost (Holzenthal et al., 2010).

However, the value of natural history collections to provide a wide range of information for biodiversity, ecology, and global change studies has recently led to extensive efforts to digitize collections (Pyke & Ehrlich, 2010). As a result, museum collection databases are increasingly going online as part of large biodiversity data-sharing projects, particularly for charismatic vertebrate groups with relatively low diversity (Guralnick & Constable, 2010). Entomology collections are much further behind in this effort, largely because they are the most diverse group of animals, and individual collections often have extremely high volumes of specimens, numbering in the millions or even tens of millions (Schuh et al., 2010).

Our study of the California med-region used existing databases of aquatic insects from a variety of museum collection databases. Unfortunately, the digitization of specimen data for these databases is not near completion. For example, at the time of this publication the Essig Museum of Entomology at the University of California, Berkeley has digitized only 2% of its estimated 6 million insect specimens. However, there are important efforts underway to digitize Entomology collections of California that have the potential to add significantly to our understanding of biodiversity and response to global change (Hill et al., 2012). These efforts will greatly facilitate assessments of biodiversity and the conservation status of species.

Beyond producing faunal lists common in analyses of species richness, biodiversity conservation is increasingly attempting to account for conservation of ecosystem function or "ecosystem services" (e.g., Chan et al., 2006). Biological traits of macroinvertebrates (and other dominant organisms) are often used as a proxy for ecosystem function in aquatic ecosystems because of the important role that they play in the food web and because ecosystem function is a product of the expression of traits (Vaughn, 2010). In our analysis of the biological traits of med and non-med EPT genera, we found that there may be little functional differences between California med and non-med species. These results contrast with those of Bonada et al. (2007) and Bonada & Dolédec (2011), who found that Mediterranean Sea-basin genera had significantly different biological traits than their temperate counterparts. One obvious explanation for the discrepancy in these results is that our analysis was limited to EPT genera, whereas med-regions may harbor much greater functional diversity in other taxonomic groups with higher tolerances to the climate extremes (Odonata, Hemiptera, Coleoptera, crustaceans, etc.). Furthermore, both of these analyses were limited to the generic level because of difficulties in identification of larval stages and the lack of available trait information at the species level. A more complete analysis of all macroinvertebrate species would require more life history information (Resh & Rosenberg, 2010) that may reveal distinct trait composition of California med rivers.

The relative lack of knowledge about freshwater biodiversity is important in light of the many factors that are contributing to freshwater ecosystem decline, especially in the drier regions of the world. Freshwater species in North America suffer extinction rates that are five times higher than those for terrestrial taxa and three times higher than coastal marine mammals (Ricciardi and Rasmussen 1999). Moreover, the extinction rate of North American freshwater fish is currently 1,000 times higher than the background rate determined from the fossil record. Because freshwater diversity is not well known, these are even likely to be underestimates (Ricciardi & Rasmussen, 1999).

Water scarcity along with very large human populations has created extremely harsh conditions for med-region freshwater organisms in California (Moyle, 1995). Most precipitation falls in the northern, high-elevation areas, while the most densely populated areas are in the southern portion of the state (Moyle et al., 2011). As a result, dams and reservoirs exist on every major stream in California, and on many smaller streams, and aqueducts take water from natural waterways to drier regions for human use (Grantham et al. 2010; Moyle 1995). Climate change presents additional threats to freshwater biota, as increasing water temperatures and variability in flow are critical limiting factors for survival of these populations (Moyle et al., 2011; Filipe et al., 2013).

Further assessment of biodiversity changes over time in this region will undoubtedly reveal declines, extirpations, and extinctions of many more taxa than previously thought. Likewise, populations of species that were rare may increase because of their ability to adapt to new habitats created. The continued development of methods to more efficiently assess biodiversity and the conservation status of organisms will enable us to define conservation priorities and mitigate impacts of climate change and intensive land use.

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Table 1 Number of species in several major groups of freshwater organisms known to occur in California med-climate streams.

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Aquatic Insects	**1116**	**880**	**60**
Ephemeroptera	**153**	**131**	**4**
Ameletidae	19	16	0
Ametropodidae	1	0	0
Baetidae	38	31	1
Caenidae	5	4	0
Ephemerellidae	24	22	0
Ephemeridae	1	1	0
Heptageniidae	33	29	0
Isonychiidae	1	1	0
Leptohyphidae	3	3	0
Leptophlebiidae	21	19	1
Polymitarcyidae	1	0	0
Potamanthidae	1	0	0
Pseudironidae	1	1	1
Siphlonuridae	4	4	1
Plecoptera	**188**	**127**	**14**
Capniidae	60	42	9
Chloroperlidae	37	25	3
Leuctridae	8	5	0
Nemouridae	19	13	0
Peltoperlidae	7	4	0
Perlidae	5	4	0
Perlodidae	38	23	1
Pteronarcyidae	3	2	0
Taeniopterygidae	11	9	1
Trichoptera	**350**	**278**	**20**
Apataniidae	6	0	0
Brachycentridae	8	8	0
Calamoceratidae	1	1	0
Glossosomatidae	25	19	2
Goeridae	2	2	0
Helicopsychidae	3	2	0
Hydropsychidae	30	25	3
Hydroptilidae	47	41	4
Lepidostomatidae	22	15	0

Taxonomic group	**Total species richness in CA**	**Species richness in CA med**	**No. of species endemic to CA med**
Leptoceridae	18	15	0
Limnephilidae	64	45	0
Odontoceridae	5	5	0
Philopotamidae	20	18	3
Phryganeidae	4	3	0
Polycentropodidae	5	3	0
Psychomyiidae	11	10	2
Rhyacophilidae	64	55	4
Sericostomatidae	2	2	0
Uenoidae	13	9	2
Odonata	**79**	**67**	**0**
Aeshnidae	9	8	0
Calopterygidae	2	2	0
Coenagrionidae	28	22	0
Cordulegasteridae	1	1	0
Corduliidae	4	3	0
Gomphidae	12	9	0
Lestidae	4	4	0
Libellulidae	19	18	0
Coleoptera	**263**	**216**	**19**
Amphizoidae	1	1	0
Dyropidae	7	5	0
Dytiscidae	103	83	5
Elmidae	25	24	3
Eulichadidae	1	1	1
Georissidae	1	1	0
Gyrinidae	8	4	1
Haliplidae	4	3	0
Heteroceridae	9	8	0
Hydraenidae	17	16	5
Hydrophilidae	78	64	4
Hydroscaphidae	1	1	0
Psephenidae	6	5	0
Ptilodactylidae	2	0	0
Hemiptera	**83**	**61**	**3**
Belostomatidae	6	4	0
Corixidae	11	9	1
Gerridae	7	5	0

Taxonomic group	**Total species richness in CA**	**Species richness in CA med**	**No. of species endemic to CA med**
Hydrometridae	1	1	0
Macroveliidae	2	2	1
Naucoridae	5	3	0
Nepidae	3	2	0
Notonectidae	10	8	0
Ochteridae	1	0	0
Saldidae	26	20	1
Veliidae	11	7	0
Crustaceans	**46**	**38**	**8**
Anisogammaridae	5	4	0
Asellidae	5	5	2
Astacidae	4	2	0
Atyidae	2	2	2
Cambaridae	2	2	0
Corophiidae	2	2	0
Crangonyctidae	8	5	4
Gammaridae	1	1	0
Grapsidae	1	1	0
Hyalellidae	3	1	0
Leptochelidae	1	1	0
Munnidae	1	1	0
Mysidae	3	3	0
Palaemonidae	3	3	0
Panopeidae	1	1	0
Talitridae	3	3	0
Tanaidae	1	1	0
Molluscs	**98**	**54**	**2**
Amnicolidae	1	1	0
Ampullariidae	1	1	0
Ancylidae	2	2	0
Corbiculidae	2	2	0
Ellobiidae	1	1	0
Hydrobiidae	19	6	0
Littoridinae	1	0	0
Lymnaeidae	13	7	0
Margaritiferidae	1	1	0
Physidae	3	3	0

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Planorbidae	14	10	0
Pleuroceridae	9	4	0
Pomatiopsidae	2	2	1
Radicinae	1	1	0
Sphaeriidae	17	7	0
Thiaridae	2	0	0
Unionidae	3	2	0
Valvatidae	4	2	1
Viviparidae	2	2	0
Fish	**110**	**71**	**9**
Acipenseridae	2	2	0
Catastomidae	12	4	1
Centrarchidae	11	11	0
Cichlidae	3	0	0
Clupeidae	2	2	0
Cottidae	8	5	1
Cyprinidae	25	17	6
Cyprinodontidae	4	0	0
Embiotocidae	1	1	0
Esocidae	1	1	0
Fundulidae	1	1	0
Gasterosteidae	2	1	0
Gobiidae	1	1	0
Ictaluridae	7	6	0
Moronidae	2	2	0
Osmeridae	4	2	0
Percidae	2	2	0
Petromyzontidae	6	4	1
Poeciliidae	4	1	0
Salmonidae	12	8	0
Amphibians	**38**	**22**	**1**
Ambystomatidae	2	2	0
Ascaphidae	1	0	0
Bufonidae	6	3	0
Dicamptodontidae	2	2	0
Hylidae	4	3	0
Pipidae	1	1	0
Plethodontidae	3	2	1

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Ranidae	12	4	0
Rhyacotritonidae	1	0	0
Salamandridae	4	4	0
Scaphiopodidae	2	1	0
Diatoms	**1,011**	**835**	**367**[(a)]
Cymbellaceae	1	1	1
Achnanthaceae	33	16	8
Achnanthidiaceae	41	34	9
Ammatoideaceae	3	3	2
Amphipleuraceae	9	7	3
Anomoeoneidaceae	2	1	0
Aulacoseiraceae	9	6	0
Bacillariaceae	129	120	45
Berkeleyaceae	2	2	1
Biddulphiaceae	3	3	3
Borziaceae	1	1	0
Brachysiraceae	4	3	2
Catenulaceae	13	12	4
Cavinulaceae	3	2	0
Chaetophoraceae	3	3	2
Chamaesiphonaceae	1	1	0
Characiaceae	4	3	3
Chlorellaceae	1	1	1
Chroococcaceae	1	0	0
Cladophoraceae	1	1	0
Closteriaceae	10	8	5
Cocconeidaceae	9	8	0
Cryptomonadaceae	1	1	1
Cyanobacteriaceae	1	1	1
Cylindrocapsaceae	1	1	1
Cymbellaceae	56	49	22
Desmidiaceae	36	28	21
Diadesmidaceae	10	9	2
Diatomaceae	1	1	1
Dichotomosiphonaceae	1	1	1
Diploneidaceae	14	12	5
Entomoneidaceae	4	4	4
Euglenaceae	13	11	8

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Eunotiaceae	31	19	6
Fragilariaceae	72	61	23
Gomphonemataceae	48	39	16
Hemidiscaceae	1	1	1
Hydrococcaceae	1	0	0
Hydrodictyaceae	11	11	6
Licmophoraceae	1	0	0
Mastogloiaceae	2	2	1
Melosiraceae	2	4	1
Merismopediaceae	8	7	4
Microcoleoideae	1	0	1
Microcystaceae	2	1	0
Microsporaceae	4	4	3
Naviculaceae	157	123	44
Neidiaceae	11	8	3
Nostocaceae	6	3	0
Oedogoniaceae	1	1	1
Oocystaceae	3	2	2
Orthoseiraceae	1	1	1
Oscillatoriaceae	9	9	8
Paraliaceae	1	0	0
Peniaceae	1	1	1
Phormidiaceae	8	5	3
Phormidioideae	1	1	1
Pinnulariaceae	24	18	7
Plagiotropidaceae	1	1	1
Pleurosigmataceae	14	13	11
Pseudanabaenaceae	4	4	2
Radiococcaceae	2	1	1
Rhoicospheniaceae	5	3	0
Rhopalodiaceae	12	12	2
Rivulariaceae	3	3	1
Scenedesmaceae	21	20	10
Schizomeridaceae	1	1	0
Schizotrichaceae	3	3	2
Scoliotropidaceae	1	1	1
Scytonemataceae	1	1	1
Selenastraceae	6	2	0

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Sellaphoraceae	18	17	7
Skeletonemaceae	1	1	1
Sphaerocystidaceae	1	1	1
Stauroneidaceae	21	17	12
Stephanodiscaceae	21	20	4
Surirellaceae	23	18	5
Synechococcaceae	1	0	0
Tabellariaceae	4	3	1
Thalassiosiraceae	8	7	6
Trebouxiophyceae	2	2	2
Treubariaceae	2	2	1
Triceratiaceae	1	1	0
Ulotrichaceae	4	4	4
Volvocaceae	2	2	2
Macrophytes	**418**	**319**	**13**
Aceraceae	3	3	0
Adoxaceae	2	1	0
Alismataceae	5	5	0
Alliaceae	1	1	0
Amaranthaceae	1	1	0
Apiaceae	13	12	2
Apocynaceae	1	1	0
Araceae	11	10	0
Araliaceae	4	4	0
Arecaceae	3	3	0
Asteraceae	27	18	2
Azollaceae	2	2	0
Balsaminaceae	1	1	0
Betulaceae	2	1	0
Blechnaceae	1	1	0
Boraginaceae	2	0	0
Brassicaceae	4	2	0
Cabombaceae	2	2	0
Calycanthaceae	1	1	0
Campanulaceae	2	0	0

Taxonomic group	**Total species richness in CA**	**Species richness in CA med**	**No. of species endemic to CA med**
Cannabaceae	2	2	0
Caryophyllaceae	6	6	0
Celastraceae	1	1	0
Chenopodiaceae	3	3	0
Commelinaceae	1	1	0
Convolvulaceae	2	2	0
Cyperaceae	28	20	0
Datiscaceae	1	1	0
Dryopteridaceae	2	1	0
Elaeagnaceae	1	1	0
Elatinaceae	2	2	0
Ericaceae	1	1	0
Fabaceae	10	8	0
Gentianaceae	1	0	0
Grossulariaceae	2	0	0
Haloragaceae	4	4	0
Hydrocharitaceae	3	3	0
Hypericaceae	2	2	0
Iridaceae	1	1	0
Isoetaceae	1	1	0
Juglandaceae	3	3	1
Juncaceae	13	11	1
Juncaginaceae	3	1	0
Lamiaceae	8	6	1
Liliaceae	4	1	0
Limnanthaceae	4	3	1
Lythraceae	4	4	0
Malvaceae	4	1	0
Melanthiaceae	2	1	0
Meliaceae	1	1	0
Menyanthaceae	1	0	0
Montiaceae	8	4	0
Moraceae	2	2	0

Taxonomic group	**Total species richness in CA**	**Species richness in CA med**	**No. of species endemic to CA med**
Myrtaceae	1	1	0
Nartheciaceae	1	0	0
Nyctaginaceae	1	1	0
Nymphaeaceae	2	2	0
Oleaceae	1	1	0
Onagraceae	10	6	0
Ophioglossaceae	7	3	0
Orchidaceae	2	2	0
Orobanchaceae	5	2	0
Papaveraceae	1	0	0
Phrymaceae	16	15	1
Pinaceae	2	1	0
Plantaginaceae	13	12	0
Platanaceae	1	1	0
Poaceae	35	29	0
Polemoniaceae	5	5	0
Polygonaceae	7	6	0
Potamogetonaceae	10	9	0
Primulaceae	1	1	0
Pteridaceae	2	2	0
Ranunculaceae	19	12	2
Rhamnaceae	1	0	0
Rosaceae	7	6	1
Rubiaceae	2	1	0
Salicaceae	19	13	0
Salvinaceae	1	1	0
Saxifragaceae	6	4	0
Scrophulariaceae	1	0	0
Simaroubaceae	1	1	0
Smilacaceae	1	0	0
Solanaceae	1	1	0
Tamaricaceae	3	3	0
Thelypteridaceae	1	1	0

Taxonomic group	Total species richness in CA	Species richness in CA med	No. of species endemic to CA med
Themidaceae	1	1	1
Typhaceae	2	2	0
Ulmaceae	1	1	0
Urticaceae	2	2	0
Valerianaceae	1	0	0
Violaceae	3	2	0
Vitaceae	1	1	0
Woodsiaceae	2	1	0
Zingiberaceae	1	0	0
Totals	**2837**	**2219**	**93**

(a) information on individual diatom species was too limited to gather detailed information on distribution, so that many species we list as occurring exclusively in the med region are very likely to occur in other areas as well.

Table 2 Species that, based on existing records, may be endemic to the med-region of California.

Taxonomic Groups	Species Name
Aquatic Insects	
Ephemeroptera	
Baetidae	*Procloeon rivulare*
Leptophlebiidae	*Paraleptophlebia quisquilia*
Pseudironidae	*Pseudiron centralis*
Siphlonuridae	*Edmundsius agilis*
Plecoptera	
Capniidae	*Bolshecapnia maculata*
Capniidae	*Capnia hitchcocki*
Capniidae	*Capnia ophiona*
Capniidae	*Capnia regilla*
Capniidae	*Capnia saratoga*
Capniidae	*Capnia valhalla*
Capniidae	*Capnia ventura*
Capniidae	*Mesocapnia bakeri*
Capniidae	*Mesocapnia bulbosa*
Chloroperlidae	*Bisancora rutriformis*
Chloroperlidae	*Suwallia shepardi*
Chloroperlidae	*Sweltsa tamalpa*
Perlodidae	*Baumannella alameda*
Taeniopterygidae	*Taenionema jeanae*
Trichoptera	
Glossosomatidae	*Agapetus joannia*
Glossosomatidae	*Glossosoma sequoia*
Hydropsychidae	*Homoplectra nigripennis*
Hydropsychidae	*Homoplectra norada*
Hydropsychidae	*Hydropsyche cora*
Hydroptilidae	*Ochrotrichia bickfordae*
Hydroptilidae	*Ochrotrichia bogani*
Hydroptilidae	*Ochrotrichia burdicki*
Hydroptilidae	*Ochrotrichia salaris*
Philopotamidae	*Chimarra butleri*
Philopotamidae	*Chimarra primula*
Philopotamidae	*Wormaldia laona*
Psychomyiidae	*Tinodes schusteri*
Psychomyiidae	*Tinodes twilus*
Rhyacophilidae	*Rhyacophila lurella*
Rhyacophilidae	*Rhyacophila reyesi*
Rhyacophilidae	*Rhyacophila tamalpaisi*
Rhyacophilidae	*Rhyacophila tehama*
Uenoidae	*Farula geyseri*
Uenoidae	*Farula honeyi*

Taxonomic Groups	Species Name
Odonata	
Coenagrionidae	*Ischnura gemina*
Coleoptera	
Dytiscidae	*Hydroporus hirsutus*
Dytiscidae	*Hydroporus klamathensis*
Dytiscidae	*Sanfilippodytes barbarensis*
Dytiscidae	*Sanfilippodytes hardyi*
Dytiscidae	*Sanfilippodytes palliatus*
Elmidae	*Dubiraphia brunnescens*
Elmidae	*Dubiraphia giulianii*
Elmidae	*Optioservus heteroclitus*
Eulichadidae	*Stenocolus scutellaris*
Gyrinidae	*Gyrinus parcus*
Hydraenidae	*Limnebius piceus*
Hydraenidae	*Ochthebius costipennis*
Hydraenidae	*Ochthebius gruwelli*
Hydraenidae	*Ochthebius leechi*
Hydraenidae	*Ochthebius martini*
Hydrophilidae	*Chaetarthria magna*
Hydrophilidae	*Chaetarthria truncata*
Hydrophilidae	*Hydrochus variolatus*
Hydrophilidae	*Laccobius insolitus*
Hemiptera	
Corixidae	*Sigara vallis*
Macroveliidae	*Oravelia pege*
Saldidae	*Saldula usingeri*
Crustaceans	
Asellidae	*Calasellus californicus*
Asellidae	*Calasellus longus*
Atyidae	*Syncaris pacifica*
Atyidae	*Syncaris pasadenae*
Crangonyctidae	*Stygobromus cherylae*
Crangonyctidae	*Stygobromus cowani*
Crangonyctidae	*Stygobromus gallawayae*
Crangonyctidae	*Stygobromus rudolphi*
Molluscs	
Pomatiopsidae	*Pomatiopsis binneyi*
Valvatidae	*Valvata virens*
Fish	
Catastomidae	*Catostomus santaanae*
Cottidae	*Cottus pitensis*
Cyprinidae	*Lavinia exilicauda*
Cyprinidae	*Lavinia parvipinnus*
Cyprinidae	*Mylopharodon conocephalus*
Cyprinidae	*Pogonichthys ciscoides*
Cyprinidae	*Pogonichthys macrolepidotus*

Taxonomic Groups	**Species Name**
Cyprinidae	*Siphatales crassicauda*
Petromyzontidae	*Lampetra hubbsi*
Amphibians	
Plethodontidae	*Hydromantes brunus*
Macrophytes	
Apiaceae	*Eryngium pinnatisectum*
Apiaceae	*Perideridia californica*
Asteraceae	*Cirsium fontinale*
Asteraceae	*Solidago guiradonis*
Juglandaceae	*Juglans hindsii*
Juncaceae	*Juncus mertensianus*
Lamiaceae	*Trichostema rubisepalum*
Limnanthaceae	*Limnanthes montana*
Phrymaceae	*Mimulus inconspicuus*
Ranunculaceae	*Delphinium patens*
Ranunculaceae	*Ranunculus bonariensis*
Rosaceae	*Drymocallis cuneifolia*
Themidaceae	*Brodiaea pallida*

Table 3 Traits and trait categories included in the biological trait analysis of 251 Ephemeroptera, Plecoptera, and Trichoptera (EPT) genera, with predicted differences between med (M) and non-med (NM) genera. Predictions labelled "M" indicate that the trait should be more prevalent in med genera, and "NM" indicates predicted prevalence in non-med genera. Traits for which there is no expected difference in occurrence in med vs. non-med regions are indicated as “—“ (predictions are based on Bonada et al. 2007 and Bonada and Dolédec (2011)). Only traits with *a priori* hypotheses ("Prediction" and corresponding “Rationale”) were tested using Wilcoxon U-tests. The results indicate non-significant results (0), significant results (p< 0.05) that follow our predictions (+), or significant results that contradict our predictions (-). Some trait categories were not tested because they were not represented in the present database.

				Results (Wilcoxon U-tests)			
Trait	**Category**	**Prediction**	**Rationale**	**EPT**	**E**	**P**	**T**
Maximum Size (mm)	<2.5	M	Better resilience capacity of smaller sizes after disturbances (floods and especially droughts)	not tested			
	2.5-5	M	(Same as above)	0	0	0	0
	5-10	NM	Less resilience capacity required (fewer disturbance related stresses), permitting larger sizes, but permanent action of flow forces constrain large sizes	0	0	0	0
	10-20	NM	(Same as above)	0	0	0	0
	20-40	M	Low flow stresses allow for larger sizes	0	0	0	0
	40-80	M	(Same as above)	0	0	0	0
	> 80	--					
Life cycle duration (yr)	<= 1 yr	M	Shorter life cycles enable greater resilience to disturbances	0	0	0	(+)
	> 1 yr	--					
Voltinism	semivoltine	NM	Environmental conditions are more stable allowing for less frequent reproduction and longer life cycles	0	0	0	(+)
	univoltine	--					
	multivoltine						
Reproduction	ovoviviparous	M	Greater resilience capacity through ovoviviparity post-disturbance	0	0	0	0
	single, free	--					
	single, fixed	--					
	endophytic	--					
	terrestrial clutches	M	Increased resistance to drying	0	not tested		0
	asexual	M	Greater resilience to disturbances	(-)	0	0	0

Trait	Category	Prediction	Rationale	Results (Wilcoxon U-tests)			
				EPT	E	P	T
Resistant stages	egg resistance	--					
	cocoons	--					
	desiccation	M	Increased resistance to drying	0	0	0	0
	diapause	M	Increased resistance to flooding and drying	0	0	0	0
	no resistance	NM	More stable environmental conditions allow for lack of resistance strategies	0	0	0	0
Locomotion and substrate relations	flight	M	Intermittent or temporary rivers favor high dispersal capacity	not tested			
	surface swimmer	M	No flow in stagnant pools during dry season favor surface swimmers	not tested			
	swimmer	M	(Same as above)	0	0	0	0
	crawler	NM	Flow forces favor crawling strategies	(-)	0	0	0
	burrower	--					
	interstitial	M	Bed drying and droughts favor interstitial life stages	0	0	0	0
	coarse particulate organic matter	NM	Response to more litter input (more dense deciduous riparian forests)	(-)	(-)	0	0
	periphyton	M	Response to more algal growth (greater sun exposure)	0	0	0	(+)
	macrophytes	M	(Same as above)	0	0	0	0
	dead animals	--					
	microinvertebrates	--					
	macroinvertebrates	--					
	vertebrates	--					
Feeding habits	gathering collector	--					
	shredder	NM	Response to more litter input (more dense deciduous riparian forests)	0	0	0	0
	scraper	M	Response to more algal growth (greater sun exposure)	0	(+)	0	0
	filtering collector	--					
	piercer	--					
	predator	--					
	parasite	--					

Table 4 Lotic species in the med region of California that have been evaluated or classified as threatened or endangered by the California Department of Fish and Game (a state agency), the U.S. Fish and Wildlife Service (a federal agency), or the IUCN (a non-governmental organization).

Taxonomic Group	**Species**	**State and Federal List**[(a)]	**IUCN Red List**[(b)]
Odonata	*Coenagrion resolutum*		LC
	Sympetrum internum		LC
	Libellula luctuosa		LC
	Ischnura gemina		VU
	Ischnura ramburii		LC
	Aeshna palmata		LC
	Enallagma carunculatum		LC
	Ischnura perparva		LC
	Libellula comanche		LC
	Libellula quadrimaculata		LC
	Orthemis ferruginea		LC
	Sympetrum illotum		LC
	Sympetrum madidum		LC
	Enallagma cyathigerum		LC
	Argia alberta		LC
	Argia lugens		LC
	Libellula croceipennis		LC
	Octogomphus specularis		LC
	Ophiogomphus bison		LC
	Calopteryx aequabilis		LC
	Erpetogomphus lampropeltis		LC
	Aeshna umbrosa		LC
	Epitheca canis		LC
	Ophiogomphus occidentis		LC
	Zoniagrion exclamationis		LC
Molluscs	*Corbicula amurensis*		DD
	Fluminicola seminalis		DD
	Gyraulus crista		LC
	Juga nigrina		LC
	Marisa cornuarietis[(c)]		LC
	Micromenetus dilatatus		LC
	Pisidium casertanum		LC

Taxonomic Group	Species	State and Federal List[(a)]	IUCN Red List[(b)]
	Pisidium variable		LC
	Pomatiopsis californica		DD
	Psidium insigne		LC
	Pyrgulopsis guiliani		VU
	Pyrgulopsis stearnsiana		LC
	Stagnicola traski		LC
	Valvata humeralis		LC
	Valvata virens		VU
	Vorticifex effusus		LC
Crustaceans	*Pacifastacus nigrescens*		EX
	Syncaris pacifica	SE, FE	EN
	Syncaris pasadenae		EX
	Pacifastacus leniusculus klamathensis[(c)]		LC
	Pacifastacus leniusculus leniusculus[(c)]		LC
	Pacifastacus leniusculus trowbridgii[(c)]		LC
	Orconectes virilis[(c)]		LC
	Procambarus clarkii[(c)]		LC
Fish[(d)]	*Acipenser medirostris, Southern Green Sturgeon*	FT	NT
	Acipenser transmontanus, White Sturgeon		LC
	Catostomus microps, Modoc Sucker	SE, FE	EN
	Catostomus santaanae, Santa Ana Sucker	FT	VU
	Cottus pitensis, Pit Sculpin		LC
	Eucyclogobius newberryi, Tidewater Goby	Withdrawn, FPD, FE	VU
	Gasterosteus aculeatus, Coastal threespine stickleback		LC
	Gasterosteus aculeatus, Unarmored threespine stickleback	SE, FE	

Taxonomic Group	Species	State and Federal List[(a)]	IUCN Red List[(b)]
	Lampetra hubbsi, Kern Brook Lamprey		NT
	Oncorhynchus mykiss, Central California coast winter steelhead	FT	
	Oncorhynchus mykiss, Central Valley steelhead	FT	
	Oncorhynchus mykiss, Little Kern golden trout	FT	
	Oncorhynchus mykiss, Northern California coast summer steelhead	FT	
	Oncorhynchus mykiss, South Central California coast steelhead	FT	
	Oncorhynchus mykiss, Southern California steelhead	FE	
	Oncorhynchus tshawytscha, California Coast fall Chinook salmon	FT	
	Oncorhynchus tshawytscha, Central Valley spring Chinook salmon	ST, FT	
	Oncorhynchus tshawytscha, Central Valley winter Chinook salmon	SE, FE	
	Pogonichthys macrolepidotus, Sacramento Splittail		EN
	Salvelinus confluentus, Bull Trout	SE, FT	
	Spirinchus thaleichthys, Longfin Smelt	ST	LC
Amphibians	*Lithobates catesbeianus*		LC
	Xenopus laevis		LC
	Anaxyrus californicus	FE	EN
	Ambystoma gracile		LC
	Taricha granulosa		LC

Taxonomic Group	Species	State and Federal List[a]	IUCN Red List[b]
	Taricha torosa		LC
	Anaxyrus punctatus		LC
	Pseudacris cadaverina		LC
	Taricha rivularis		LC
	Dicamptodon tenebrosus		LC
	Dicamptodon ensatus		NT
	Spea hammondii		NT
	Rana boylii		NT
	Rana draytonii		VU
	Rana mucosa	SCE, FE	
	Hydromantes brunus	ST	VU
Macrophytes	*Circium fontinale*	SE, FE	
	Cyperus squarrosus		LC
	Eriastrum densifolium	SE, FE	
	Ficus carica		LC
	Juncus effusus		LC
	Lemna gibba		LC
	Lemna minor		LC
	Lemna trisulca		LC
	Lilaeopsis masonii	SR	
	Lilium pardalinum	SE, FE	
	Limnanthes bakeri	SR	
	Najas marina		LC
	Picea sitchensis		LC
	Pinus ponderosa		LC
	Potamogeton crispus		LC
	Potamogeton natans		LC
	Potamogeton nodosus		LC
	Potamogeton pusillus		LC
	Sidalcea oregana	SE, FE	
	Sparganium emersum		LC
	Stuckenia pectinata		LC
	Trichostema austromontanum	FT	
	Typha angustifolia		LC
	Typha domingensis		LC
	Washingtonia filifera		NT

Taxonomic Group	Species	State and Federal List[(a)]	IUCN Red List[(b)]
	Wolffia arrhiza		LC

(a) SE=State Listed as Endangered, ST=State listed as Threatened, SR=State listed as Rare, SCE=State Candidate (Endangered), FE = Federally listed as Endangered, FT = Federally listed as Threatened, FPD =Federally Proposed (Delisting)

(b) LC=Least Concern, DD=Data Deficient NT=Near Threatened, VU=Vulnerable, EN=Endangered, EX=Extinct

(c) Species is not native to California

(d) Many classifications for fish are based on subspecies and specific populations. Separate populations of the same species often have different categories of threat, and all are shown here.

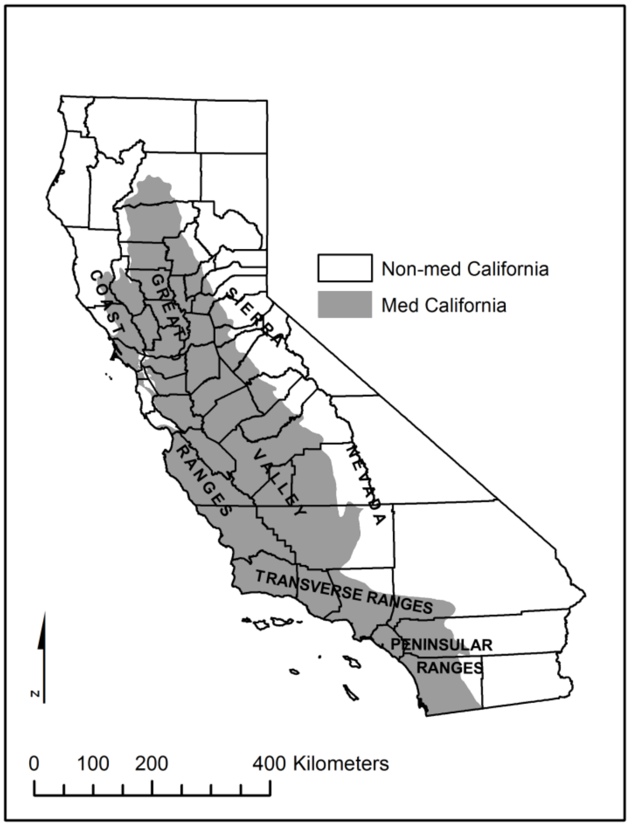

Fig. 1 Med-climate region of California. Major geological features such as mountain ranges are labeled. Lines represent county divisions. The Great Valley is often referred to as the California Central Valley.

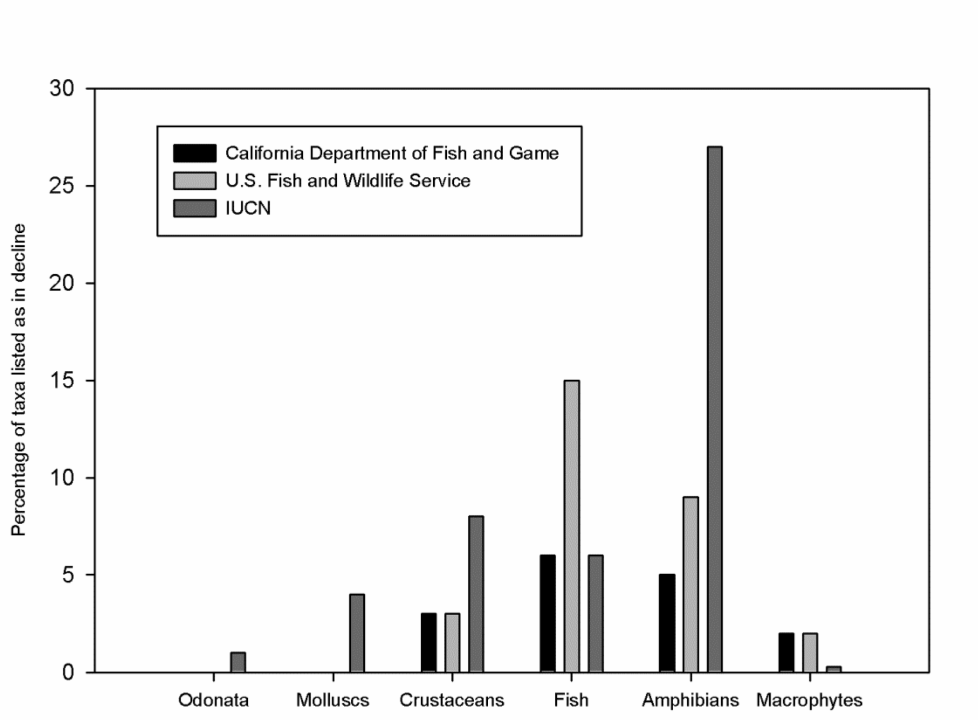

Fig. 2 Percentage of lotic med CA taxa listed as in decline (vulnerable, threatened or endangered) or extinct by the California Department of Fish and Game, U.S. Fish and Wildlife Service, and the IUCN.

CHAPTER 2

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

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

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 1914-15 for Odonata (dragonflies and damselflies) adults throughout central California and northwestern 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. Migratory species occurred frequently in highly populated sites, while habitat specialists occurred less often. 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.

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 & 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. 2009; DeWalt et al. 2005; Favret & Dewalt, 2002) and in Europe (Fochetti & 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 & Holzenthal, 2010; Resh & 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 & 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 & 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 & 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 & 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 & Thompson 2010). In addition, habitat specialists are known to have higher local extinction in areas with increased urbanization, while generalists often do not (Goertzen & 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 one hundred 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 1914-15 (Kennedy 1917). Here, we compare Odonata assemblages from C.H. Kennedy’s historical survey to resurveys conducted at the same sites in 2011-13. We then 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 1914-15 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 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, 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 two weeks of the original calendar dates of his collections. Kennedy’s notes indicate that he generally visited individual sites for more than three hours during each visit. Therefore, we also visited each site for more than three hours, unless the habitat was highly degraded and there was little to no Odonata activity. The total time spent surveying averaged 4.6 ± 3.3 hours (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 (R Development Core Team 2013). Site and an era indicator (i.e. 1914-15 survey or 2011-13 resurveys) were both included as random effects. The model is defined as follows:

Species richness = intercept + minimum temperature + total precipitation + human population + random effects (site, era).

Change in Community Similarity

In order to determine whether Odonata assemblages have become more similar across sites since the 1914-15 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 = number of species present in both assemblages, b = number of species present only in the first assemblage, and c = 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 1914-15, 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 in order 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:

Species detection = intercept + era x low dispersal + era x migrant
+ era x habitat specialist + era x forest specialist + era x lotic specialist
+ era x tolerance value + era x generation time + era x diapause
+ era x elevation preference + random effects (family, genus, species, site).

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). To compare site-level minimum temperature values to trends occurring across California and Nevada, we averaged annual minimum temperatures across the study sites over the respective calendar years of the 1914-15 and 2011-13 resurveys.

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:

Species occurrence = intercept + minimum temperature x migrant
+ minimum temperature x habitat specialist + minimum temperature x diapause
+ total precipitation x migrant + total precipitation x habitat specialist
+ total precipitation x diapause + human population x migrant
+ human population x habitat specialist + human population x diapause
+ random effects (family, genus, species, site, era).

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 2011-13 resurveys, we collected and observed a total of 69 species, while Kennedy observed a total of 80 species across the 45. 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 2011-13 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. There were nine additional species in 2011-13 that were rare in Kennedy's survey (one or two occurrences; Table 3) that we did not observe.

Overall, a total of 52 species declined (65%) in relative frequency of sites when compared to the 1914-15 surveys, while 29 species increased (36%). Fifty-two species were considered habitat specialists, and 34 (65%) of them declined since 1914-15. Out of the 16 species with the largest declines since 1914-15, 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 1914-15. The average percentage of generalists at each site increased from about 55% in 1914-15 to 73% in 2011-13 (t=5.28, p<0.0001). Out of the 14 species with the largest increases since 1914-15, all but three (*Argia vivida*, *Argia emma* and *Enallagma clausum*) were habitat generalists.

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 1914-15 and 37 in 2011-13 (p = 0.22). Total species richness within the California Mediterranean declined from 51 in 1914-15 to 45 in 2011-13, declined within the Great Basin shrub steppe from 44 in 1914-15 to 32 in 2011-13, and remained similar in the Northern California coastal forests (37 in 1914-15 and 38 in 2011-13) and the Sierra Nevada forests (34 in 1914-15 and 34 in 2011-13; 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 1914-15 and 2011-13 (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 1914-15 surveys to 2011-13 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 1914-15 to -1.9 ˚C (±5.3) in 2011-13 during the water year, and average total precipitation across sites decreased from 785 mm (±492) in 1914-15 to 585 mm (±421) in 2011-13 (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 1914-15 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 (-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).

Discussion

Change in Occurrence

Two currently common species, *Enallagma civile* and *Libellula luctuosa*, were not present at all during Kennedy's 1914-15 surveys (Table 3). *E. 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 & Kalkman 2008), changes in predators (e.g. McPeek 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 & 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 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; McKinney 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-llosera & 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 & 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*, *P. 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 1914-15 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 current survey. 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 & 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 & 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 & 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 & 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 & 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 & 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 & Suhling 2013; Samways & 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; McKinney 2006; McKinney 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 & Kerr 2007).

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Table 1. Summary of effort and environmental variables in the 1914-15 surveys and 2011-13 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 - 2082)	585 (64 - 1926)	-200
Human population	6,069 (0 - 53,181)	88,889 (0 - 956,142)	82,820

Table 2. Predicted increase or decline in biological traits over time.

Trait	Explanation	Predicted change	Reference
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, 3013
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	(-)	EPA Rapid Bioassessment Protocol
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: 0-2000 m, high: only known from higher elevations	(-)	Habitat descriptions in Manolis (2003)

Table 3. Comparison of species occupancy from 1914-15 surveys and 2011-13 resurveys at 45 sites throughout California and Nevada. 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.

Species Name	1914-1915	2011-2013	Occurrence Change	Relative Change	Specialization
Lestes congener	14	3	-11	-0.0217	G
Sympetrum pallipes	18	7	-11	-0.0220	G
Sympetrum obtrusum	9	2	-7	-0.0138	S
Sympetrum danae	6	0	-6	-0.0117	S
Macromia magnifica	9	3	-6	-0.0119	S
Ophiogomphus occidentis	5	0	-5	-0.0097	S
Progomphus borealis	7	2	-5	-0.0099	S
Ophiogomphus morrisoni	8	3	-5	-0.0100	S
Aeshna interrupta	6	2	-4	-0.0080	S
Stylurus olivaceus	6	2	-4	-0.0080	S
Hetaerina americana	11	7	-4	-0.0084	S
Libellula nodisticta	3	0	-3	-0.0058	S
Sympetrum costiferum	3	0	-3	-0.0058	S
Coenagrion resolutum	4	1	-3	-0.0059	S
Ophiogomphus bison	4	1	-3	-0.0059	S
Sympetrum semicinctum	9	6	-3	-0.0063	G
Archilestes californicus	2	0	-2	-0.0039	S
Ischnura gemina	2	0	-2	-0.0039	S
Lestes unguiculatus	2	0	-2	-0.0039	S
Leucorrhinia glacialis	2	0	-2	-0.0039	S
Ophiogomphus severus	1	0	-1	-0.0019	S
Sympetrum internum	2	0	-2	-0.0039	G
Aeshna umbrosa	1	0	-1	-0.0019	S
Epitheca spinigera	1	0	-1	-0.0019	S
Plathemis subornata	1	0	-1	-0.0019	S
Enallagma praevarum	5	9	4	0.0071	G
Argia vivida	14	18	4	0.0064	G
Argia emma	15	19	4	0.0063	S
Enallagma clausum	1	6	5	0.0093	S
Sympetrum corruptum	21	27	6	0.0095	G
Ischnura cervula	19	26	7	0.0116	G
Pachydiplax longipennis	5	13	8	0.0146	G

Species Name	1914-1915	2011-2013	Occurrence Change	Relative Change	Specialization
Rhionaeschna multicolor	23	31	8	0.0131	G
Libellula luctuosa	0	9	9	0.0168	G
Libellula saturata	12	21	9	0.0159	G
Tramea lacerata	7	21	14	0.0256	G
Pantala hymenaea	4	19	15	0.0277	G
Anax junius	13	28	15	0.0270	G
Enallagma civile	0	18	18	0.0336	G
Total Occurrences	275	304			

Table 4. Total and average species richness for 1914-15 and 2011-13 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 minimum temperature, total precipitation and human population on Odonata species richness for 1914-15 surveys and 2011-13 resurveys. Significant relationships are bolded.

	Estimate	Std. error	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**

Table 6. Number of increases and decreases in Jaccard Similarity Index Scores for site comparisons, from 1914-15 surveys to 2011-13 resurveys. Significant differences in number of increases over decreases in similarity are bolded.

	# Sites	Total comparisons	Increases	Decreases	Sign test p-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

Table 7. Multi-species model estimates for the effects of time period (era, from 1914-15 to 2011-13), biological traits, and interactions on Odonata species detection. 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.

Parameter	Estimate	Std. error	Z-value	P-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 x era	-0.44	0.41	-1.07	0.284	-0.36
Migrant x era	**1.49**	**0.26**	**5.71**	**0.000**	**3.42**
Habitat specialist x era	**-0.37**	**0.17**	**-2.18**	**0.029**	**-0.31**
Forest specialist x era	0.07	0.23	0.31	0.754	0.07
Lotic specialist x era	0.18	0.21	0.87	0.385	0.20
Tolerance value x era	-0.01	0.04	-0.24	0.809	-0.01
Generation time x era	-0.11	0.39	-0.28	0.778	-0.10
Diapause x era	**-0.45**	**0.17**	**-2.74**	**0.006**	**-0.36**
Elevation preference x era	-0.01	0.16	-0.09	0.929	-0.01

Table 8. Multi-species model estimates for the effects of temperature, precipitation, human population, species traits, and interactions on Odonata species detection for 1914-15 surveys and 2011-13 resurveys. 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.

Parameter	Estimate	Std. error	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 x migrant	-0.04	0.14	-0.29	0.775	-0.04
Minimum temperature x habitat specialist	**-0.47**	**0.06**	**-7.44**	**<0.001**	**-0.38**
Minimum temperature x diapause	**-0.54**	**0.07**	**-8.04**	**<0.001**	**-0.41**
Total precipitation x migrant	**-0.64**	**0.17**	**-3.72**	**<0.001**	**-0.47**
Total precipitation x habitat specialist	**0.20**	**0.07**	**3.06**	**0.002**	**0.22**
Total precipitation x diapause	**0.44**	**0.07**	**6.50**	**<0.001**	**0.55**
Human population x migrant	0.00	0.11	-0.03	0.977	0.00
Human population x habitat specialist	**-0.28**	**0.10**	**-2.72**	**0.007**	**-0.24**
Human Population x diapause	-0.12	0.09	-1.23	0.218	-0.11

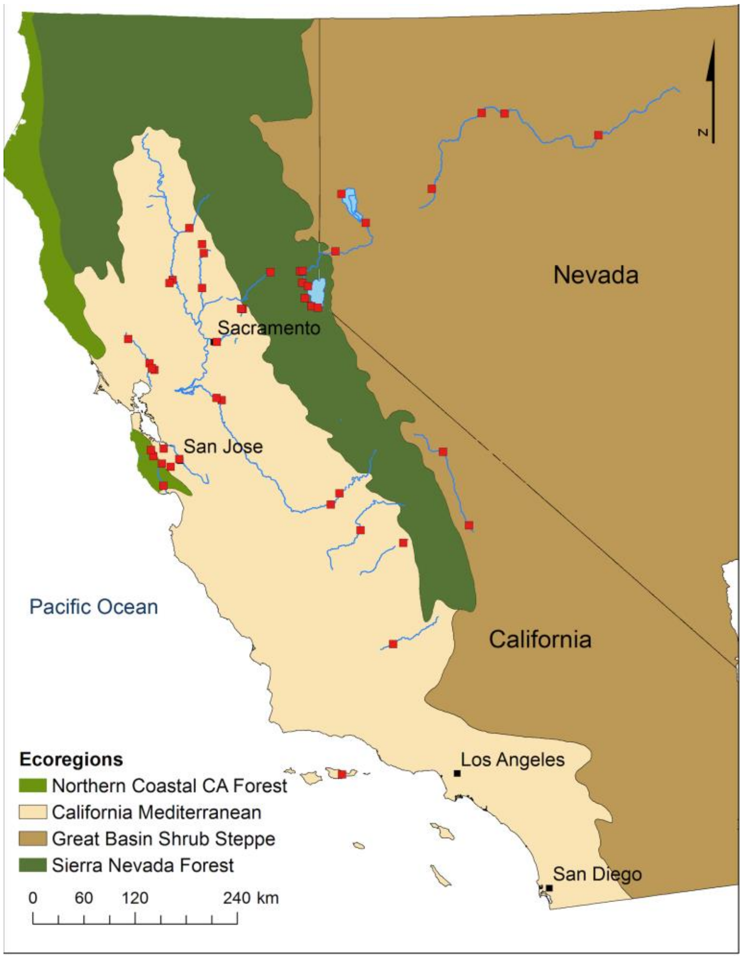

Fig. 1 Map of study sites and ecoregions.

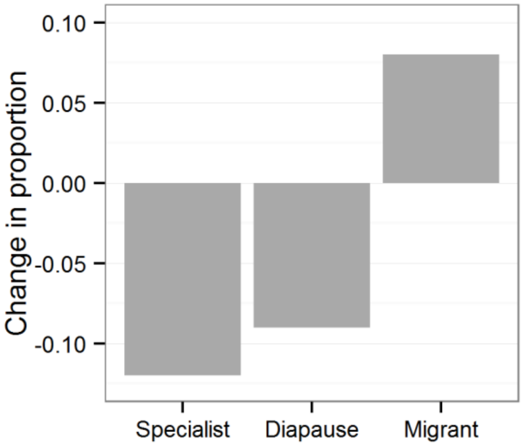

Fig. 2 Proportional change in occurrences of migrant species, species with overwintering diapause, and habitat specialists from the 1914-15 surveys to 2011-13 resurveys.

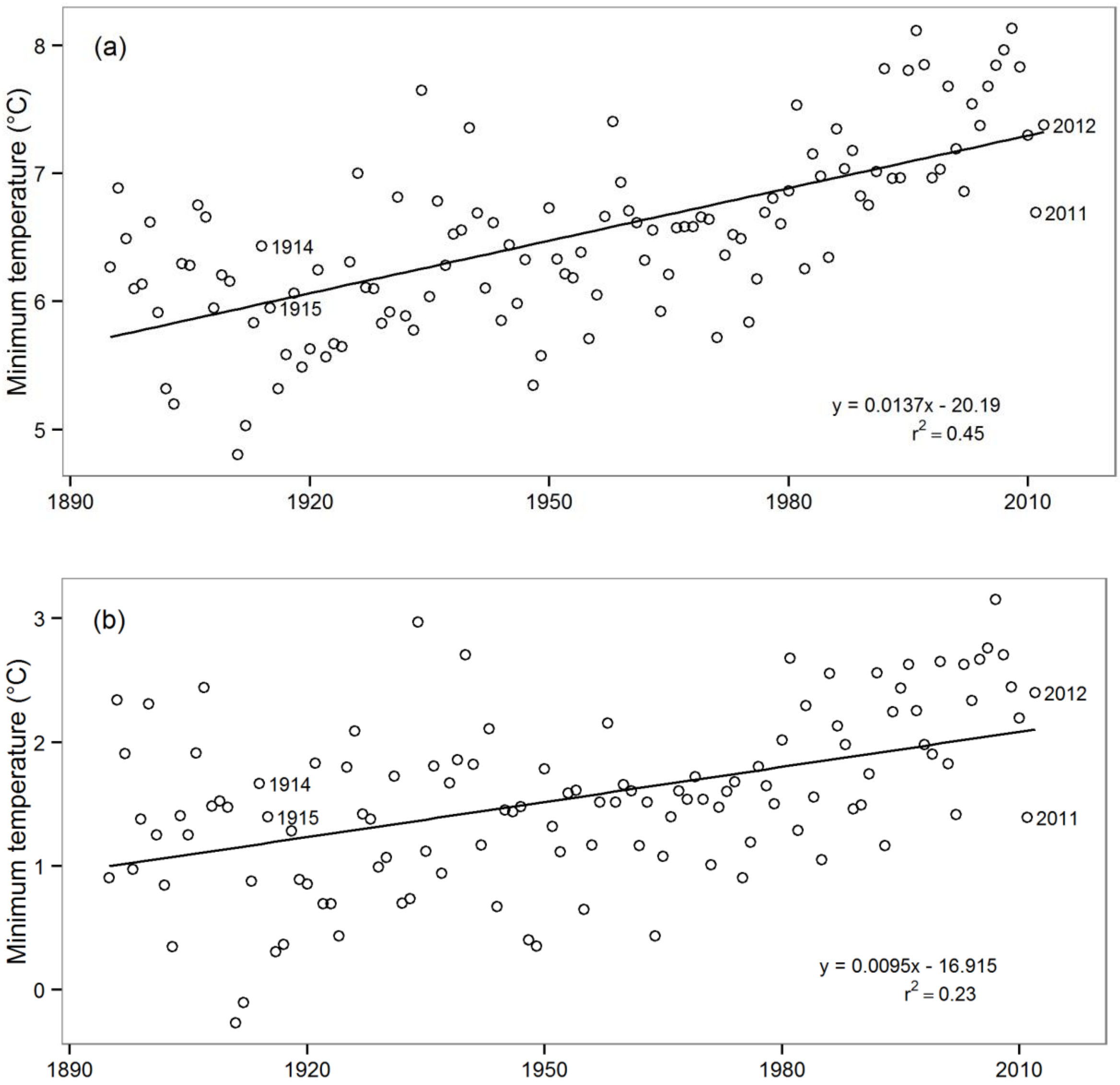

Fig. 3 Average annual minimum temperature, over the calendar year, from 1895 to 2012 across (a) California and (b) Nevada.

CHAPTER 3

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

Joan E. Ball-Damerow, Leithen K. M'Gonigle, and Vincent H. Resh

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

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 north-western 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 richness of dragonflies, but not less-mobile damselflies. In contrast, local habitat type influenced the richness 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.

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; Clausnitzer et al. 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 larval 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 & 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.

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 1914-15, 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. 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 three-year study period. For each individual site visit, we recorded the amount of time spent surveying (average 2.4 hours ±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 larval 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 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).

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 also may 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 larval 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 larvae 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 effected 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:

Visit-level species richness ~ intercept + visit effort + lotic habitat type
+ lentic habitat type + canopy cover + emergent vegetation
+ visit degree-days + visit total precipitation + site elevation
+ site agriculture + site urbanization + random effects (site, year).

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:

Visit-level species occurrence ~ intercept + visit effort
+ lotic habitat x lotic species + lentic habitat x lentic species
+ site canopy cover x forest specialist + emergent vegetation
+ visit degree-days x dragonfly + visit degree-days x migratory species
+ visit degree-days x habitat specialist + visit total precipitation x dragonfly
+ visit total precipitation x migratory species + site elevation x habitat specialist
+ site agriculture x habitat specialist + site urbanization x habitat specialist
+ site urbanization x migrant + random effects (genus, species, site, year).

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). 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 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 larvae 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 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).

Although our study region in California and Nevada is relatively arid, sites had significant variation in precipitation during the wet season (70-2040 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; Bêche et al. 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 specialist species in order to protect the widest variety species (e.g., Korkeamaki & 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; Clausnitzer et al. 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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Table 1. Variables hypothesized to influence the occupancy rate and detection of Odonata species. 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 one-km buffer radius of the site. Agriculture is the percent agricultural land calculated within a one-km buffer radius of the site.

	Predicted Effect								
Variable	Species Occurrence	Richness	Dragonfly/ Damselfly	Habitat Specialist	Forest Specialist	Lotic/Lentic Associated	Migrant	Data Source	Mean Value (Min-Max)
Visit Effort (hours)	+	+	+/+	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 (97-4295)
Total Precip. (mm)	+	+	+/0	n/a	n/a	n/a	n/a	GHCN	540 mm (70-2040)
Elevation (m)	-	-	n/a	+	n/a	n/a	n/a	NED	576 (1.7-2535)
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)

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. Significant values are bolded.

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 (hours)**	**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

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. 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.

Parameter		Estimate	Std. Error	Z Value	P-Value
	(Intercept)	-3.77	0.29	-13.24	<0.001
Survey	**Visit Effort (hours)**	**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 x Lotic Species**	**0.38**	**0.09**	**4.31**	**<0.001**
	Lentic Habitat x Lentic Species	**0.33**	**0.08**	**4.28**	**<0.001**
	Canopy Cover x Forest Specialist	**0.35**	**0.05**	**6.86**	**<0.001**
	Degree-days x Dragonfly	**0.11**	**0.04**	**2.57**	**0.01**
	Degree-days x Migrant	**0.14**	**0.03**	**5.10**	**<0.001**
	Total Precipitation x Dragonfly	**0.08**	**0.04**	**2.04**	**0.04**
	Elevation x Habitat Specialist	**0.29**	**0.04**	**7.11**	**<0.001**
	Urbanization x Habitat Specialist	**-0.34**	**0.06**	**-5.37**	**<0.001**

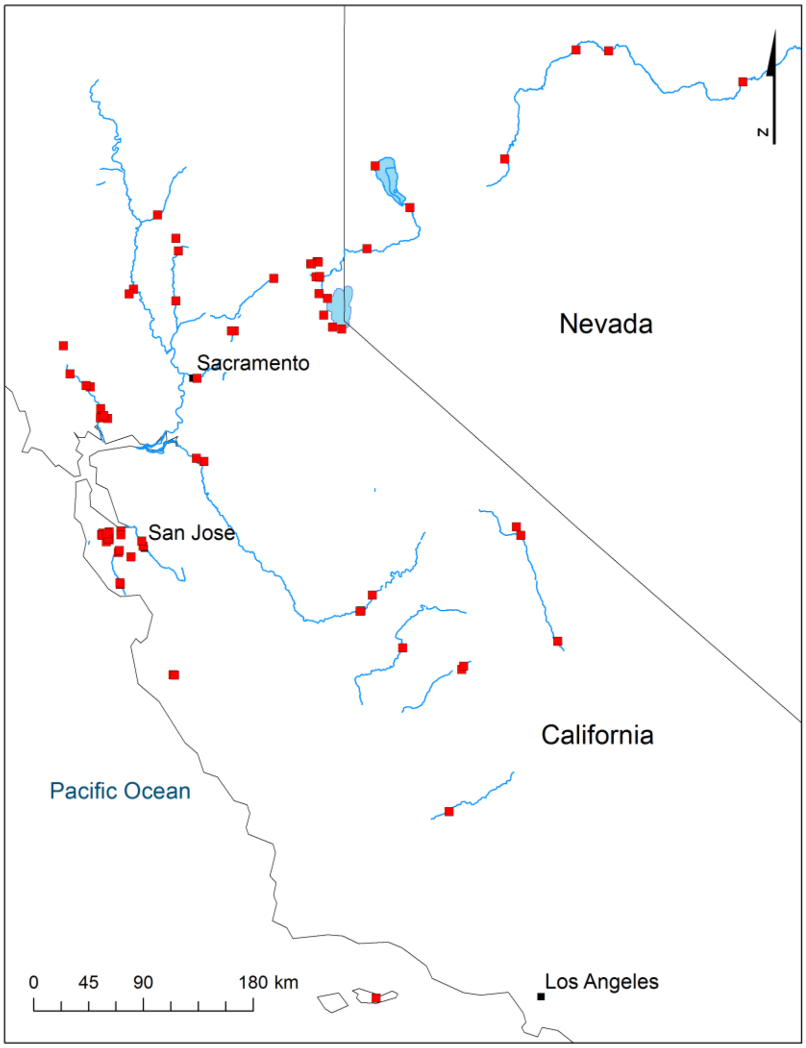

Fig. 1 Map of study sites and major rivers and lakes sampled throughout central California and north-western Nevada, USA

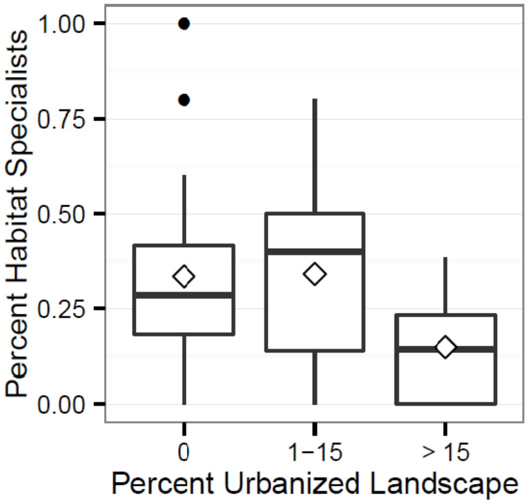

Fig. 2 Percentage of habitat specialists at sites with 0%, 1-15%, and >15% high and medium intensity development within a surrounding one-km buffer radius.

CHAPTER 4

California dragonfly and damselfly (Odonata) database: temporal and spatial distribution of species records collected over the past century

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Abstract

The recently completed Odonata database for California consists of statewide specimen-records from the major entomology collections of the state, large Odonata collections outside of the state, previous literature, historical and recent field surveys, and from enthusiast-group observations. The database includes 32,025 total records and 19,000 unique records for 106 species of dragonflies and damselflies, with records spanning 1879-2013. Records have been geographically referenced using the point-radius method to assign coordinates and an uncertainty radius to specimen locations. In addition to describing techniques used in data acquisition, georeferencing, and quality control, we present assessments of the temporal, spatial, and taxonomic distribution of records. We use this information to identify biases in the data, and to determine changes in species prevalence, latitudinal ranges, and elevation ranges when comparing records before 1976 and after 1979. The average latitude of where records occurred increased by 78 km over these time periods. While average elevation did not change significantly, the average minimum-elevation across species declined by 108 m. Odonata distribution may be generally shifting northwards as temperature warms and to lower minimum elevations in response to increased summer water-availability in low-elevation agricultural regions. The unexpected decline in elevation may also be partially the result of bias in recent collections towards centers of human population, which tend to occur at lower elevations. This study emphasizes the need to address temporal, spatial, and taxonomic biases in museum and observational records in order to produce reliable conclusions from such data.

Introduction

Natural history specimens are arguably the most valuable records of the historical occurrence of organisms. In contrast to scientific publications, which usually are most relevant for the first ten years following their appearance, information from specimens become more valuable with age (Winker 2004). Museum records that are backed by voucher specimens also allow researchers to verify species identification. In addition to their traditional use in taxonomy and biogeography studies, specimens can provide a wealth of information concerning changes in morphology, genetic and biochemical composition, and the distribution and diversity of organisms over time (Cao et al. 2013, Graham et al. 2004, O'Connell et al. 2004, Pyke and Ehrlich 2010, Winker 2004). However, large-scale applied and ecological studies using museum specimens are exceedingly difficult to conduct without a database of existing records. While the development of digital catalogs of natural history specimens began in 1970, by 2010 only ~ 3% of total records worldwide were estimated to be available online through the mobilization efforts of the Global Biodiversity Information Facility (GBIF 2014; Ariño 2010).

Many vertebrate collections have complete or near-complete databases of their specimens, along with ancillary information such as photos, field notes, and published manuscripts associated with particular specimens (e.g., Guralnick and Constable 2010, Pyke and Ehrlich 2010). However, databases for insects and other invertebrates have lagged far behind vertebrates (Schuh et al. 2010). This is largely because the task of databasing information from millions of small specimens, which represent the most diverse animal group on the planet, is enormous. In addition, these collections often lack the necessary resources to meet desired specimen curation because insects tend to undergo continual taxonomic revision (DeWalt et al. 2005). Therefore, many have considered digitization of huge collections of insects with tiny and highly abbreviated labels to be impossible (Schuh et al. 2010). However, in response to a growing need for specimen data in research, more insect and other large natural history collections are in the process of undergoing or beginning digitization (e.g., Abbott 2005, Favret and DeWalt 2002, Graham et al. 2004, Hill et al. 2012, Schuh et al. 2010). In the United States, the National Science Foundation (2014) has made such efforts possible through funding initiatives, including the Advancing Digitization of Biodiversity Collections (ADBC) and the Thematic Collections Network (TCN).

Along with digitization, however, comes the responsibility of database curators and data-users to acknowledge and address the many biases that exist in specimen data. Because the approach of natural history collection acquisition and management has traditionally focused on taxonomic work and the special interests of curators and enthusiasts (Graham et al. 2004), the data are usually biased in regards to the species collected and the temporal and spatial distribution of records (Pyke and Ehrlich 2010). For example, collectors have often focused collecting efforts on rare, large, and charismatic species while neglecting more common or cosmopolitan species (Winker 2004). Collections also tend to occur along roads, railroad tracks, or near centers of human population (Graham et al. 2004, Pyke and Ehrlich 2010). There is usually a strong correlation between collection effort, or number of records, and the number of species documented for a given time period or region (Fattorini 2013). Therefore, well-sampled regions may have better species representation than less-sampled areas as a result of sampling effort. Such biases present in natural history collections can be reduced by incorporating as much data as possible in occurrence-based analyses of the data. For example, compiling records from multiple institutions may help reduce the problem of localized collecting from any one collection (Pyke and Ehrlich 2010, Soberon et al. 2000).

The present study summarizes a recently completed database of Odonata records from throughout the state of California, USA, including both specimens and observational records. This group of aquatic insects provided a good starting point for a statewide database of insect specimens because they are less diverse than most insect orders, have well-known taxonomy (Clausnitzer et al. 2009), are charismatic to the general public, and have naturalist sightings that are available to supplement recent occurrence records (Abbott 2005, Odonata Central 2014). Odonata are also known to be useful indicators of freshwater ecosystem health, and are thus likely to contribute to our understanding of general response to changes in aquatic habitat and water quality (e.g., Clausnitzer 2003, Smith et al. 2007). Here, we outline the methods used in the development of the California Odonata database. We then present the spatial and temporal distribution of records to identify data gaps and biases. We determine contributions of different collection types (e.g., university and government institutions, observation-based records) to total number of records and unique county records. Finally, we assess the prevalence of records for each Odonata species before 1976 and after 1979 to determine both potential taxonomic biases and changes in species prevalence, altitude, and elevation ranges over time. We chose the time periods of before 1976 and after 1979 because they have approximately equal numbers of records, and the time period beginning in 1980 marks the beginning of accelerated temperature warming.

Methods

Odonata specimen database

We developed a database of Odonata occurrence records in conjunction with a larger project, known as Calbug, whose goal is to database over one million California arthropod specimens (Calbug 2014). Calbug is a collaborative project among the ten major entomology collections in California, including: the California Academy of Sciences (CASENT), California State Collection of Arthropods (CSCA), Los Angeles County Museum (LACM), San Diego Natural History Museum (SDNHM), Santa Barbara Museum of Natural History (SBMNH), Essig Museum of Entomology of the University of California at Berkeley (EMEC), Bohart Museum of Entomology of the University of California at Davis (UCBME), Entomology Research Museum of the University of California at Riverside (UCRCENT), Museum of Natural History of the University of California at Santa Cruz (UCSC), and the Oakland Museum of California (OMC). The Odonata database includes records from CASENT, CSCA, LACM, EMEC, UCBME, SBMNH, SDNHM, UCRCENT, and OMC.

In addition to the Calbug institutions, we obtained specimen data from the two largest Odonata collections in the United States, the Museum of Zoology at the University of Michigan (UMMZI) and the Florida State Collection of Arthropods (FSCA), which includes records from International Odonata Research Institute (IORI), Louisiana State Arthropod Collection (LSUC), and the Museum of Zoology Pontifical Catholic University of Ecuador (QCAZ) collections. We then incorporated data from other online databases that contain California odonate material, including that of the Illinois Natural History Survey (INHS 2014), and the National Museum of Natural History (NMNH 2014). We also included California odonate occurrence records from the personal collections of D.R. Paulson (DRPC), R.W. Garrison (RWGC), S.D. Gaimari (SDGC), and the author (J.E.B-D, Ball-Damerow et al. 2014). Finally, the odonate records of C.H. Kennedy (1917), collected throughout central California in 1914-15 are incorporated as a private collection. These records are included in the Essig museum's online specimen database (Table 1, Essig Museum of Entomology Collections Specimen Database 2014).

Odonata was a high priority group for the Calbug project, which began in 2010. At the start of the project, we directly entered data from specimen labels into the Essig database, and assigned each specimen a Unique Identifier (UID) that is associated with the physical specimen and its database record. The Essig database uses Linux, Apache HTTP Server, MySQL, and Perl/PHP (LAMP) technology, and currently contains 117 fields based on Darwin Core standards. A Darwin Core-Archive is created monthly and made available to GBIF and other aggregators via the Berkeley Natural History Museums (BNHM) IPT service.

Since 2011, we have photographed specimens with their collection labels as the first stage of the data collection process. Further details on the imaging process are described on the Calbug website (2014). The images are then uploaded into the Essig database with species name and UID information, and stored in the database as part of the specimen record. Individuals may then enter label information for specimen records online through the Essig database, using the magnified specimen image.

Observation-based records

In addition to specimen collections, we also included occurrence data from Odonata Central and CalOdes enthusiast observations, of which records have often been photo-vouchered and verified by odonate experts. Odonata Central (2014) is a North American database with georeferenced records, and includes photo-vouchered sightings, records from literature, and some specimen-based data (Abbott 2005). CalOdes is a California statewide dragonfly enthusiast group composed of around 125 members who track and submit lists of species observed at specific locations and dates (Dragonflies of California, 2014).

Data quality

To facilitate quality control during data entry, the Essig database uses controlled vocabularies, such as dropdown lists, date range validation, and species name authority files to validate names. Hierarchical information is automatically filled in for geography and taxonomy.

Following data entry, we conducted a data checking procedure to minimize likely data-entry errors. This included an assessment of records with the same localities for spelling errors and to determine whether locations were associated with the correct county in the state. The data entry form of the database automatically filled information from one record to the next so that records with the same information in a series did not have to be entered multiple times. To minimize carry-over errors, we therefore checked records with adjacent UIDs for questionable repeated fields, such as collector or date. Finally, we spot checked all fields for a portion of specimens against the specimen label photograph.

Odonata have been relatively well-curated in these collections over time, so that correct specimen identification was assumed in most cases. An Odonata specialist, T. Manolis (2003), recently checked most taxonomic identifications of Odonata specimens from the Calbug institutions. Odonata specimens at UMMZI and FSCA have also been curated by odonate specialists, including L.K. Gloyd and M.F. O’Brien at UMMZI, and W.F. Mauffray at FSCA.

We compared all specimen records to current county records and known distribution ranges as a method to check for outlier records. Each specimen that fell outside of current county records for the species was checked for accurate identification and potential data entry errors. From these records, we retained only those with verified species identification and locality information. Finally, we corrected any species with outdated names, based on taxonomic classifications in Odonata Central (2014).

Georeferencing

We georeferenced occurrence localities using the standardized point-radius method (Wieczorek et al. 2004). This method outlines a series of rules to assign geographic coordinates to text descriptions of locations. Using this standard, we also assigned an uncertainty estimate (i.e. radius) based on common sources of uncertainty, such as the extent of a named place (e.g., Berkeley, California) and the distance precision provided for an offset direction (e.g., 4 miles north of Berkeley, California, which has a distance precision of 1 mile). In most cases, we used multiple online georeferencing tools, including Geolocate (Rios and Bart 2010), Georeferencing Calculator (Wieczorek et al. 2004), ACME Mapper (2014), Geographic Names Information System (GNIS; 2014), and Earth Point (2014).

After all records were georeferenced, we spot checked a portion of records for accuracy. In addition, we checked all localities with listed counties that did not match county polygons using ArcGIS Desktop, release 10.1 (ESRI 2012). We then corrected any aberrant records or further investigated related records, as needed.

Taxonomic, temporal and spatial summary of records

We first summarize the number of species within each of the families found in the state. To demonstrate the temporal and spatial coverage of species occurrence records, we then summarized records by decade, by county, and in maps of occurrence locations. For this and all subsequent analyses, we removed any species considered to be vagrant, with only one sighting in the state. We determined species richness and the total number of specimens before 1900 and by decade in the following years. We then calculated species richness and total number of records by county for the entire period of record. In order to assess the effect of effort on species richness by county, we plotted the total number of species against the number of records for each county. We also used this information to identify regions that are currently underrepresented in the collections. Finally, we mapped all Odonata occurrence locations before 1976 and after 1979 to illustrate the spatial distribution of records for these time periods.

Contribution of collection types to county records

The four collection types included in the database were the Calbug institutions (California University and government collections), non-Calbug (non-California) institutions, private collections of odonate specialists, and observation-based records. We first summarized the total number of records from each data source. To illustrate how different collections have contributed to our knowledge of spatial distribution of odonates in the state, we determined the number of unique county records from each of the major collection types. We summarized the number of unique county records (by species and county) shared by one, two, three, or all four types.

Species occurrence records

The final goal of this paper was to assess the prevalence of records for individual Odonata species before 1976 and after 1979 to determine both potential taxonomic biases and changes in species prevalence, altitude, and elevation ranges over time. We chose these time periods because they have comparable numbers of unique-species occurrence records (8,431 before 1976 and 9,156 after 1979). The four year gap, including the years of 1976-1979, separates the two time periods for temporal comparison while maximizing our ability to achieve similar numbers of records. Moreover, temperature began increasing rapidly starting around 1980 as a result of climate change (IPCC 2013). We removed all species that were recorded in fewer than two instances because these were considered to be vagrant species. We then determined the first and last year of documented occurrence, and the total number of records before 1976 and after 1979. We considered the total number of unique records for each time period to be a proxy for collection effort. To account for differences in collection effort, we divided the number of unique occurrences of each species by the total number of unique occurrences across all species for the respective time period. We then identified species with changes in occurrence records that are likely to result from taxonomic biases, and those that may have legitimately increased or declined in prevalence. Related studies by Ball-Damerow et al. (2014) and Manolis (2003), and expert opinion were applied to distinguish between species with actual change in prevalence over time and species with change likely resulting from taxonomic collection biases.

To determine whether species have expanded to higher latitudes or elevations, we calculated the average and range of latitude and elevation for each species before 1976 and after 1979. Any records with greater than 4 km error radius were removed from this analysis. Wilcoxon signed-rank tests were performed to determine whether the median difference in latitude and elevation means between the two time periods were significantly different.

Results

Database summary

There were 32,025 records from all combined sources (Appendix A, Table 2). The majority of records (21,648) came from Calbug efforts. CalOdes, Odonata Central, recent field collections (Ball-Damerow et al. 2014), and C.H. Kennedy's collections (Kennedy 1917) contributed 6777, 1492, 2016, and 1190 records, respectively (Table 2). Many of these records were not unique, and the summed total number of unique species, year, and locality combinations for all data sources was 19,000, and the total species, year, and county combinations was 13,255 (Table 2).

Taxonomic, temporal and spatial summary of records

There are currently 106 species within nine families that are known to occur in the state, including nine species of Aeshnidae, two species of Calopterygidae, 30 species of Coenagrionidae, one species of Cordulegastridae, six species of Corduliidae, 12 species of Gomphidae, seven species of Lestidae, 38 species of Libellulidae, and one species of Petaluridae. The earliest records in the database were from 1879, and include two specimens of *Argia vivida* Hagen from the Santa Ana River in Southern California, and several records of *Hetaerina americana* (Fabricius) and *Libellula saturata* Uhler in Colton, San Bernardino County, California. These specimens are all held at INHS. The last year of record in the database was 2013.

The first peak in Odonata collections in California occurred in 1914-1915 with C.H. Kennedy's collections throughout the state (Kennedy 1917, Fig. 1). Subsequent peaks occurred in the mid-1950s, 1960s, and 1970s, with the largest collections from D. Paulson, R. Garrison, and S. Dunkle (Fig. 1). Most of the recent records come from CalOdes sightings and field surveys by J.E.Ball-Damerow over the period of 2010-2013.

The total number of species found throughout the state varied only slightly by decade, except for time periods when there were less than ~ 1,200 total records, e.g., before 1900 and 1900-1910. The time period with the highest number of records and species was 2000-2013, with 9,535 records and 106 species, followed by the 1990s, with 99 species and only 1,623 total records (Fig. 2). The 1910s, which include C.H. Kennedy's surveys, contribute 2,485 total records for 84 species (Fig. 2).

There was an exponential relationship between the total number of unique records from a given county and species richness observed (Fig. 3). The richness increased dramatically through ~ 800 total records, leveling off at ~ 58 species. Therefore, many counties with less than 800 records are likely to show higher species richness with increased sampling. The least-sampled county was Kings County, with only 28 records and 22 total species (Table 3). Riverside County was the most sampled with 2,108 unique records and 58 species observed (Table 3).

Most counties supported 40-60 species. Counties that were well above or below the confidence interval may be either relatively species-rich or species-poor (Fig. 3). Siskiyou, Shasta, Inyo, Placer, and Lake Counties were relatively rich in species, while some species-poor counties included Los Angeles, Stanislaus, Yolo, Kern, Colusa, and Ventura (Fig. 3).

A map of specimen localities for both time periods demonstrates some additional spatial bias and data gaps (Fig. 4). Dense clusters of records exist around urban centers, including the San Francisco Bay area, Sacramento, and major cities in southern California, such as Santa Barbara, Los Angeles, San Diego, and Riverside. The least sampled and/or occupied area is the desert region in the southeast of the state. While the number of total records was higher before 1976, the spatial distribution of records before 1976 and after 1979 is similar.

Contribution of collection types to county records

Calbug institutions contributed the highest number of total records with 14,207 total records, followed by observation-based records with 8, 269 total records (Table 1). Non-Calbug institutions and private collections provided 5,803 and 3,746 total records, respectively.

The observation-based records contributed the highest number of unique county records with 538 (by species and county only), followed by the Calbug institutions with 353 unique records (Fig. 5). Non-Calbug institutions and private collections contributed 87 and 83 unique county records, respectively. There were 705 county records originated from two of the four collection types, 594 records originated from three types, and 370 records originating from all four collection types (Fig. 5).

Species occurrence records

There were 8,642 unique species occurrence records (i.e. unique locality and date) before 1976, and 9,175 unique occurrence records after 1979. The most commonly sampled species before 1976 were *Argia vivida*, *Sympetrum corruptum* Hagen, *Libellula saturata*, *Enallagma carunculatum* Morse, and *Ischnura cervula* Selys. The most commonly sampled or observed species after 1979 were *Argia vivida*, *Sympetrum corruptum, Ischnura cervula, Libellula saturata*, and *Anax junius* (Drury) (Table 4). The least sampled species after 1979 were *Enallagma basidens* Calvert, *Somatochlora albicincta* (Burmeister), *Epitheca spinigera* (Selys), *Stylurus intricatus* (Selys), and *Ophiogomphus severus* Hagen (Table 4). *Aeshna canadensis* Walker, *Tramea calverti* Muttkowski, and *Sympetrum vicinum* (Hagen) were not observed before 1998, 1988, and 1980, respectively. *Enallagma basidens*, *Sympetrum albicincta*, and *Nehalennia irene* (Hagen) were only observed one time prior to 1976 (Table 4).

Thirty-seven species decreased in relative occurrence in the two time periods examined, while 66 species increased (Table 4). Species with the highest increases in relative occurrence were *Anax junius*, *Tramea lacerata* Hagen, *Libellula forensis* Hagen, and *Libellula luctuosa* Burmeister. Species with the greatest declines in relative occurrence were *Argia vivida*, *Sympetrum corruptum, Enallagma annexum* (Hagen), *Ischnura denticollis* (Burmeister), and *Enallagma carunculatum* (Table 4). Many of the species with the highest declines are likely the result of differences in sampling approaches in the recent data, much of which were observation-based, as compared to the older specimen data, which was entirely collection-based. Species with the highest declines, that also match patterns of decline in a recent resurvey study by Ball-Damerow *et al*. (2014), include *Hetaerina americana*, *Sympetrum illotum* (Hagen), *Octogomphus specularis* (Hagen), and *Cordulegaster dorsalis* Hagen.

In comparing the average and range of latitude and elevation across individual species occurrence localities, we excluded all records with an error radius of greater than 4 km. The total number of unique records before 1976 available was then 5,142 and the total number of unique records after 1979 was 7,785. The median average latitude across all species increased by 0.7˚ (±0.82, $p<0.001$), indicating an average shift of around 78 km northwards (Table 5). Average minimum latitude declined slightly by 0.12˚ (±1.1, $p=0.01$), and average maximum latitude increased by 0.59˚ (±1.3, $p<0.001$, Table 5). Neither average nor average maximum elevation across species changed significantly over the two time periods, but average minimum elevation declined by 108 m (±360 m, $p=0.003$; Table 5).

Discussion

The California Odonata database provides an overview of common patterns to be expected in the temporal distribution of museum records in California. For odonates, peaks in specimen acquisition occurred in 1914-15 as a result of C.H. Kennedy's work (Kennedy 1917), with subsequent peaks in the 1950s, 1960s and 1970s through the combined work of several collectors. After this mid-20th century time period, specimen acquisition was slower. The largest peak in the Odonata database has occurred since 2000, and represents mostly observation-based records obtained from odonate enthusiasts.

Previous work has noted a recent decline in specimen acquisition of natural history museums over the past 30-40 years that corresponds with declines in funding for many of these institutions (Pyke and Ehrlich 2010). However, observation-based records now provide a valuable complement to specimen records in documenting change in species prevalence and distribution, especially when such records are photo-vouchered and vetted (e.g., Breed et al. 2013, Pyke and Ehrlich 2010, Soberon et al. 2000).

The present study also identified spatial biases and data gaps, which should be addressed in any distributional analyses and in designing future sampling investigations of California odonates. As demonstrated in a previous spatial analysis of Odonata collection data in North America, collections are often located near more highly populated regions (e.g., Hassall and Thompson 2010). Sampling locations for California odonates are clustered around urban areas, such as the San Francisco Bay area, Sacramento, Los Angeles, and San Diego. The more sparsely populated desert region in the southeast has very few records, which may also be the result of a lack of freshwater habitat in the region (Fig 4).

Species richness is not strongly associated with total number of records at the statewide scale (Fig 2), while it is at the county scale (Fig 3). During the 1980s and 1990s, there was a significant drop in the total number of records without a parallel drop in species richness. It seems that after 1,500 records species richness for the state levels off at around 100 species, which is close to the total number known resident species in the state (106 species). Even in 1980, with 1,265 total records, species richness dropped only to 77 species (Fig 2). There is a stronger exponential relationship between the total number of records and species richness observed in a given county (Fig. 3). While species richness leveled off at around 58 species per county with at least 600 records, there were some obvious outliers that could represent relatively species rich or poor counties. In particular, Shasta County had 78 species recorded with only 514 records, which is likely because it is located in the warmest region with relatively high precipitation and aquatic habitat. In contrast, counties with below average species richness given the number of records were all dry regions in the Central Valley or southern California. Similarly, Hassall and Thompson (2010) found that collection effort, in addition to warm temperature and water availability, plays a major role in species richness of odonates observed in various regions of North America. Future sampling, particularly in under-sampled regions and in warm areas with higher freshwater habitat availability (e.g., Sutter County and Lake County), is therefore likely to yield additional species.

Each of the different collection types—Calbug (i.e. California) institutions, non-Calbug institutions, private collections, and observation-based records—contributed significantly to the total number of records and to county records for species. The Calbug institutions had the highest total number of records, followed by observation-based records, which had just over half the number of total records as Calbug. However, observations contributed significantly more county records for species. The goal of many enthusiasts is to find new county records, which likely explains this difference. We find that recent observation-based records have greatly contributed to our knowledge of the spatial distribution of odonate species in California.

Apparent changes in species prevalence according to occurrence records are sometimes the result of variation in taxonomic biases, particularly in comparing natural history specimens and observation-based records (Table 4). According to existing occurrence records, two species with the highest decline in prevalence over time were two of the most common species in the state, *Argia vivida* and *Sympetrum corrupum*. Many individuals reporting species observations to CalOdes or Odonata Central may have neglected these species in at least some of their lists, perhaps because these collectors considered less-common species to be more interesting or noteworthy. Another potential problem with observation-based data is the difficulty in identifying certain species in the field. In general, the most difficult group to identify is the genus *Enallagma* (particularly *E. boreale* and *E. annexum*), and many enthusiasts report them as *Enallagma sp*. or as “bluets.” Less experienced enthusiasts in particular may avoid reporting this group or other difficult to identify species, such as *Argia agrioides* and *Argia nahuana*. In contrast, Odonata taxonomists contributing to specimen records from the early and mid-20th century often focused on these groups, which were in need of taxonomic revision (e.g., Garrison 1984). As a result of this known discrepancy, such species should not be included in comparing specimen and observation-based data unless analysis methods address collecting biases, or only include results of certain collectors less likely to demonstrate this taxonomic bias. In general, charismatic, rare, and colorful species are often more likely to be present in both specimen collections and in observation-based lists (e.g., Dunn 2005).

Species that have increased in prevalence over time, however, often demonstrate more reliable results than those with apparent declines (Szabo et al. 2010). Many of the species with the highest increases in relative occurrence also demonstrated increased prevalence in a recent resurvey study (Ball-Damerow et al. 2014, Table 4). Eight out of the ten species with the highest increases in prevalence were habitat generalists, nine species were widespread throughout the state, and all ten were found across a wide range of elevation from sea level to around 2,000 m. Similarly, previous studies have demonstrated that widespread, habitat generalist species have expanded considerably over time (Ball-Damerow et al. 2014, Dupont et al. 2011, Julliard et al. 2004, Korkeamaki and Suhonen 2002). The two most conspicuous migratory species, *Anax junius* and *Tramea lacerata,* demonstrated the highest increases in prevalence. In a related resurvey study, Ball-Damerow et al. (2014) found that four out of the five migratory species in the state were among those with the highest increases in prevalence, including *A. junius* and *T. lacerata*. The other two migratory species that increased in the resurvey study were *Sympetrum corruptum* and *Pantala hymenaea*, both of which are more drab-colored, less conspicuous, and may therefore be less reported in recent observation-based lists (Ball-Damerow et al. 2014).

Odonata species in California have expanded northwards by an average of around 78 km and demonstrated an average increase in northern range margins of 65 km. This shift is unlikely to be the result of location bias, considering that overall distribution of sampled sites was similar across the two time periods (Fig 4), and favorite collecting sites are not likely to shift north in this way. Similarly, a study of 37 species of British Odonata showed a northward shift at the range margin of about 74 km when comparing records from 1960-70 and 1985-1995 (Hickling et al. 2005). Overall, a wide range of taxa are shifting northwards and to higher elevations as a result of increasing temperatures (e.g., Angert et al. 2011, Hickling et al. 2006, Parmesan 2006).

However, we also observed a decline in the average minimum elevation across species. This could be the result of increases in dry-season water habitats throughout low elevation areas of the Central Valley with increased irrigation for agriculture (Ball-Damerow et al. 2014). This region of the state was previously drier and may have supported fewer odonates in the early 20th century. In contrast, mountainous regions generally have higher rainfall and more natural aquatic habitat. The unexpected decline in elevation could also be a result of more recent spatial bias to collect near centers of human population, which also tend to occur at lower elevations.

Conclusions

The California Odonata database is one of the largest state-level databases for this order of insects in North America. This database provides a valuable source of information to determine change in Odonata communities and species distribution in the region over time. The timespan of the collection, from the late 1800s through 2013, coincides with unprecedented human population growth, redistribution of water throughout an agriculture-intensive state, and large-scale land use change (Mount 1995). One of the most powerful applications of this database is its use as a data-exploration tool. For example, researchers may identify particular species, regions, or even collectors that warrant further study or that may be amenable to analyses of change over time. Further investigation will undoubtedly yield discoveries concerning changes in Odonata biology and distribution over time. Moreover, comparisons of our California odonate data to that of other regions or groups of organisms may provide insight into the general use of Odonata as biological indicators of change over time and more general principles of global change biology.

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Table 1. All contributing data sources, abbreviations, and total number of specimens.

Source Collection	Abbreviation	# Specimens
CalBug Institutions		14,207
California Academy of Science	CASENT	2,876
UC Riverside	CIS	531
California State Collection of Arthopods	CSCA	24
Essig Museum	EMEC	5,550
LA County Museum	LACMENT	2,032
Oakland Museum	OMC	107
Santa Barbara Museum of Natural History	SBMNHENT	153
San Diego Natural History Museum	SDNHM	88
UC Bohart Museum	UCBME	2,776
UC Riverside	UCRCENT	70
non-CalBug Institutions		5,803
Florida State Collection of Arthropods	FSCA	65
International Odonata Research Institute (at FSCA)	IORI	3,230
Louisiana State University	LSUC	48
Museum of Zoology - Pontifical Catholic University of Ecuador (P.U.C.E)	QCAZ	12
Illinois Natural History Survey	INHS	96
University of Michigan Museum	UMMZI	1,425
US National Museum	USNM	927
Personal		3,746
C.H. Kennedy	CHK	1,190
D.R. Paulson	DRPC	930
R.W. Garrison	RWGC	576
S.D. Gaimari	SDGC	132
J.E. Ball-Damerow field collections	JEBD	918
Observations		8,269
Cal Odes	Cal Odes	6,777
Odonata Central	Odonata Central	1,492
Grand Total		**32,025**

Table 2. Summary of total California Odonata records, and unique species records by year and either locality or county. Specimen database includes Calbug Institutions (California University and government-based collections), non-Calbug institutions, and private collections.

Data Source	Total Records	Unique Locality Records	Unique County Records
Specimen database	21,648	11,149	8,716
C.H. Kennedy (1917)	1,190	527	404
J.E. B-D field collections	918	856	514
CalOdes	6,777	5,463	2,698
Odonata Central	1,492	1,005	923
Totals	32,025	19,000	13,255

Table 3. Total number of records and species for each county.

County	Total Records	Species Richness	County	Total Records	Species Richness
Kings	28	22	Napa	492	47
Sutter	33	17	Alameda	496	47
San Benito	56	25	San Mateo	504	45
Alpine	93	30	Shasta	514	78
Amador	109	41	Sacramento	524	46
Glenn	111	33	Plumas	530	55
Tehama	123	46	Placer	533	65
Lake	153	48	Fresno	547	54
San Joaquin	157	31	Imperial	562	39
Madera	169	41	Modoc	580	64
San Francisco	177	23	Mono	598	46
Calaveras	179	39	Butte	664	56
San Luis Obispo	180	37	Lassen	668	68
Santa Cruz	191	45	Santa Barbara	701	44
Merced	199	21	Yolo	710	44
Mariposa	209	39	Humboldt	731	57
Del Norte	211	41	Colusa	776	53
Solano	235	38	Nevada	777	56
Sierra	268	48	Mendocino	892	54
Yuba	283	40	Stanislaus	904	42
Trinity	306	50	El Dorado	924	57
Marin	314	40	Sonoma	956	58
Monterey	332	48	San Bernardino	1038	57
Tulare	372	46	Siskiyou	1136	68
Tuolumne	372	45	Santa Clara	1202	51
Orange	437	35	Inyo	1548	59
Contra Costa	445	39	San Diego	1759	58
Ventura	474	35	Los Angeles	1804	45
Kern	487	49	Riverside	2108	58

Table 4. Summary of species records, including earliest and latest observation or specimen collection date, unique occurrences (by site and year) before 1976 and after 1979, and the change in relative occurrence in unique records. Bolded records show the same relationship (i.e. increase or decrease in species prevalence) reported in Ball-Damerow et al. (2014). Records that are likely to be a result of taxonomic biases, such as failure to collect common species or spcies that are difficult to identify, and a focus on rare or charismatic species, are indicated by *.

Family	Species	Earliest Year	Latest Year	Before 1975	After 1980	Change
Coenagrionidae	*Argia vivida**	1879	2013	767	535	-232
Libellulidae	*Sympetrum corruptum**	1892	2013	612	414	-198
Coenagrionidae	*Enallagma annexum**	1900	2013	268	134	-134
Coenagrionidae	*Ischnura denticollis**	1900	2013	256	126	-130
Coenagrionidae	*Enallagma carunculatum**	1900	2013	329	218	-111
Coenagrionidae	*Amphiagrion abbreviatum*	1904	2013	168	70	-98
Calopterygidae	***Hetaerina americana***	**1879**	**2013**	**304**	**220**	**-84**
Coenagrionidae	*Argia nahuana**	1894	2013	115	35	-80
Libellulidae	***Sympetrum illotum***	**1892**	**2013**	**270**	**205**	**-65**
Coenagrionidae	*Enallagma praevarum**	1900	2013	103	67	-36
Gomphidae	***Octogomphus specularis***	**1900**	**2013**	**97**	**61**	**-36**
Coenagrionidae	*Enallagma civile**	1926	2013	195	167	-28
Libellulidae	*Pantala hymenaea**	1912	2013	141	114	-27
Cordulegastridae	***Cordulegaster dorsalis***	**1900**	**2013**	**139**	**118**	**-21**
Coenagrionidae	*Telebasis salva*	1900	2013	86	63	-23
Coenagrionidae	*Enallagma boreale**	1903	2013	92	71	-21
Libellulidae	*Paltothemis lineatipes**	1914	2013	103	84	-19
Lestidae	***Archilestes californicus***	**1900**	**2012**	**61**	**48**	**-13**
Libellulidae	***Libellula nodisticta***	**1894**	**2013**	**51**	**39**	**-12**
Libellulidae	*Libellula comanche*	1914	2013	50	38	-12
Lestidae	***Lestes congener***	**1900**	**2013**	**64**	**53**	**-11**
Lestidae	***Lestes dryas***	**1910**	**2013**	**89**	**80**	**-9**
Libellulidae	***Sympetrum pallipes***	**1894**	**2013**	**130**	**125**	**-5**
Libellulidae	*Leucorrhinia hudsonica*	1914	2013	42	32	-10
Coenagrionidae	*Enallagma anna**	1915	2012	26	19	-7
Coenagrionidae	*Enallagma clausum**	1938	2013	19	12	-7
Libellulidae	*Plathemis subornata*	1915	2013	34	28	-6
Libellulidae	***Sympetrum danae***	**1914**	**2013**	**33**	**27**	**-6**
Coenagrionidae	*Ischnura barberi*	1897	2013	59	55	-4
Gomphidae	***Ophiogomphus bison***	**1907**	**2013**	**58**	**55**	**-3**
Libellulidae	***Sympetrum obtrusum***	**1914**	**2013**	**39**	**36**	**-3**
Libellulidae	*Libellula croceipennis*	1914	2013	22	19	-3
Aeshnidae	*Aeshna walkeri*	1900	2013	41	40	-1
Lestidae	*Archilestes grandis*	1897	2012	25	24	-1
Libellulidae	*Erythemis collocata**	1900	2013	216	227	11

Family	Species	Earliest Year	Latest Year	Before 1975	After 1980	Change
Libellulidae	***Sympetrum semicinctum***	**1909**	**2013**	**61**	**63**	**2**
Coenagrionidae	***Coenagrion resolutum***	**1914**	**2011**	**13**	**13**	**0**
Aeshnidae	*Aeshna interrupta*	1914	2013	50	53	3
Lestidae	*Lestes disjunctus*	1912	2013	62	66	4
Coenagrionidae	*Ischnura gemina**	1900	2013	12	13	1
Gomphidae	*Stylurus intricatus*	1915	2012	6	7	1
Gomphidae	*Erpetogomphus compositus*	1914	2013	48	52	4
Lestidae	*Lestes unguiculatus*	1914	2013	10	13	3
Coenagrionidae	*Enallagma basidens*	1974	2012	1	4	3
Corduliidae	*Cordulia shurtleffii*	1914	2013	32	37	5
Coenagrionidae	*Argia hinei*	1915	2013	12	16	4
Gomphidae	*Stylurus plagiatus**	1965	2013	4	8	4
Corduliidae	*Epitheca spinigera*	1914	2013	2	6	4
Corduliidae	*Somatochlora albicincta*	1952	2013	1	5	4
Coenagrionidae	*Argia moesta*	1938	2013	17	22	5
Libellulidae	*Orthemis ferruginea*	1935	2013	16	21	5
Gomphidae	*Ophiogomphus severus**	1914	2013	3	8	5
Gomphidae	***Progomphus borealis***	**1900**	**2013**	**61**	**70**	**9**
Libellulidae	*Sympetrum internum**	1914	2013	12	18	6
Coenagrionidae	*Argia alberta*	1915	2013	19	26	7
Coenagrionidae	*Nehalennia irene**	1973	2013	1	9	8
Lestidae	***Lestes stultus***	**1903**	**2013**	**45**	**56**	**11**
Gomphidae	*Erpetogomphus lampropeltis*	1915	2013	10	19	9
Gomphidae	*Ophiogomphus morrisoni**	1914	2013	23	33	10
Libellulidae	***Libellula saturata***	**1879**	**2013**	**354**	**385**	**31**
Libellulidae	*Sympetrum madidum**	1897	2013	59	72	13
Corduliidae	*Somatochlora semicircularis*	1914	2013	21	32	11
Libellulidae	*Libellula quadrimaculata*	1914	2013	80	95	15
Coenagrionidae	*Argia sedula*	1945	2013	26	38	12
Coenagrionidae	*Zoniagrion exclamationis*	1911	2013	51	65	14
Libellulidae	*Libellula composita**	1915	2013	11	23	12
Aeshnidae	*Aeshna canadensis*	1998	2012	0	12	12
Coenagrionidae	*Ischnura erratica*	1900	2013	15	29	14
Coenagrionidae	*Ischnura hastata*	1938	2013	4	18	14
Libellulidae	*Tramea calverti*	1988	2011	0	14	14
Gomphidae	*Stylurus olivaceus**	1914	2012	5	21	16
Libellulidae	*Macrodiplax balteata*	1947	2013	2	19	17
Libellulidae	*Leucorrhinia glacialis**	1914	2013	15	33	18
Libellulidae	*Sympetrum costiferum**	1934	2013	11	29	18
Aeshnidae	*Aeshna palmata**	1914	2013	34	54	20

Family	Species	Earliest Year	Latest Year	Before 1975	After 1980	Change
Gomphidae	*Ophiogomphus occidentis**	1914	2013	17	36	19
Libellulidae	*Sympetrum vicinum*	1980	2012	0	19	19
Calopterygidae	*Calopteryx aequabilis*	1951	2013	7	27	20
Libellulidae	*Brachymesia furcata*	1930	2013	7	28	21
Libellulidae	*Ladona julia*	1953	2013	4	25	21
Libellulidae	***Pachydiplax longipennis***	**1900**	**2013**	**189**	**222**	**33**
Aeshnidae	*Aeshna umbrosa*	1915	2012	16	40	24
Coenagrionidae	*Ischnura ramburii*	1930	2013	7	32	25
Libellulidae	*Leucorrhinia intacta*	1918	2013	15	44	29
Coenagrionidae	*Argia agrioides*	1907	2013	71	104	33
Libellulidae	*Perithemis intensa*	1934	2013	8	38	30
Coenagrionidae	***Ischnura perparva***	**1898**	**2013**	**247**	**292**	**45**
Gomphidae	*Gomphus kurilis*	1905	2013	68	104	36
Corduliidae	*Macromia magnifica**	1900	2013	27	61	34
Libellulidae	*Pantala flavescens*	1915	2013	20	55	35
Coenagrionidae	*Argia lugens*	1901	2013	86	126	40
Aeshnidae	*Anax walsinghami**	1915	2013	19	56	37
Libellulidae	*Brechmorhoga mendax*	1901	2013	31	69	38
Libellulidae	*Tramea onusta*	1907	2013	31	69	38
Petaluridae	*Tanypteryx hageni**	1918	2013	22	61	39
Libellulidae	*Plathemis lydia*	1912	2013	157	208	51
Coenagrionidae	***Argia emma***	**1910**	**2013**	**72**	**119**	**47**
Aeshnidae	*Rhionaeschna californica*	1897	2013	92	144	52
Coenagrionidae	***Ischnura cervula***	**1902**	**2013**	**317**	**394**	**77**
Corduliidae	*Epitheca canis*	1914	2013	16	77	61
Aeshnidae	***Rhionaeschna multicolor***	**1898**	**2013**	**257**	**345**	**88**
Libellulidae	*Libellula pulchella*	1905	2013	84	166	82
Libellulidae	***Libellula luctuosa***	**1929**	**2013**	**54**	**143**	**89**
Libellulidae	*Libellula forensis*	1900	2013	85	220	135
Libellulidae	***Tramea lacerata***	**1900**	**2013**	**107**	**254**	**147**
Aeshnidae	***Anax junius***	**1900**	**2013**	**196**	**361**	**165**
Total number of unique occurrences:				8642	9175	

Table 5. Summaries of change in unique species latitude and elevation values before 1976 and after 1979. Unique records represent unique combinations of species, locality coordinates, and year. Records included in this assessment have an error radius ≤ 4 km.

	Average Change	Standard Deviation	Wilcoxon Rank-Sign Test	P-Value
Avg Latitude	**0.70° (78 km)**	**0.82**	**V= 542**	**<0.001**
Min Latitude	**-0.12° (-13 km)**	**1.12**	**V=3429**	**0.01**
Max Latitude	**0.59° (65 km)**	**1.28**	**V=643**	**<0.001**
Avg Elevation (m)	-49	248	V=2730	0.37
Min Elevation (m)	**-108**	**360**	**V=3327**	**0.003**
Max Elevation (m)	49	613	V=2099	0.19

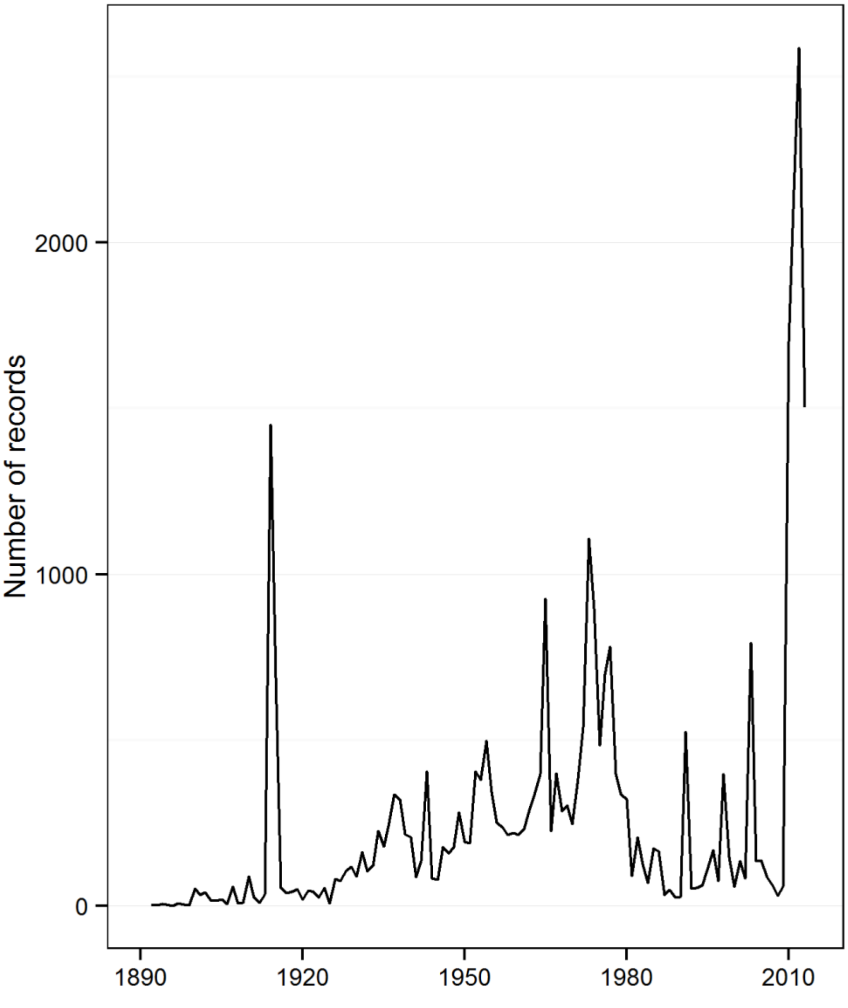

Fig 1. Total number of California Odonata records per year.

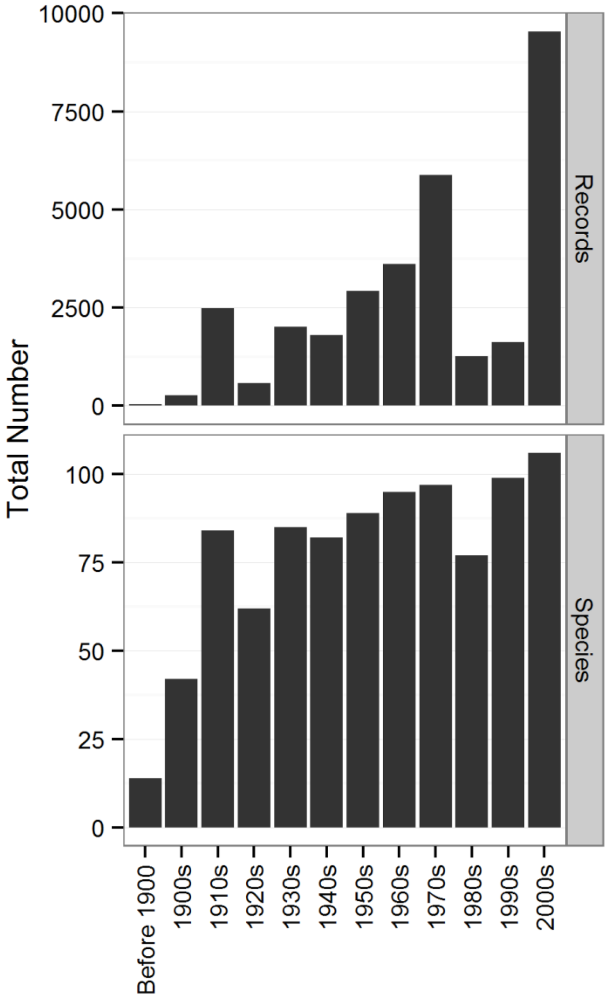

Fig 2. Total number of records and number of species by decade.

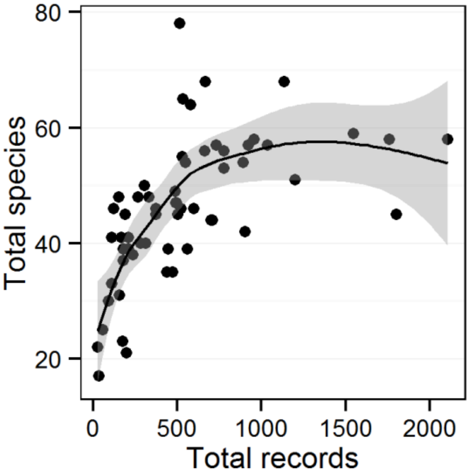

Fig 3. Relationship between species richness and total number of records by county, where each point represents a California county.

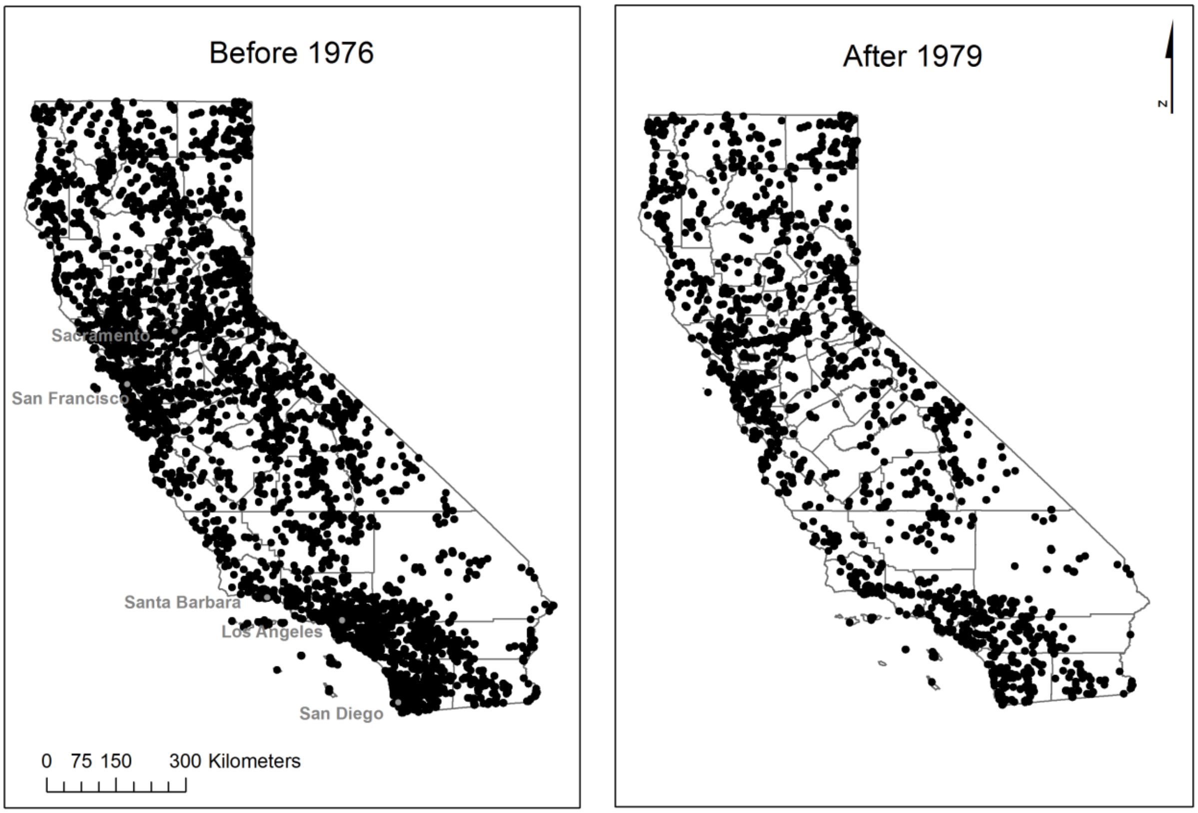

Fig 4. Spatial distribution of California records before 1976, and after 1979.

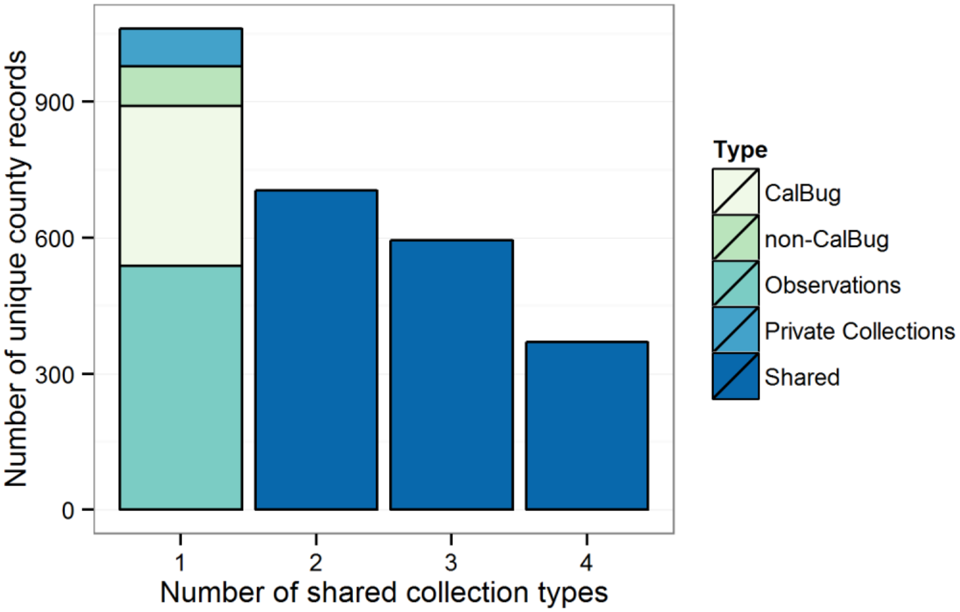

Fig 5. Number of unique county records for each collection type (Calbug collaborating institutions, non-Calbug institutions, observations - Cal Odes and Odonata Central, and private collections), and number of unique county records with two, three, and four shared data types.

CHAPTER 5

Historical records indicate changes in California dragonfly and damselfly (Odonata) assemblages and their species detection rates over the past century

J.E. Ball-Damerow, G. Rapacciuolo & V.H. Resh

Historical records indicate changes in California dragonfly and damselfly (Odonata) assemblages and their species detection rates over the past century

Abstract

Museum and observation-based records of species occurrence are the primary source of information to document change in distribution over time. However, these unstandardized data contain biases with regards to uneven sampling effort. In the present study, we use several methods to correct for sampling biases in a dataset of Odonata (damselflies and dragonflies) records assembled from unstandardized sources. The goal was to examine changes in species richness, community similarity, and probability of detection over the past century at locations throughout California, USA. We first determined changes in site-level species richness and community similarity before and after 1975. To determine change in region-level richness, we calculated non-parametric incidence-based estimators for each time period. We then modelled variation in probability of detection using Bayesian generalized linear models (GLMs). In these models, we included the number of species recorded and the Julian date of the collection event to account for sampling effort and season, and climate variables. Finally, we used linear mixed-effects models to determine the attributes of species that increased or declined over time. While site-level species richness has not changed, Odonata assemblages have become more similar over the past century. Probabilities of detection for many species have also increased or declined. For example, species with higher optimum temperatures showed greater increases in detection probability than those with lower optima. Highly mobile migratory species have increased while habitat specialists have declined. In addition, difficult-to-identify species were detected less in recent years, which is likely the result of lower reporting rates in surveys. Odonata communities are becoming more homogenous with the expansion of habitat generalists and the decline of specialists. A combination of sampling biases, species traits, and climate have influenced the probability of detection of Odonata species over the last century.

Introduction

Widespread changes in land use and climate have altered and continue to influence the existence, abundance, and distribution of organisms throughout the world (e.g., Jetz *et al.*, 2007; Forister *et al.*, 2010; Gaston, 2011; Bartomeus *et al.*, 2013). Historical data on species occurrences have therefore become increasingly valuable in assessments of change in the biology and distribution of organisms over time (e.g., Shaffer *et al.*, 1998; Soberon *et al.*, 2000; Guralnick & Van Cleve, 2005; Pyke & Ehrlich, 2010). Specimen data in museums are the most widely available and arguably most valuable form of occurrence data because the presence of specimens enables verification of species' identity and examination of genetic composition (Pyke & Ehrlich, 2010).

Specimen- and observation-based datasets covering long time periods contain information from numerous collectors, and inevitably have intrinsic spatial, temporal, and taxonomic biases (Graham *et al.*, 2004; Guralnick & Van Cleve, 2005; Hassall & Thompson, 2010; Szabo *et al.*, 2010). For example, a majority of collectors tend to sample along roads or rivers, and near towns or biological-research stations (Graham *et al.*, 2004; Pyke & Ehrlich, 2010). Certain species may also exist more or less often in collections and species lists, because collectors often favor rare and charismatic species, and may neglect common and cosmopolitan taxa (e.g Guralnick & Van Cleve, 2005; Jeppsson *et al.*, 2010; Toth *et al.*, 2014). Furthermore, these preferences can change over time (Jeppsson *et al.*, 2010).

Analyses using information from specimens and species observations must therefore account for common biases (Pyke & Ehrlich, 2010). Richness estimators, originally developed for standardized ecological samples, have shown promise in reducing bias found in observed species richness values for museum specimen datasets (Soberon *et al.*, 2000; Petersen *et al.*, 2003; Meier & Dikow, 2004; Guralnick & Van Cleve, 2005).

Recently, studies have employed list-length analysis to adjust for varying collector effort (Szabo *et al.*, 2010; Breed *et al.*, 2013; Isaac *et al.*, 2014). This approach uses the number of species reported as a proxy for effort (Breed *et al.*, 2013). However, this list-length analysis has previously been used only for analyses involving observation-based lists (Szabo *et al.*, 2010; Breed *et al.*, 2013; van Strien *et al.*, 2013). To our knowledge no previous studies have applied list length analysis to museum records.

In the present study, we examine changes in Odonata richness, community similarity, and species' detection probabilities from 1900-2013 using a combination of museum-specimen data and observation-based lists. These charismatic aquatic insects have been relatively well-sampled over time, and we have sufficient data to study climate and land-use change impacts (Ball-Damerow *et al.*, In Review). Our specific goals for the present study are to: (i) determine average site-level changes in species richness and community similarity before and after 1975; (ii) compare observed and estimated region-level (statewide and by ecoregion) species richness before and after 1975; (iii) determine changes in the detection probabilities of the most well-recorded species between 1900-2013 in relation to list-length, year, time of year, and climate; and (iv) identify biological traits that are associated with increases or declines in detection probabilities.

Methods

Study Area

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

Since the early 1900s, urbanization has greatly expanded throughout the western USA; with the human population in California increasing from ~ 2.7 to over 37 million (California Department of Finance, 2010). Coastal and valley regions of California, in particular, have been covered in impervious surfaces and crops (Mount, 1995), and 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 USA now exhibit altered water quality, stream flow, and habitat structure compared to their original state (Mount 1995).

Data Selection

Species occurrence data were from a database of California Odonata records, described in Ball-Damerow et al. (In Review). Species nomenclature was standardized according to the most up-to-date source for Odonata in North America (Odonata Central, 2014). We focused on historical occurrence records from this database from 1900 to 2013, which include geographically referenced museum-specimens, literature records (i.e., Kennedy, 1917), enthusiast observation-records, and field studies (Ball-Damerow et al. In Review). The field studies were part of a recent resurvey study that resampled sites in 2011-2013 originally sampled in 1914-1915 for Odonata (Ball-Damerow *et al.*, 2014). As described in Ball-Damerow et al. (In Review), sites were georeferenced using the standardized point-radius method in which coordinates and an uncertainty radius are assigned to text descriptions of locations (Wieczorek *et al.*, 2004). We excluded specimens with an uncertainty radius greater than 20 km, and sites with fewer than 3 species listed for a given collection date.

To ensure that results were not driven by the resurvey data, we conducted all analyses using two datasets, one of which included data from all data sources (21,027 records), and the other excluded data from the Kennedy's surveys (1917) and the resurvey study (19,145 records). After determining that removing the resurvey data did not significantly alter the results for any of the analyses, we present results using all data sources.

Data filtering for species richness and community similarity

For analyses of species richness and community similarity, we first compiled data into two time periods, before and during 1975 (historic), and after 1975 (modern). In addition, coordinates for each specimen were assigned to a grid cell of 20 km^2, so that multiple coordinates within the same grid cell were considered as the same site. To reduce the effect of seasonality on richness values, we include only records within the peak summer flying season of June through August. Lists collected in the same grid cell but on different dates of the historic or modern time period were collapsed into a single list representing species' composition at that grid cell for the respective period. Finally, we included only sites that were sampled in both time periods.

Site-level change in species richness

Observed species richness was the number of species recorded at each site for the historic and modern periods. We then calculated a metric for degree of change in species richness to account for differences in collection effort (as in Dekoninck *et al.*, 2013):
Trend = $[S_{curr} – (\alpha S_{hist})]/[(\alpha S_{hist})+S_{curr}]$, where
S_{curr}= species richness for the modern period, S_{hist}= species richness for the historic period, and α is a correction factor to account for differences in sampling intensity and methods between the time periods. We calculated the correction factor by dividing the sum of S_{curr} by the sum of S_{hist}.

Site-level change in community similarity

To determine whether Odonata assemblages have become more similar across sites since 1975, we 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 = number of species present in both assemblages, b = number of species present only in the first assemblage, and c = number of species present only in the second assemblage (Rahel, 2002). We then subtracted each pairwise Jaccard Index for sites before 1975 from the same pairwise comparison for sites after 1975 (Marchetti *et al.*, 2001). Finally, we determined the proportion of pairwise comparisons that increased or decreased in community similarity over time, and conducted binomial tests to determine if there were significantly more increases in similarity than decreases.

Region-level species richness estimators

We calculated non-parametric incidence-based species richness estimators statewide and for each ecoregion. These richness estimators use relative rarity and commonness of species over multiple samples to minimize bias in estimates. Because previous studies have recommended at least ten subsamples to produce reliable estimates of richness (Petersen *et al.*, 2003; Beck & Kitching, 2007), we included all sample dates for each site within the respective ecoregion as individual subsamples for overall richness estimates. Estimators in this study were calculated using EstimateS software (Colwell, 2013) with 100 randomizations of sample order, and include Incidence-Based Coverage Estimator (ICE; Chao *et al.*, 2000), first and second order jackknife (Burnham & Overton, 1979), and bootstrap (Smith & Vanbelle, 1984) estimators.

Generating species lists for list length analysis

To generate species' lists, we assigned each record from the initial dataset to a collection event, defined by unique combinations of latitude, longitude, year, and Julian date of collection. We grouped records by their collection event and generated lists of unique species detected at each event. The list-length value for subsequent analyses is therefore the number of species for the collection event. We excluded any lists with less than three species. The total number of lists was 1,947 with 106 Odonata species from at least one collection event.

Change in probability of detection for individual species

For each species, we generated binary detection-nondetection data for each unique collection event. To determine which species had sufficient data for a reliable estimation of temporal trends in probability of detection, we defined three time periods of approximately similar duration and number of records (≤1941, 1941-1980, 1981-2013). We only modeled species detected in at least ten lists during each time period. The final dataset therefore included 42 Odonata species.

We used Bayesian generalized linear models (GLMs) with a binomial error structure to model variation in probability of detection among collection events. To examine changes in probability of detection over time, we included the year of collection as a predictor in GLMs. Changes in the probability of detection of odonates may also be the result of changes in climate, particularly minimum temperature and total precipitation (e.g., Ball-Damerow *et al.*, 2014). To account for the effects of climate on species' probability of detection, we included minimum temperature and total precipitation in our GLMs. We obtained climate data from the PRISM Climate Group (2013) at a four km resolution. For each collection event, corresponding climate values included the mean minimum temperature and the total precipitation during the collection year. All raster operations were done using the raster package (Hijmans, 2014) in the statistical program R, version 3.0.1 (R Core Team, 2013).

Changes in probability of detection may also be the result of sampling biases. Sampling effort likely influences the probability of detection (e.g., Hassall & Thompson, 2010). Higher detection probability is also likely to occur during the peak summer flying season. We therefore included the length of species lists to account for sampling effort and Julian date to account for time of year in our GLMs.

For each species, we built the following full model of probability of detection:

$$logit(p_j) = \alpha_j + \beta_1 \times year_j + \beta_2 \times list\ length_j + \beta_3 \times day_j + \beta_4 \times day_j^2 + \beta_5 \times \min temp_j + \beta_6 \times \min temp_j^2 + \beta_7 \times tot\ precip_j + \beta_8 \times tot\ precip_j^2,$$

where p_j is the probability to detect the species at collection event j, α_j is the intercept, β_1 is the linear effect of year of collection event j, β_2 is the linear effect of list length of collection event j (log-transforming original list-length values), β_3 and β_4 are the linear and quadratic effects of Julian date j, β_5 and β_6 are the linear and quadratic effects of minimum temperature at collection event j, and β_7 and β_8 are the linear and quadratic effects of total precipitation at collection event j.

In addition to the full model, we built a null model (only including the intercept α_j) for each species as well as the following subset of models: YR: A model with only the intercept α_j and β_1; noYR: A model with all effects, except β_1; noLL: A model with all effects, except β_2; noDAY: A model with all effects, except β_3 and β_4; and noCLIM: A model with all effects, except β_5, β_6, β_7 and β_8.

We fitted all Bayesian models using JAGS 3.3.0 (Plummer, 2012) accessed via the R package R2jags (Su & Yajima, 2014), using code adapted from Kery & Schaub (2011). We chose conventional vague priors for all parameters using normal distributions with mean = 0 and standard deviation = 0.0001. We standardized values of all predictors by centering them on a mean of zero, rescaling them by the standard deviation of the original predictor values. We used the 95% credible intervals computed by JAGS to describe the precision of estimates for each parameter (Kery, 2010). For each model, we ran three Markov chains with 10,000 iterations each and discarded the first half as burn-in. These specifications were sufficient to achieve convergence of all parameters based on the Gelman-Rubin Rhat statistic (Rhat < 1.1).

Model performance was compared among each species' various models of detection probability using: 1) the percentage of deviance for the null model that was explained by the fitted model, and 2) the Deviance Information Criterion (DIC). Among models of the same data set, the smaller the DIC, the better was the model. Differences in DIC >10 between two models indicate essentially no support for the inferior model (Spiegelhalter *et al.*, 2002). For each species, we used full models to estimate optimum values of minimum temperature, total precipitation, and Julian date. We then estimated the marginal effect of each variable on probability of detection by keeping the other modelled variables constant at their mean. The optimum value for a given variable was the value within that variable's observed range that corresponded to the species' maximum probability of detection.

Effect of species' attributes on change in detection probability over time

We predicted that the prevalence of several species attributes within Odonata assemblages would have changed over time in response to climate or habitat alterations (Table

1). To assess these predictions, we modeled estimates of β_1 (the linear effect of year on probability of detection *p*) as a function of species attributes (from Table 1), using linear mixed effects models in the R package lme4 (Bates *et al.*, 2013). We first generated global models of β_1 (the linear effect of year on probability of detection *p*) as a function species attributes (Table 1). In addition, we included family and genus as random effects to account for shared natural history among species.

To identify the most important variables among the full set, as well as quantifying the relative importance of their effect on temporal trends, we used an information-theoretic approach (Burnham & Anderson, 2002). For each response, we generated a pool of models including all potential combinations of the global set of explanatory variables, and an intercept-only model. We identified a best-fitting model based on the AICc (Akaike's information criterion corrected for small sample sizes) and a best-fitting model subset including all models whose AICc differed by less than four from the best-fitting model's AICc (i.e., ΔAIC < 4). We recalculated ΔAIC's and corresponding Akaike weights, which represent the probability that a given model, m_i, out of *i* alternative models is the best model given the data (Burnham & Anderson 2002), based on the identified best-fitting model subset. Finally, we estimated each explanatory variable's relative importance by summing the Akaike weights of all models within the best-fitting subset that included the variable. Average coefficients for variables in the model were then calculated by taking the mean of the coefficients from the set of best-fitting models (i.e. all models with ΔAIC < 4) weighted by the Akaike weight of each given model.

Results

Site-level change in species richness

Average site-level species richness across all sites was 10.4 (±6.7) before 1975 and 12 (±8.0) after 1975, increasing by 1.5 species (±8.5; Table 2). Within individual ecoregions, the greatest change in unadjusted species richness values occurred in Northern California Coastal Forests, which also had the highest increase in total number of records (Table 2). The California Mediterranean, Great Basin Shrub Steppe, and Sierra Nevada Forests all increased in unadjusted species richness (Table 2). Change in trend estimates across all sites was -0.03 (±0.4), and estimates for individual ecoregions ranged from -0.1 (±0.4) in the California Mediterranean and Great Basin Shrub Steppe to 0.1 (±0.3) in the Northern California Coastal Forests (Table 2), indicating that there was no significant change in site-level species richness after adjusting for effort.

Site-level change in community similarity

Community similarity across all sites significantly increased after 1975 (Table 3). When comparing Jaccard similarity indices across all sites between the two time periods, there were 3,275 increases and 1,805 decreases (probability of increase = 59%, p<0.001). There were also significantly more increases in Jaccard indices across sites within the California Mediterranean ecoregion (61%, p<0.001) and the Sierra Nevada Forests (53%, p<0.001). The number of increases was not significantly greater than decreases for sites within the Great Basin Shrub Steppe or the Northern California Coastal Forests (Table 3).

Region-level species richness estimators

Species richness estimators produced values that were greater than observed species richness (Table 4). Observed species at the sites examined across California was 96 species for the historic and 102 species for the modern period. The average species richness estimator value for California was ~107 species (±5.4) for the historic period (which is ~ the same as the total known resident species in the state to date) and ~ 112 species (±4.6) for the modern. Estimated species richness for individual ecoregions ranged from 34.5 (±1.6; Northern California Coastal Forests) to 74.8 (±4.1; Great Basin Shrub Steppe and Sierra Nevada Mountains) in the historic period, and from 56.9 (±10.9; Coastal Forests) to 84.6 (±15; Sierra Nevada Mountains) in the modern. The difference between estimator values and observed species richness ranged from 3.5 to 12.6 (Table 4).

According to species richness estimators, species richness increased by an average of 5.1 species over the state (6 observed), 22.4 for the Northern California Coastal Forests (15 observed), 15.6 for the Sierra Nevada Mountains (9 observed), 10.6 for California Mediterranean (6 observed), and 1.1 for the Great Basin Shrub Steppe (0 observed). The Northern California Coastal Forests had the highest increase in species richness according to both observed and estimated values but also had least amount of data, with only 15 samples before 1975 and 33 samples after 1975 (Table 4).

Average differences between estimated and observed richness values were highest for Chao2 and second order Jackknife estimators (average of 12.6), followed by first order Jackknife (11.1), ICE (7.6), and Bootstrap (5.3). Chao2 produced one unreasonable species richness estimate for the Sierra Nevada Mountains of 113.9 species, which was 42 higher than observed species richness.

Change in probability of detection for individual species

The full model explained the highest variation in probability of detection for most species (Table 5). Of the set of species for which the full model explained the highest deviance in probability of detection (n = 27), about half of these (n = 15) had the null model as their lowest DIC model. Presumably, this is because the penalty for added model terms in the full model outweighs the increase in explained deviance. For 23 of the total set of 42 species, the year slope estimate from the full model was significantly different from zero (Table 5), indicating that their probability of detection has changed over time. For nearly all species, the list length slope estimate from the full model was significantly different from 0, which suggests that sampling effort plays a significant role in probability of detection.

There were ten species for which the full model had the lowest DIC and the year slope estimate did not overlap zero (Table 6; Fig. 2). Four of these species declined in probability of detection: *Ischnura denticollis*, *Enallagma annexum*, *Enallagma carunculatum*, and *Sympetrum pallipes*. The remaining six species increased in detection probability: *Rhionaeschna multicolor, Pachydiplax longipennis, Libellula saturata, Libellula forensis, Tramea lacerata,* and *Anax junius*. Species that increased in detection probability generally had higher minimum temperature optima (7.6 ˚C – 16.3 ˚C), with the exception of *Libellula forensis* (1. 6 ˚C). In contrast, the species with declining detection probability generally had lower minimum temperature optima (-4.5 ˚C – 5 ˚C), with the exception of *Ischnura denticollis* (7.35 ˚C). The two species with the highest increases in probability of detection (*T. lacerata* and *A. junius*) were also associated with relatively low total precipitation optima (0.97 mm and 0.70 mm, respectively; Table 6).

Effect of species' attributes on change in detection probability over time

Several species attributes were consistently present in the best models of change in detection probability over time (Table 7). Species identification difficulty (Id), migratory species (Mig), precipitation optima (Precip), and habitat specialization (Spec) were all included in 12 out of the 14 best models (Table 7). Species that are difficult to identify and habitat specialists declined in detection probability, while migratory species and species with higher precipitation optima increased in probability of detection over time (Table 8).

Discussion

Site-level change in species richness and community similarity

Our study demonstrates that after adjusting for total effort for modern and historic periods, there was no change in average site-level species richness across California or within individual ecoregions (Table 2). However, assemblages have become more similar across sites (Table 3). These results corroborate those of a recent resurvey study of Odonata in the region (Ball-Damerow *et al.*, 2014). Habitat generalist species likely compensate for loss of habitat specialists, which leads to the increased similarity of Odonata assemblages across sites (Rahel, 2002). Similar homogenization has occurred in numerous studies of organisms, such as fish across California (Marchetti *et al.*, 2001), freshwater organisms in North America (Rahel, 2002), plant communities across metropolitan areas of the USA (McKinney, 2008), and butterfly species across Canada (White & Kerr, 2007).

Region-level species richness estimators

Species richness estimators indicate that observed Odonata richness in California is likely to be lower than true richness. However, evaluating the performance of such estimators is difficult because we do not know the true richness (e.g., Hortal *et al.*, 2006; Fattorini, 2013). In the historic period, only 96 species were observed while estimators predicted an average of 107 species. This is promising with regard to the accuracy of estimators because there are ~106 currently known resident species in the state when considering all data from both time periods, in addition to a few species that are likely to be vagrants (Manolis, 2003). After 1975, observed richness increased to 102 species with estimator values averaging ~112 species, a value closely matching that of total observed species in the state (111), including rare species considered to be vagrant (and not included in the analysis).

Our results indicate that current knowledge of statewide odonate richness in California may be close to complete, when considering total known species found in the state. However, according to estimators, individual ecoregions are likely to have 4-12 more species than was observed before 1975, and 10-12 more species than observed after 1975. Previous studies have also shown that estimators provide higher estimates of richness with lower bias (Guralnick & Van Cleve, 2005).

In contrast, the change in richness when comparing estimator values from the modern and historic periods is generally less than that of the change in observed richness. For example, observed richness increased by 15 species in the Northern California Coastal Forest ecoregion, but richness increased far less (7.4 species) when averaging richness estimators. The Northern California Coastal Forests region also had the least amount of data available, which likely influenced this discrepancy. In the ecoregion with the most data, California Mediterranean, observed richness indicated an increase of 6 species, while estimators indicated an increase of 4.6 species (a discrepancy of only 1.4 species). In the present study, the number of records available seemed to influence both observed and estimated richness at the ecoregion scale. However, the more conservative values for change in richness with estimators indicate that total effort influences estimated richness less than observed richness.

Museum data collected over long time periods does not constitute a random sample because they are gathered from multiple people with different methods (Guralnick & Van Cleve, 2005). Richness estimators were initially developed for ecological samples, and it is still unclear to what degree museum specimens with uneven sampling violate statistical assumptions and how this affects results (Meier & Dikow, 2004; Guralnick & Van Cleve, 2005). However, previous studies have demonstrated that differences in estimated species richness from different subsampling schemes were small (Petersen *et al.*, 2003; Guralnick & Van Cleve, 2005; Hortal *et al.*, 2006). Furthermore, studies of species richness estimation using museum specimen databases have revealed that estimation curves produce similar results to those of ecological samples (Soberon *et al.*, 2000; Petersen *et al.*, 2003). Our results and previous studies have shown that these estimators help reduce bias when applied to museum and observation-based data (e.g., Guralnick & Van Cleve, 2005).

Change in detection probability for individual species and species attributes

We found that the combined effects of collection year, Julian date, list length, and climate explained variation in detection probability of Odonata better than a null model or any subset of variables for a majority of species. The significant effect of year indicated that species detection probabilities have changed over time. Other studies have indicated that while many odonate species have increased over time in occurrence rates, other species have declined in California (Ball-Damerow *et al.*, 2014), Europe (Korkeamaki & Suhonen, 2002), and Africa (Suhling *et al.*, 2006). In addition, individual species are known to have particular flying seasons, as outlined in many field guides (e.g., Manolis, 2003, for California), so that date is likely to have varying effects based on the species examined (Corbet, 2004). There were zero species where removing the list length or climate variables produced the best model, indicating that these variables are particularly important for Odonata detection. Hassall and Thompson (2010) also found that collection effort, in addition to warmer temperature and higher water availability, largely determine occurrence of odonates in North America.

Three species that declined in detection probability (*Enallagma annexum, Enallagma carunculatum,* and *Ischnura denticollis*) are relatively small sized and/or may be difficult for many enthusiasts to locate and identify in the field. In addition, we found that species that are difficult to identify generally had lower detection probability overall. These species may be less reported in recent observation-based surveys, particularly *Enallagma spp*. (Ball-Damerow *et al.*, In Review). However, we found that *Sympetrum pallipes* has a lower temperature optimum, and may be declining with increased minimum temperatures. In addition, *Enallagma annexum* is typically found in more humid areas (Manolis, 2003), and may have declined in response to recent extended drought experienced in the western USA (Cook *et al.*, 2004). Finally, we found that habitat specialists generally declined in detection probability. Many previous studies have reported similar declines in specialist species in recent years, as a result of land use and climate change (e.g., Korkeamaki & Suhonen, 2002; Clark *et al.*, 2007; Ball-Damerow *et al.*, 2014).

Species that increased in detection probability typically had higher temperature optima, with the exception of *Libellula forensis*. Previous studies have shown that warm-adapted groups, such as Odonata, have expanded their ranges in response to climate warming (e.g., Hickling *et al.*, 2005; Hickling *et al.*, 2006; Ball-Damerow *et al.*, 2014). The two species with highest increases in detection probability (*Anax junius* and *Tramea lacerata*) are migratory species that are highly visible, and have two of the highest temperature optima of species in our study. A recent resurvey study in the region also reported these two species as among those with the highest increases in detection rates (Ball-Damerow *et al.*, 2014). The remaining species with increases in detection were all highly mobile habitat generalists. Research 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). These species may therefore be less vulnerable to habitat fragmentation (Dupont *et al.*, 2011).

Shifts in phenology (e.g., Dingemanse & Kalkman, 2008), changes in predators (e.g., McPeek, 1998), competition with introduced species, and other species interactions undoubtedly contribute to Odonata detection rates (Corbet 2004). We note that, although not measured here, such factors are likely to be at least partially responsible for changes in Odonata detection rates in our dataset.

Conclusions

Our study has demonstrated that Odonata species composition and detection rates have changed in California over the past century. We found list length to be an effective measure of effort with lists created using museum data and observation records, and may be the most important factor influencing detection probability in our study. Without such a measure to account for effort, results are likely to be highly biased (e.g., Hassall & Thompson, 2010; Breed *et al.*, 2013). Species identification difficulty is also important to consider, especially when using a combination of museum data collected by specialists and data collected by enthusiasts. After accounting for such nuisance parameters, our data from museum specimens and observation-based lists corroborated findings from a more standardized resurvey study (Ball-Damerow *et al.*, 2014) demonstrating that California odonate assemblages are becoming more similar with the expansion of highly mobile habitat generalists and the decline of habitat specialists. Continued warming temperatures and homogenization of the landscape will undoubtedly contribute further to this trend (Rahel, 2002; McKinney, 2006; White & Kerr, 2007).

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Table 1. Predicted increase or decline in biological traits of Odonata over time.

Trait	Explanation	Predicted Change	Reference
Low Dispersal (Low Disp; 0/1)	limited distribution, not known to move far from natal habitat	(-)	Corbet, 2004
Identify (0/1)	species difficult to identify in the field	(-)	Expert opinion
Migrant (0/1)	migrate annually, includes 5 species in CA	(+)	May, 3013
Specialization (0/1)	require certain habitat types to complete life cycle, such as flowing water or high elevation	(-)	Habitat descriptions in Manolis (2003)
Forest (0/1)	specialized to occur within forested regions	(-)	Habitat descriptions in Manolis (2003)
Lotic (0/1)	specialized to occur within streams or rivers	(-)	Habitat descriptions in Manolis (2003)
Tolerance (1-10)	sensitivity to poor water quality, usually organic pollution	(-)	EPA Rapid Bioassessment Protocol
Generation Time (Gen; long, short)	long-lived species generation times > 1 year, short-lived species ≤ 1 year	(-)	Bêche et al., 2006 (genus-level); Corbet, 2006
Diapause (0/1)	presence or absence of overwintering egg diapause to resist dessication and/or cold temperatures	(-)	Bêche et al., 2006 (genus-level); Corbet, 2004
Endophytic (0/1)	oviposits within emergent vegetation	(0)	Behavior descriptions in Manolis (2003)
Elevation (low, low-mid, high)	rough estimates of elevation preferences, including low: 0-900 m, low-mid: 0-2000 m, high: only known from higher elevations	(-)	Habitat descriptions in Manolis (2003)

Table 2. Average site-level species richness of Odonata before and after 1975. Values are calculated for peak flying months of Odonata, from June through August. TR = total number of records, SR = species richness, change = change in richness since 1975, trend = richness adjusted by the total number of records (see text for details).

	TR Before 1975	TR After 1975	SR Before 1975	SR After 1975	SR Change	Trend
All Sources	14.3 (±13)	17.3 (±17.5)	10.4 (±6.7)	12 (±8.0)	1.5 (±8.5)	-0.03 (±0.4)
CA Mediterranean	14.7 (±13.8)	15.9 (±17.1)	10.7 (±6.7)	11.3 (±7.5)	0.5 (±8.7)	-0.1 (±0.4)
Great Basin Shrub Steppe	13.4 (±12.3)	16.4 (±14.2)	10.0 (±6.8)	11.9 (±8.1)	1.9 (±8.2)	-0.1 (±0.4)
Northern CA Coastal Forests	15.1 (±18.5)	22.6 (±22.5)	10.7 (±9.3)	14.2 (±9.9)	3.6 (±7.5)	0.1 (±0.3)
Sierra Nevada Forests	13.2 (±12)	19.3 (±19.9)	9.6 (±6.6)	12.6 8.5)	3.0 (±7.5)	0.0 (±0.3)

Table 3. Number of increases and decreases in Jaccard Similarity Index Scores for site comparisons, from before and after 1975. Significant differences in Jaccard Similarity Index Scores are bolded.

	All Regions	**CA Mediterranean**	Great Basin Shrub Steppe	Northern CA Coastal Forests	**Sierra Nevada Forests**
# Sites	**106**	**94**	22	5	**32**
Total Comparisons	**5565**	**1596**	231	10	**496**
Increases	**3275**	**978**	127	8	**286**
Decreases	**1805**	**565**	85	2	**169**
No Change	**485**	**53**	19	0	**41**
Sign Test P-Value	**<0.001**	**<0.001**	0.15	0.11	**<0.001**
Prob. Of Increase	**0.59**	**0.61**	0.55	0.80	**0.58**
Confidence Interval	**0.58**	**0.59**	0.48	0.44	**0.53**
	0.60	**0.64**	0.62	0.97	**0.62**

Table 4. Species richness estimators of Odonata for the state of California and its ecoregions before and after 1975. Richness estimates include specimen and observation records from 1900-2013 during peak Odonata flying months of June through August.

	S_{obs}	No. Samples	ICE Mean	Chao 2 Mean	Jack 1 Mean	Jack 2 Mean	Bootstrap Mean	Averages	Avg. estimator value - S_{obs}
Pre 1975									
California	96	286	102.4	107.0	108.0	114.9	101.4	106.7	10.7
Northern California Coastal Forests	31	15	33.0	33.9	35.7	36.8	33.3	34.5	3.5
California Mediterranean	66	153	68.9	74.1	73.0	76.9	69.3	72.4	6.4
Great Basin Shrub Steppe	64	69	73.0	73.3	76.8	80.8	70.3	74.8	10.8
Sierra Nevada Mountains	63	69	73.0	73.3	76.8	80.8	70.3	74.8	11.8
Post 1975									
California	102	350	108.9	111.1	113.0	119.0	107.0	111.8	9.8
Northern California Coastal Forests	46	33	53.1	60.7	56.7	63.4	50.7	56.9	10.9
California Mediterranean	72	192	82.6	82.2	83.9	88.9	77.5	83.0	11.0
Great Basin Shrub Steppe	64	50	76.4	72.5	78.7	80.9	71.5	76.0	12.0
Sierra Nevada Mountains	72	110	80.6	113.9	84.9	95.7	77.4	84.6	12.6
Change									
California	6	64	6.5	4.2	5.0	4.0	5.7	5.1	-0.9
Northern California Coastal Forests	15	18	20.1	26.8	21.0	26.6	17.4	22.4	7.4
California Mediterranean	6	39	13.7	8.1	11.0	12.0	8.2	10.6	4.6
Great Basin Shrub Steppe	0	-19	3.4	-0.8	1.9	0.1	1.1	1.1	1.1
Sierra Nevada Mountains	9	41	7.6	40.6	8.1	14.9	7.0	15.6	6.6

Table 5: Overall fit of the 7 alternative models across the final set of Odonate species (n = 42), using two alternative datasets. Abbreviations: Lowest DIC = number of species for which the model has the lowest DIC; Highest Deviance = number of species for which the model explains the highest amount of deviance; Year slope ≠ 0 = number of species for which the model's year slope does not overlap 0; List length slope ≠ 0 = number of species for which the model's list length slope does not overlap 0; Day slope ≠ 0 = number of species for which the model's day slope does not overlap 0.

	null	**YR**	**noYR**	**noLL**	**noDAY**	**noCLIM**	**full**
All Sources							
Lowest DIC	15	0	5	0	6	0	16
Highest Deviance	-	0	14	0	1	0	27
Year slope ≠ 0	-	26	-	25	24	23	23
List length slope ≠ 0	-	-	39	-	40	40	41
No Surveys							
Lowest DIC	15	0	10	1	4	0	12
Highest Deviance	-	0	14	1	3	0	27
Year slope ≠ 0	-	25	-	27	20	25	22
List length slope ≠ 0	-	-	38	-	41	40	40

Table 6: Summary of the full model for all species for which the full model had the lowest DIC and the year slope estimate did not overlap 0. Reported are the number of presences within the full set of lists used (n); the mean estimates for the year and list length slopes (with 95% confidence intervals); optima for minimum temperature (Opt. temp.; °C), total precipitation (Opt. precip.; mm), and day of year (1 – 366); and deviance explained by the full model.

Species	**n**	**Year slope**	**List length slope (95% C.I.)**	**Opt. Temp**	**Opt. Precip.**	**Opt. Day**	**Expl. Dev.**
Ischnura denticollis	231	-0.59 (-0.74, -0.44)	0.54 (0.40, 0.70)	7.35	1.13	365.69	0.14
Enallagma annexum	113	-0.43 (-0.56, -0.30)	0.53 (0.39, 0.66)	2.45	156.32	175.11	0.07
Enallagma carunculatum	360	-0.31 (-0.43, -0.18)	0.86 (0.73, 0.99)	5.03	0.73	2.10	0.13
Sympetrum pallipes	145	-0.27 (-0.46, -0.07)	0.77 (0.56, 0.97)	-4.48	199.16	365.87	0.28
Rhionaeschna multicolor	426	0.21 (0.08, 0.33)	0.89 (0.76, 1.01)	7.56	0.91	365.83	0.17
Pachydiplax longipennis	320	0.29 (0.13, 0.44)	0.87 (0.72, 1.01)	15.80	331.47	193.03	0.23
Libellula saturata	539	0.30 (0.18, 0.44)	0.97 (0.85, 1.10)	9.09	0.84	181.53	0.23
Libellula forensis	259	0.38 (0.22, 0.56)	0.99 (0.84, 1.15)	1.65	331.52	151.16	0.23
Tramea lacerata	299	0.62 (0.44, 0.80)	1.01 (0.85, 1.16)	11.96	0.97	219.86	0.27
Anax junius	426	0.66 (0.51, 0.81)	0.97 (0.83, 1.11)	16.30	0.70	365.97	0.23

Table 7: Summary of all trait models with an AIC difference of less than 4 compared to the lowest AIC model.

Model predictors	**df**	**logLik**	**AICc**	**ΔAIC**	**AIC weight**
Id, Mig, Precip, Spec	8	7.93	4.51	0.00	0.22
Id, Mig, Precip, Spec, Gen	9	9.02	5.58	1.07	0.13
Id, Mig, Precip, Spec, LowDisp	9	8.54	6.54	2.03	0.08
Mig, Precip, Spec, Gen	8	6.78	6.80	2.30	0.07
Id, Mig, Precip, Spec, Tol	9	8.36	6.90	2.40	0.07
Id, Mig, Precip, Spec, Temp	9	8.33	6.97	2.46	0.06
Id, Mig, Precip, Spec, For	9	8.21	7.20	2.70	0.06
Id, Mig, Precip, Spec, Diap	9	8.16	7.31	2.80	0.05
Id, Mig, Precip, Spec, Endo	9	8.03	7.57	3.06	0.05
Id, Mig, Precip, Spec, Gen, Lot	10	9.72	7.66	3.15	0.05
Id, Mig, Precip, Spec, Elev	9	7.95	7.73	3.22	0.04
Id, Mig, Precip, Spec, Lot	9	7.93	7.76	3.25	0.04
Id, Mig, Precip, Spec, For, Gen	10	9.52	8.06	3.55	0.04
Mig, Precip, Spec	7	4.58	8.14	3.63	0.04

Table 8: Model-averaged coefficients for the effect of traits on Odonata detection probability trends based on all trait models with an AIC difference of less than 4 compared to the lowest AIC model. Terms included in the lowest AIC model are in bold.

	Coefficient	**Std. error**	**z value**	**p value**
Intercept	0.004	0.213	0.020	0.984
Identify	**-0.209**	**0.083**	**2.533**	**0.011***
Migrant	**0.544**	**0.135**	**4.022**	**0.000*****
Opt precipitation	**0.091**	**0.030**	**3.044**	**0.002****
Habitat Specialist	**-0.297**	**0.066**	**4.535**	**0.000*****
Gen	0.262	0.149	1.756	0.079
Low Dispersal	0.182	0.160	1.142	0.253
Tolerance	-0.028	0.016	1.689	0.091
Opt temperature	0.035	0.037	0.954	0.340
Forest	-0.084	0.093	0.906	0.365
Diapause	-0.081	0.091	0.894	0.372
Endophytic	-0.062	0.139	0.445	0.656
Lotic specialist	-0.097	0.134	0.720	0.472
Elevation	-0.023	0.106	0.213	0.831

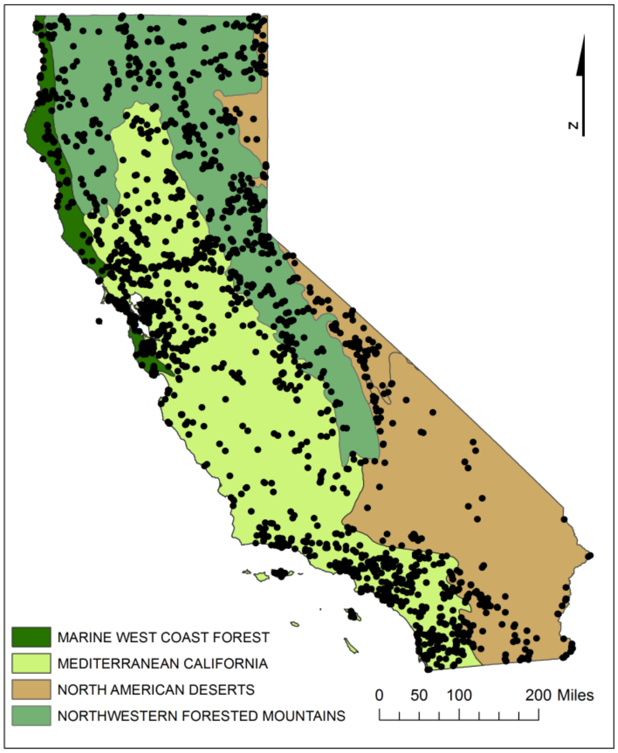

Fig. 1. Odonata species occurrence locations and ecoregions within California, USA.

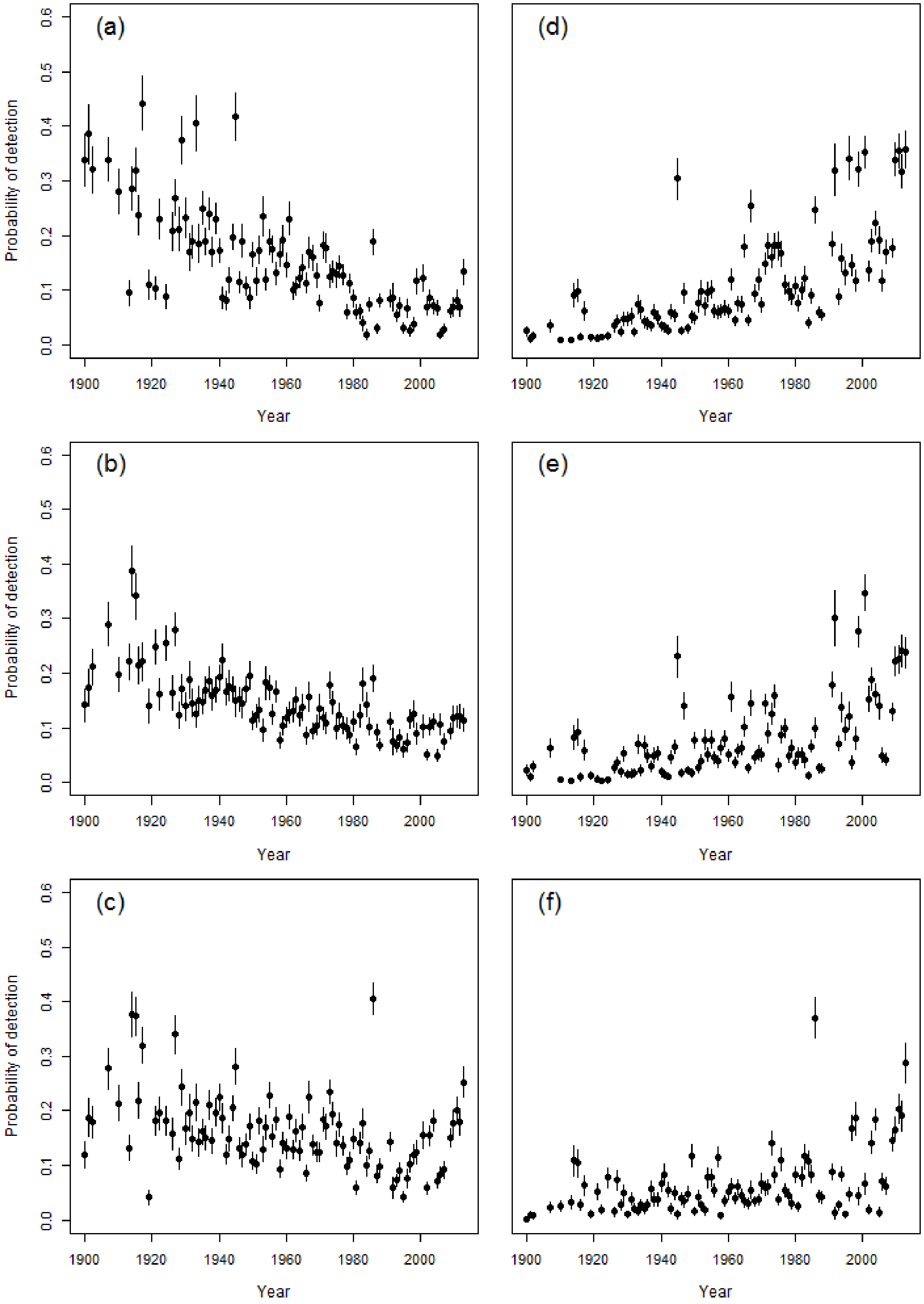

Fig. 2. Modelled probability of appearing in a list over time for the 6 species showing the most significant trends (declining: (a) *Ischnura denticollis,* (b) *Enallagma annexum,*(c) *Enallagma*

carunculatum; increasing: (d) *Anax junius*, (e) *Tramea lacerata*, (f) *Libellula forensis*). Figures show mean (points) and standard deviation (arrows) of probability of detection in each year as predicted by the full model of each species.