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Detecting long-term occupancy changes in Californian odonates from natural history and citizen science records

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Abstract

In a world of rapid environmental change, effective biodiversity conservation and management relies on our ability to detect changes in species occurrence. While long-term, standardized monitoring is ideal for detecting change, such monitoring is costly and rare. An alternative approach is to use historical records from natural history collections as a baseline to compare with recent observations. Here, we combine natural history collection data with citizen science observations within a hierarchical Bayesian occupancy modeling framework to identify changes in the occupancy of Californian dragonflies and damselflies (Odonata) over the past century. We model changes in the probability of occupancy of 34 odonate species across years and as a function of climate, after correcting for likely variation in detection probability using proxies for recorder effort and seasonal variation. We then examine whether biological traits can help explain variation in temporal trends. Models built using only opportunistic records identify significant changes in occupancy across years for 14 species, with eight of those showing significant declines and six showing significant increases in occupancy in the period 1900-2013. These changes are consistent with estimates obtained using more standardized resurvey data, regardless of whether resurvey data are used individually or in conjunction with the opportunistic dataset. We find that species increasing in occupancy over time are also those whose occupancy tends to increase with higher minimum temperatures, which suggests that these species may be benefiting from increasing temperatures across California. Furthermore, these species are also mostly habitat generalists, whilst a number of habitat specialists display some of the largest declines in occupancy across years. Our approach

enables more robust estimates of temporal trends from opportunistic specimen and observation data, thus facilitating the use of these data in biodiversity conservation and management.

Keywords: Bayesian occupancy models, Population change, Natural history collections, Citizen science, Detection bias, Dragonflies, Traits, Temperature, NIMBLE

Introduction

Natural history collections house an estimated 2.5–3 billion biological specimens globally (Graham et al. 2004; O'Connell et al. 2004; Pyke and Ehrlich 2010), some of which date as far back as the 18th century. There are no other sources that provide this much biodiversity data on a comparable timescale. The growing demand for long-term temporal biodiversity trends makes natural history collection data particularly appealing for species conservation and climate change impact assessments. However, estimating trends from natural history collections requires a careful assessment of data quality and biases (e.g., Boakes et al. 2010). Historical specimens were often collected in a haphazard and opportunistic manner, largely dependent on the behavior of collectors (Ponder et al. 2001; Graham et al. 2004; Hortal et al. 2006). For instance, the number of specimens collected is often positively correlated with the population density and accessibility of an area (Ballesteros-Mejia et al. 2013; Meyer et al. 2015), and collectors often focus on rare or charismatic species (e.g., Jeppsson et al. 2010). Natural history collections also contain biases related to the location, age and size of the institution (Ferro and Flick 2015). As a result, large regions may have been under-sampled or not sampled at all (Pyke and Ehrlich 2010; Ruete 2015). These spatial biases are compounded when comparing specimen collections and observations over time (Isaac and Pocock 2015). While recording biases in natural history collections have long been documented (e.g., Shaffer et al. 1998), progress has been slow in devising suitable approaches to address these biases and reduce uncertainty in estimates of biodiversity change over time derived from these data.

During recent efforts toward mass digitization of natural history collections (Lister et al. 2011; Beaman and Cellinese 2012), there has been a parallel surge in the availability and use of species observations reported online by citizen scientists (e.g., eBird, www.ebird. org; Silvertown 2009). Despite important differences (Guralnick and Van Cleeve 2005; Boakes et al. 2010), natural history and citizen science data are subject to the same fundamental spatial and temporal sources of recording bias (Isaac et al. 2014; Isaac and Pocock 2015; Ruete 2015). Contrary to natural history collection data, there has been much progress in devising approaches to account for recording

biases when extracting signals of change from citizen science data (Isaac et al. 2014). However, it remains unclear whether methods developed to estimate changes in species abundance and distribution from citizen science data can work with natural history collection data (but see Zeilinger et al. 2017). This is an exciting prospect, as a successful application of these novel methods to natural history records may unlock the potential held in natural history collections for aiding conservation and management. Furthermore, doing so may facilitate the integration of natural history and citizen science data, which are complementary. For instance, while natural history records generally stretch much further into the past (i.e., centuries) than citizen science records, citizen science observations often have a much better coverage for recent decades (e.g., Ball-Damerow et al. 2015). Combining the strengths of these two data sources should increase both the temporal extent and resolution of species temporal trend estimates.

One intuitive and effective approach to statistically correct for uneven recorder intensity is to use the number of species recorded during each sampling visit (the list length, L; Isaac et al. 2014) as a proxy for recorder effort (Roberts et al. 2007; Szabo et al. 2010; Breed et al. 2013; Barnes et al. 2014). Adding a covariate for list length may enable distinguishing true absences from failures to detect and record a focal species, since list length is positively associated with collector effort and therefore collection probability (Roberts et al. 2007; Isaac and Pocock 2015). This approach is particularly powerful when combined with occupancy models, which model the recording (detection) process separately from the ecological process that underlies the species' true occupancy (van Strien et al. 2013; Isaac et al. 2014; Hefley and Hooten 2016). For example, the ecological process might capture the likelihood that a species was present at as site given certain climatic parameters, whilst the detection process would separately model whether the species was likely to have been recorded when present given the effort expended during a collection event (potentially captured using list length). This approach is intuitive for citizen science data because these data are often reported in the form of species lists, each of a given length (Isaac and Pocock 2015). Previous studies using citizen science data have successfully used the list length to correct for recorder effort and improve estimates of species' temporal trends (e.g., Szabo et al. 2010; Breed et al. 2013; Barnes et al. 2014; van Strien et al. 2010, 2013, 2015). However, digitized natural history records—particularly those spanning multiple institutions—have not typically been collected this way, making it more challenging to define unique species lists from which to derive list lengths. One way to address this is to assume that natural history records can be compiled into meaningful lists similar to citizen science lists based on the location and time in which they were collected. This assumption has

previously been used to aggregate natural history records in analyses of biodiversity change over space and time (e.g., Bartomeus et al. 2013; van Strien et al. 2015; Zeilinger et al. 2017).

In this paper, we examine long-term changes in the occupancy of Californian odonates from an integrated database of natural history and citizen science records using Bayesian occupancy models. Odonata are good candidates to study changes over time, because they are indicators of ecosystem health (Clausnitzer 2003; Smith et al. 2007), have a wide range of environmental tolerances and are responsive to ecosystem conditions in relation to broadscale factors—such as climate (Hickling et al. 2006) and urbanization (Samways and Steytler 1996; Suhling et al. 2006; Smith et al. 2007). Furthermore, Californian odonates have been relatively well-sampled over time and most existing records from 1900 to 2013—including both citizen science and natural history records—are accessible through a recentlyintegrated digital database (Ball-Damerow et al. 2015). Our specific objective was to test whether natural history and citizen science records can help us identify which odonate species have declined and which have increased in California over the period 1900–2013. The degree to which species increase or decline over time in response to environmental changes is likely to depend on their biological traits (Williams et al. 2008; Angert et al. 2011; Foden et al. 2013). For example, among odonate species, habitat generalists have been found to increase and habitat specialists to decrease, not only in California (Ball-Damerow et al. 2014a) but also Great Britain (Powney et al. 2015). Therefore, we also test whether variation in modeled occupancy trends among species can be explained by four biological traits that have previously been linked with changes in odonates (Hassall et al. 2007; Angert et al. 2011; Ball-Damerow et al. 2014a; Powney et al. 2015). We assess whether our estimates of change in odonate species occupancy are reasonable by comparing them with previous estimates of change from a standardized resurvey study in California (Ball-Damerow et al. 2014a). Our ultimate goal is to enable a more widespread use of natural history records, together with citizen science observations, within conservation and management by demonstrating how careful treatment of these combined data can generate reliable estimates of temporal trends in biodiversity.

Methods

Species records and lists

We obtained species occurrence data from a database of California Odonata, including over 32,000 specimen and observation-based records (https://doi.org/10.3897/zookeys.482. 8453; Ball-Damerow et al. 2015). The database contains 19,000 unique georeferenced records for 106 species of

dragonflies and damselflies spanning the period 1879–2013 throughout the state (Ball-Damerow et al. 2015). Historical 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). Museum specimen data exhibited a decline in records for recent decades, a pattern common to other natural history collection datasets (Tewksbury et al. 2014; Zeilinger et al. 2017). To augment contemporary records, we also included occurrence data from Odonata Central and CalOdes enthusiast observations, of which records have often been photovouchered and verified by odonate experts. Odonata Central (2014) is a North American database with georeferenced records, and includes photovouchered sightings, records from literature, and some specimen-based data (Abbott and Broglie 2005). CalOdes is a California statewide dragonfly enthusiast group, with members who track and submit species lists (Dragonflies of California 2014).

We aggregated species records based on unique combinations of georeferenced longitude and latitude, Julian day, and year. Hereafter, we refer to these aggregates as species lists (Fig. 1). We then overlaid a 20-km resolution grid onto our study area and assigned each list to the grid cell where it was collected. To minimize uncertainty related to georeferencing error, we excluded lists collected at locations with an uncertainty radius greater than the grid cell size (i.e., 20 km).

Occupancy models

To improve the likelihood of suitable model convergence, we excluded 65 odonate species with less than 50 records both before and after 1975; we selected this cutoff to ensure a comparable recording intensity between the two broad time periods. We modeled changes in the occupancy of the remaining 41 species using a hierarchical occupancy model—also known as a binomial-binomial mixture model—as described in Royle and Kery (2007). This model explicitly models the detection process separately from the ecological (occupancy) process, while simultaneously correcting for zero-inflation in our dataset—a consequence of imperfect detection (Martin et al. 2005). It is important to note that, contrary to usual datasets used for occupancy modeling, our data did not include repeated visits to a site within a closed time period. However, we were able to identify the separate occupancy and detection latent states by using non-overlapping sets of covariates within the two sub-models (Solymos et al. 2012).

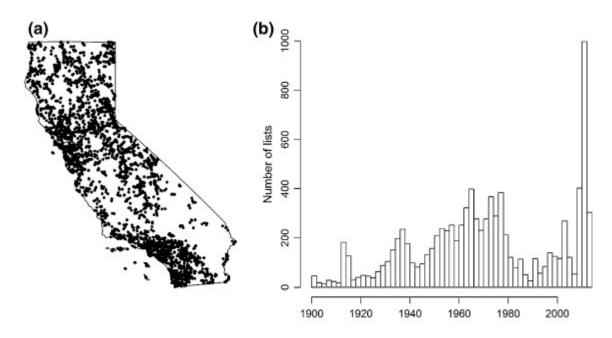


Fig. 1 Spatiotemporal distribution of Odonata species occurrence records used in this study. a Locations of Odonata species lists compiled from specimen and occurrence records throughout California, USA, and b number of lists at two year intervals over the period of study, from 1900 to 2013

Since our primary goal was to estimate how the occupancy of each species varied across years—a measure of the species' temporal trend in occupancy —we included the year in which a list was recorded as the first parameter in the occupancy sub-model. Additionally, since occupancy is known to vary across California based on climate (Ball-Damerow et al. 2014a, b), we also included the mean minimum temperature and mean total precipitation in the cell and year of collection within the occupancy sub-model. Yearly values for these climatic variables were obtained from the PRISM Climate Group (2014) at a 4-km resolution. Before including both temperature and precipitation in our models, we ensured that these variables were not strongly correlated with each other or with Julian day within our study area (Table S1). Finally, we controlled for unaccounted spatial relationships among sites by adding a random effect of grid cell to our occupancy sub-model. In effect, this led to estimating a different intercept α for each cell *i*. Therefore, we specified the following occupancy sub-model:

$$logit(\psi_{sit}) = \alpha_i + \beta_1 * year_{st} + \beta_2 * temperature_{it} + \beta_3 * precipitation_{st}$$
 (1)

where ψ_{sit} represents a species' occupancy in site s, within grid cell i, at time t; here, sites are defined as the unique latitude and longitude coordinates of each list, grid cells are 20 \times 20 km cells defined above, and time is the combination of Julian day and year.

For the detection sub-model, we accounted for variation in recorder effort among lists by including a list-length term (Breed et al. 2013; Isaac et al. 2014; Szabo et al. 2010)—the log of the number of species recorded in a list (L)—and for effects of season by including a linear and quadratic terms for Julian day (day) as follows (modified from van Strien et al. 2013):

$$logit(p_{st}) = \alpha + \beta_4 * L_{st} + \beta_5 * day_{st} + \beta_6 * day_{st}^2$$
(2)

Contrary to previous applications of these models to citizen science data (e.g. Szabo et al. 2010), we did not exclude lists with particularly short lengths but rather modeled all lists in the same way. Including all available data was shown to improve temporal trend estimates generated using occupancy models from unstructured data (Kamp et al. 2016). We standardized all continuous predictors to facilitate the interpretation of the relative importance of model coefficients (Schielzeth 2010).

In addition to opportunistic natural history and citizen science records, the database we used included records from historical surveys and targeted modern resurveys previously analyzed in Ball-Damerow et al. (2014a). To ensure that such standardized resurvey study data did not drive the species-level trends in occupancy modeled and similarities with results from Ball-Damerow et al. (2014a), we re-ran all hierarchical occupancy models after the exclusion of all resurvey records analyzed in Ball-Damerow et al. (2014a). We hereafter refer to this alternative dataset as "opportunistic", and compare it with the "full" dataset.

Occupancy models were fit using the Markov chain Monte Carlo (MCMC) engine provided with the NIMBLE package (version 0.6–3) for R 3.3.2 (NIMBLE Development Team 2015; R Core Team 2016; de Valpine et al. 2016). To improve efficiency of MCMC mixing, we set up MCMC samplers as described in Zeilinger et al. (2017). Briefly, we used block sampling algorithms to jointly sample the linear coefficients within each sub-model, and the standard deviation of the site random effect was sampled on the logarithmic scale with generalized Gibbs sampling framework of Liu and Sabatti (2000). We also used a custom distribution to remove latent states from the model and further improve MCMC efficiency (Turek et al. 2016). We used uninformative priors and three MCMC chains each with 500,000–1,000,000 iterations (depending on the species) and a burn-in period of 100,000. Convergence was verified by calculating the Gelman-Rubin diagnostic and effective sample size (Gelman and Rubin 1992; Gelman et al. 2004).

After running each model for up to 1,000,000 iterations, models for a number of species did not display suitable convergence across all model parameters.

This was especially the case for models generated using opportunistic data only. As a result, we excluded from our analyses species whose models did not suitably converge. Regardless of the dataset used, we only kept species based on the following quantitative thresholds: Gelman-Rubin $\mathring{r} < 1.1$ (Gelman et al. 2004) and effective sample size >700 (i.e., more than triple the ruleof-thumb commonly used by phylogeneticists to assess suitable convergence of tree topology posteriors; Drummond et al. 2006) across all model parameters. We confirmed successful convergence of these species through visual inspection of MCMC chain histories. This exclusion process resulted in final species datasets of 34 and 24 species for the complete dataset and the opportunistic dataset, respectively. Throughout the paper, we only present results based on these sets of species.

Trait correlates of occupancy change

We tested four hypotheses of the effect of species' attributes on yearly change in reporting rates (i.e., increasing versus decreasing) based on results from a resurvey study of Californian odonates (Ball-Damerow et al. 2014a). Following Ball-Damerow et al. (2014a), we hypothesized that: (i) habitat specialists, which require certain habitat types (e.g., flowing water or high elevation) to complete their life cycle, would show decreases in occupancy; (ii) migratory species, which have a tropical origin and are warmadapted would show increases in occupancy; (iii) species that undergo overwintering diapause to withstand colder temperatures would show decreases in occupancy; and (iv) species adapted to warmer temperatures would show increases in occupancy due to overall warming across California (Hassall and Thompson 2008). We obtained information on the first three traits from regional Odonata field guides (Manolis 2003; Paulson 2009) supplemented by expert knowledge (D. Paulson, pers. comm.)—and coded each as a binary 0/1 variable based on whether the species displayed the trait or not. We determined temperature preference using the mean posterior estimate of the minimum temperature parameter β_2 (see Eq. 1) generated by our occupancy models. To test the four hypotheses simultaneously, we used linear mixed effects models with a normal error structure in the R package Ime4 (Bates et al. 2013). We modeled the mean posterior estimate of the year parameter β_1 as a function of the linear effects of habitat specialism, migratory behavior, diapause and temperature preference. To account for shared natural history among species, we also included family and genus as random effects in the model. We calculated the conditional and marginal coefficient of determination for the linear mixedeffect model using the method developed by Nakagawa and Schielzeth (2012).

Results

Changes in species' occupancy

Across all species, list length was positively related to probability of detection, indicating that all species were more likely to be detected on longer lists (Fig. 2). This relationship was significant in all species except *Archilestes californicus*, a specialist to lotic water. Whenever significant (i.e., 95% CI intervals not overlapping 0), linear and quadratic parameters for Julian day indicated realistic polynomial relationships between probability of detection and seasonality (Table S3, S4). List length and Julian day parameter estimates were largely consistent between the full and opportunistic datasets (Fig. 2; Tables S3, S4).

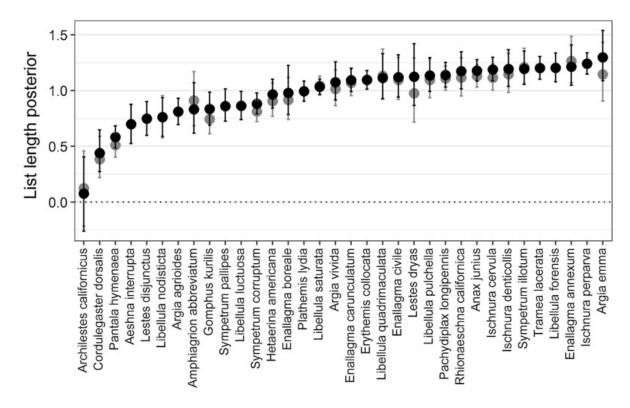


Fig. 2 Posterior estimates of the list length parameter β_4 —a proxy for recorder effort—for 34 species of Californian odonates generated using Bayesian occupancy models. Indicated are the means $\pm 95\%$ confidence intervals derived from the list length posterior distribution for each species. Occupancy models were run either using all databased odonate records (black points) or using opportunistic records only (grey points; note these are only shown for 24 species with reliable estimates)

After accounting for variation in probability of detection, we found significant changes in probability of occupancy across years for 25 of the 34 species (74%) in the full dataset and 16 out of 24 species (67%) in the opportunistic dataset (Table 1). According to both datasets, eight species showed

significant declines across years (Libellula nodisticta, Ischnura denticollis, Enallagma carunculatum, Enallagma annexum, Amphiagrion abbreviatum, Enallagma boreale, Sympetrum illotum, Hetaerina americana), while six species showed significant increases across years (Libellula saturata, Anax junius, Pachydiplax longipennis, Enallagma civile, Libellula pulchella, Ischnura cervula). Four of the declining species (I. denticollis, E. carunculatum, E. annexum, E. boreale) are smaller damselflies that may be less-frequently reported in more recent enthusiast observation records, while three of the other declining species are habitat specialists (L. nodisticta, A. abbreviatum, H. americana). By contrast, all six species identified as expanding are habitat generalists.

Estimates of yearly change in species' occupancy obtained from the full and opportunistic datasets were significantly positively correlated with each other (r = 0.46, $t_{22} = 2.45$, p < 0.05). Furthermore, estimates from occupancy models were also positively correlated with estimates of occupancy derived from the resurvey study of Ball-Damerow et al. (2014a), though this correlation was weak for estimates generated using opportunistic data only (full vs resurvey estimates: r = 0.41, $t_{32} = 2.58$, p < 0.05; opportunistic vs. resurvey estimates: r = 0.19, $t_{22} = 0.89$, p = >0.05). Finally, estimates of the effects of minimum temperature and total precipitation on probability of occupancy were largely consistent with known preferences (Manolis 2003; Paulson 2009) across all species modeled (Tables S5, S6).

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simultaneously, we used linear mixed effects models with a normal error structure in the $\bf R$ package lme4 (Bates et al. 2013). We modeled the mean posterior estimate of the year parameter β_1 as a function of the linear effects of habitat specialism, migratory behavior, diapause and temperature preference. To account for shared natural history among species, we also included family and genus as random effects in the model. We calculated the conditional and marginal coefficient of determination for the linear mixed-effect model using the method developed by Nakagawa and Schielzeth (2012).

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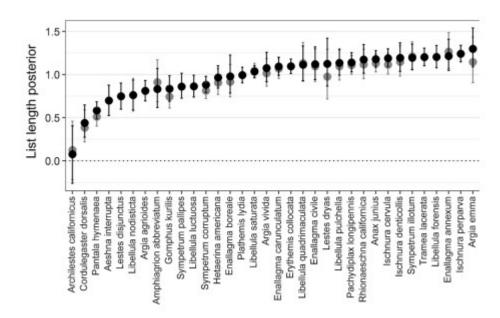


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Trait correlates of occupancy change

Based on the full dataset, the four species' traits we examined accounted for 62% of the variation in yearly trends across species (Table 2). Temperature preference—the mean posterior of the temperature parameter β_2 from our occupancy models—was the only significant predictor of increase or decline (i.e., its coefficient ± 2 standard error did not overlap zero; Table 2). Species whose probability of occupancy increased with minimum temperature showed significantly higher increases in occupancy from 1900 to 2013 than species whose probability of occupancy decreased with minimum temperature (Fig. 3). The positive association between yearly increase in probability of occupancy and temperature preference was robust to the uncertainty in estimates of yearly trends (Table S7). Despite not being

statistically significant, there was a negative relationship between occupancy change and habitat specialism, with habitat specialists generally displaying lower increases or larger declines than habitat generalists. Although the direction of these effects remained unchanged when yearly trends were derived from the opportunistic dataset, the explanatory power of trait-based models decreased substantially, with random effects accounting for most of the explained variation (Table 2). The much lower explanatory power of trait predictors within the opportunistic dataset is likely a consequence of the reduced species set, and the ensuing loss of statistical power. Migratory behavior and diapause did not appear to be strongly related with yearly changes in species occupancy in this analysis.

Table 1 Estimates of temporal change in occupancy for 35 odonate species in California

Species	Full dataset			Opportunistic dataset			Survey
	Year posterior	î	ESS	Year posterior	î	ESS	change
Libellula nodisticta	-16.16 (-29.89, -6.73)	1(1)	1200	-16.13 (-32.64, -5.71)	1(1)	1254	-3
Aeshna interrupta	-3.46 (-10.44, 1.91)	1(1)	5344				-4
Ischnura perparva	-0.87 (-1.76, -0.31)	1(1)	4905				2
Ischnura denticollis	-0.71 (-1.02, -0.47)	1(1)	11443	-0.62 (-0.94, -0.35)	1(1)	13912	1
Enallagma carunculatum	-0.68 (-1.16, -0.35)	1(1)	10813	-0.58 (-1.1, -0.22)	1(1)	8980	-1
Sympetrum pallipes	-0.63 (-1.73, -0.13)	1(1)	3030				-11
Enallagma annexum	-0.61 (-0.92, -0.36)	1(1)	12833	-0.68 (-1, -0.41)	1(1)	14295	1
Amphiagrion abbreviatum	-0.56 (-0.86, -0.3)	1(1)	19521	-0.58 (-0.97, -0.28)	1(1)	10911	-1
Enallagma boreale	-0.51 (-0.85, -0.23)	1(1)	17600	-0.9 (-1.86, -0.34)	1(1)	3596	2
Sympetrum illotum	-0.37 (-0.65, -0.13)	1(1)	15440	-0.46 (-0.78, -0.2)	1(1)	12700	-2
Lestes dryas	-0.33 (-0.68, -0.01)	1(1)	29804	0.05 (-0.36, 0.48)	1(1)	26139	-2
Hetaerina americana	-0.32 (-0.57, -0.1)	1(1)	22746	-0.24 (-0.49, -0.01)	1(1)		-4
Sympetrum corruptum	-0.21 (-0.39, -0.04)	. ,	45132	-0.18 (-0.39, 0.01)	1(1)	40821	6
Cordulegaster dorsalis	-0.01 (-0.22, 0.2)	1(1)	46203	0.12 (-0.14, 0.39)	1(1)	37685	-2
Argia vivida	0.01 (-0.1, 0.11)	1(1)	49598	-0.08 (-0.21, 0.04)	1(1)		4
Argia emma	0.12 (-0.16, 0.39)	1(1)	39129	0.53 (0.11, 0.97)	1(1)	26725	4
Libellula quadrimaculata	0.16 (-0.47, 0.84)	1(1)	18122	0.35 (-0.12, 0.9)	1(1)	16797	0
Rhionaeschna californica	0.19 (-0.33, 0.65)	1(1)	18662	0.27 (-0.38, 0.82)	1(1)	11589	1
Archilestes californicus	0.23 (-0.04, 0.5)	1(1)	63733	0.27 (0, 0.54)	1(1)	61600	-2
Gomphus kurilis	0.36 (-0.07, 0.87)	1(1)	30253	19.26 (0.99, 39.85)	1(1)	894	1
Ischnura cervula	0.4 (0.15, 0.68)	1(1)	29586	0.54 (0.26, 0.88)	1(1)	21734	7
Libellula pulchella	0.45 (0.12, 0.86)	1(1)	20142	0.89 (0.43, 1.6)	1(1)	7591	1
Libellula forensis	0.68 (0.23, 1.37)	1(1)	8779				(
Enallagma civile	0.7 (0.41, 1.1)	1(1)	10527	0.41 (0.15, 0.72)	1(1)	25485	18
Pachydiplax longipennis	0.72 (0.41, 1.13)	1(1)	19647	0.7 (0.29, 1.28)	1(1)	14839	8
Anax junius	0.99 (0.67, 1.45)	1(1)	9871	0.87 (0.61, 1.19)	1(1)	31980	15
Lestes disjunctus	1.9 (-4.53, 9.02)	1(1)	8746				2
Erythemis collocata	13.07 (2.92, 27.35)	1(1)	2672				-2
Libellula saturata	13.15 (3.07, 26.54)	1(1)	887	0.57 (0.11, 1.19)	1(1)	8457	9
Plathemis lydia	21.89 (5.1, 50.39)	1(1)	1553				-1
Pantala hymenaea	23.77 (5.78, 49.19)	1(1)	1416	4.13 (-23.46, 26.14)	1(1)	946	15
Argia agrioides	27.64 (10.25, 51.5)	1(1)	1238				(
Libellula luctuosa	33.75 (13.34, 58.57)	1(1)	866				9
Tramea lacerata	36.98 (14.67, 64.14)	1(1)	730				14

For each species, temporal changes in occupancy are estimated using the posterior mean (±95% CI interval) of the year parameter generated using hierarchical Bayesian occupancy models. Occupancy models were run either using all odonate records (i.e., full dataset) or using opportunistic records only. However, suitable model convergence (according to the criteria detailed in the Methods section) could not be achieved for all species using the opportunistic dataset; hence, estimates for these species are not presented. Also presented are values of Rubin-Gelman ř and effective sample size (ESS) corresponding to each model parameter estimate. Estimates of

yearly occupancy change from occupancy models are compared with changes in occurrence rates derived from a standardized resurvey study (i.e., "Survey change" column, Ball-Damerow et al. 2014a), for the species for which these are available. Bolded estimates are significant (i.e., 95% Cl do not overlap 0) and light grey rows indicate consistently significant estimates between the full and opportunistic datasets

Table 2 Fixed effects from the linear mixed-effects model describing variation in the yearly trend of species' occupancy as a function of species' temperature preference, migratory behavior, specialization, and diapause

Fixed effect	Full data:	$set(R^2 = $	0.62)	Opportunistic dataset ($R^2 = 0.08$)			
	Coefficient	S. E.	t value	Coefficient	S. E.	t value	
(Intercept)	2.429	1.889	1.286	3.516	3.312	1.062	
Temperature	0.436	0.076	5.723	0.195	0.088	2.23	
Specialist	-1.790	2.675	-0.669	-1.780	1.789	-0.995	
Migrant	2.863	5.011	0.571	-3.475	4.864	-0.714	
Diapause	1.546	3.025	0.511	1.508	2.352	0.641	

Yearly trends were obtained using either the full or the opportunistic datasets. Models also include family and genus as random effects. Estimated coefficients, standard error (SE), and t value for each trait are indicated. The marginal R² for each model (estimates of the coefficient of determination for the fixed effects alone) are also reported. Conditional R² (estimates of the coefficient of determination for fixed and random effects combined) were 0.62 and 0.86 for the full and opportunistic data models, respectively. Rows in grey indicate statistically significant traits

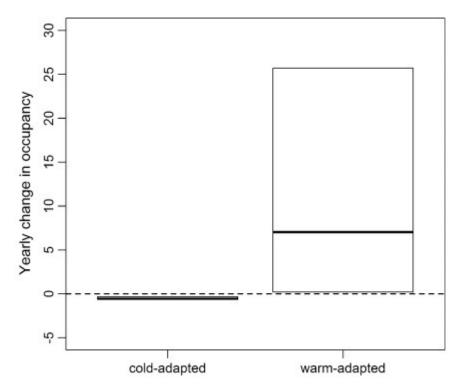


Fig. 3 Yearly change in occupancy for cold- versus warm-adapted species. Yearly changes in occupancy are the mean of the posterior distribution for the year parameter β , as estimated from occupancy models on the full dataset. Cold-adapted and warm-adapted species are species whose probability of occurrence showed a negative and positive association with minimum temperature, respectively. Yearly trends are only included for the 21 species displaying both yearly trends and temperature preferences that were statistically significant (i.e. 95% C.I. intervals for the posterior distribution of the relevant parameter did not overlap 0) on the full dataset. Black lines represents medians and the box shows the middle 50% yearly trend estimates for cold- and warm-adapted species

Discussion

Using hierarchical Bayesian occupancy models to account for variation in recorder effort on probability of detection, we identified long-term changes in the occupancy of Californian odonates from a combined dataset of natural history specimens and citizen science observations. Our estimates of temporal change are in line with previous accounts based on replicated standardized surveys, which mostly took place in central California (BallDamerow et al. 2014a), and the biology of these taxa (Hassall et al. 2007; Hassall and Thompson 2008; Angert et al. 2011; Powney et al. 2015). This analysis demonstrates that data aggregation and statistical correction

for recording bias may increase our ability to identify species' occupancy changes over time from natural history collection data, thus improving our confidence to use these data for detecting long-term changes.

Changes in species' occupancy

Based on a dataset of opportunistic specimen and observation records, we identified significant declines in occupancy for eight species and significant increases in occupancy for six species of odonates across California from 1900 to 2013. These estimates of occupancy change were largely consistent, whether repeated standardized surveys were excluded or incorporated with the opportunistic dataset (see Table 1). Five of the six species displaying significant increases based on both full and opportunistic data were also identified as having the largest increases in the resurvey study done in this region, including L. saturata, A. junius, P. longipennis, and E. civile (Ball-Damerow et al. 2014a; Table 1). Similarly, two species (L. nodisticta and H. americana) identified as declining significantly in both the full and opportunistic dataset were also found to be declining in the resurvey study (i.e. a decline in occurrence rate of greater than 2 occurrences; Ball-Damerow et al. 2014a; Table 1). Despite these similarities, it is important to note that the resurvey study was limited to 45 sites throughout central California, and did not encompass the entire state of California. Therefore, the distribution of some species included in this study shows little overlap with the resurvey study area (Ball-Damerow et al. 2014a).

Regardless of whether survey data were included, our occupancy models also identified specific relationships with minimum temperature that closely corresponded to information on temperature and elevation preferences available in field guides (Manolis 2003; Paulson 2009). Many of the species associated with higher temperatures also showed increases in occupancy in the resurvey study (Ball-Damerow et al. 2014a). Occupancy models using opportunistic datasets may enable the identification of climatic preferences for less well-studied groups—where temperature preferences are unknown—and predict future increases or declines given climate change.

Trait correlates of occupancy change

Identifying the biological traits associated with increases or declines in occupancy may provide a way to predict likely changes for species that cannot be modeled satisfactorily, for example if they are hard to detect or have low reporting rates over time. We found that species whose probability of occupancy increased with temperature also showed the highest increases in occupancy from 1900 to 2013. Warm-adapted odonate species are expected to benefit from increasing temperatures (Hickling et al. 2005; Hassall and Thompson 2008) as they may experience faster growth rates

and longer reproductive periods with increasing winter temperatures (Harrington et al. 2001). Despite not being statistically significant in our trait model, specialization was also a useful predictor of yearly trend in occupancy (Fig. S1), as all six species displaying significant increases in both full and opportunistic datasets were habitat generalists. Ecological generalization often promotes rates of colonization in a variety of organisms, including Odonata (Powney et al. 2015), while specialization has the opposite effect (e.g., Warren et al. 2001; Ruesink 2005; Vall-llosera and Sol 2009; Dupont et al. 2011). Similarly, generalist species are also less likely to become locally extinct (Korkeamaki and Suhonen 2002).

Addressing biases in opportunistic species occurrence records

Standardized historical data across large regions and time periods are often unavailable. In these cases, integrating opportunistic records from multiple sources and selecting appropriate statistical models may be the only feasible option to generate estimates of biodiversity changes over time. Nevertheless, data aggregation and statistical approaches only partially address biases resulting from opportunistic data, as there is no complete substitute for standardization when comparing samples across space and time.

Firstly, the approach we present here may only be feasible for a limited set of the species for which data are available. 106 odonate species were recorded at least once in our full dataset (see Fig. 1) but we could only generate satisfactory estimates of probability of occupancy for 34 and 24 species from the full and opportunistic datasets, respectively. Species were excluded from these final sets because they fell short of the thresholds we set for either the minimum number of records over time (i.e., 50 records both pre- and post-1975) or suitable convergence of occupancy models (i.e. Gelman-Rubin $\dot{r} < 1.1$ and effective sample size >700 across all model parameters). As a result of these necessary filtering steps, we were unable to model or include estimates for several species of interest. Many of the species with the highest declines in the resurvey study could not be examined here, as they did not pass our filter for the minimum number of records across time. These species, which tend to be less well recorded, are often habitat specialists and are likely subject to the highest declines across large regions and time periods (Clavel et al. 2011; Ball-Damerow et al. 2014b; Powney et al. 2015). The data filtering criterion we employed may be too restrictive for habitat specialists, which are likely to occupy a lower number of sites and have inherently fewer co-occurring species. Complementing natural history collection and citizen science data with standardized surveys—for example by targeting historical distribution strongholds—may be necessary to reliably identify declines in these species.

Moreover, our final set of yearly change estimates derived from opportunistic data also excluded three of the species that are known to have increased most in recent years (*P. hymenaea*, *T. lacerata*, and *L. luctuosa*; Ball-Damerow et al. 2014a; Table 1). *L. luctuosa* in particular is well-documented to have entered California in the 1930s and subsequently has spread and become common throughout the state (Manolis 2003). Although estimates for all three species from opportunistic records did indicate yearly increases, we chose not to present these estimates because 95% confidence intervals around some of the model parameters were subject to excessive uncertainty. Therefore, although we had to exclude a large set of species from our analyses, we are confident that our conservative criteria led to the inclusion of only the most robust estimates of occupancy change. We advise the use of similarly restrictive filters to ensure reliable occupancy estimates are obtained from opportunistic data.

The estimates of occupancy change we present may still be affected by variation in detection probability. For example, our models identified significant declines identified for four species (I. denticollis, E. carunculatum, E. annexum, E. boreale); these declines were not detected in the resurvey study, and these particular species are all small damselflies that are common but more difficult to identify in the field. As a result, there may be low reporting rates by enthusiasts for these species in recent years and could have impacted detection estimates from occupancy models. Isaac et al. (2014) found that particular scenarios of change in species detectability could affect estimates of occupancy derived from models using list length as a proxy for recorder effort. However, the approach we adopted here separate occupancy and detection sub-models with a list length covariate and a spatial random effect—was the most robust across all scenarios of spatiotemporal variation in recorder effort (Isaac et al. 2014). Similar occupancy models have previously been used to provide consistent estimates of temporal change from opportunistic data on dragonflies (van Strien et al. 2010), butterflies (Breed et al. 2013), birds (Link et al. 2006), owl prey populations (van Strien et al. 2015), and an insect pest (Zeilinger et al. 2017). Although Isaac et al. (2014) do indicate that a reduction in effort per visit over time could affect the ability of occupancy models to identify declines in species occupancy, there was a slight increase in list length across years in our dataset (Spearman's rank correlation: $\rho = 0.25$, p < 0.001). As a result, our estimates of decline are unlikely to be subject to large residual effects of recorder bias. In any case, we strongly believe these estimates represent the most robust estimates of change that can currently be obtained from this dataset.

Facilitating the use of natural history collections to support conservation and management

Progress in the use of natural history collection data for extracting temporal trends in biodiversity has been hindered by the inability to properly address variation in recorder effort across space and time. We have shown here that, even when precise information on recorder effort is unavailable, useful proxies can be calculated from occurrence records themselves. Across all species we modeled the probability of detection increased with the list length—the total number of species recorded during a sampling event. After accounting for variation in detection probability using list length and Julian day, we identified realistic increases in occupancy across years for several warm-adapted, generalist and migratory species, as well as significant decreases for at least two specialist species known to have been declining in recent decades.

Serious obstacles remain when using opportunistic records to determine change over time. Although we started with an unusually detailed and extensive database, our fairly stringent requirements for data availability and certainty in parameter estimates resulted in a limited number of species in the final dataset. Furthermore, the fact that several small and harder to identify damselflies were found to be declining, despite being common, could point to residual effects of recorder bias. Despite these issues, we derived robust estimates of long-term change that were generally comparable with those obtained from resurvey records (Ball-Damerow et al. 2014a) and showed that our approach can be useful for detecting long-term changes across a number of species. Therefore, we also provide access to the R code used to run the hierarchical Bayesian occupancy models presented in this study (https://github.com/giorap/odonata-occupancy-change), in the hope that this may facilitate future applications of these approaches to natural history collection data. We emphasize the necessity to develop a priori expectations for species responses throughout this process and to examine critically all model output for potential residual effects of bias.

Our study highlights three key ways in which natural history collection data could contribute to generating knowledge of long-term biodiversity changes more readily. First, aggregating natural history collection data from multiple sources into species lists with a given spatial and temporal footprint will enable leveraging existing approaches for modeling variation in detection probability across sets of species lists. Second, combining natural history collection data with other sources of opportunistic occurrence data such as citizen science observations will increase the temporal extent and temporal resolution of the dataset. Finally, identifying the traits associated with change in the species that satisfy data demands will enable predicting likely

changes for species that lack the necessary occurrence data. Such multifaceted approach will ensure that the growing availability of digitized natural history collections data can help meet the growing demand for temporal biodiversity trends to support conservation and management decisions.

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