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Altitudinal shifts of the native and introduced flora of California in the context of 20th-century warming

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ABSTRACT

Aim The differential responses of plant species to climate change are of great interest and grave concern for scientists and conservationists. One underexploited resource for better understanding these changes are the records held by herbaria. Using these records to assess the responses of different groups of species across the entire flora of California, we sought to quantify the magnitude of species elevational shifts, to measure differences in shifts among functional groups and between native and introduced species, and to evaluate whether these shifts were related to the conservation of thermal niches.

Location California.

Methods To characterize these shifts in California, we used 681,609 georeferenced herbarium records to estimate mean shifts in elevational and climatic space of 4426 plant taxa. We developed and employed a statistical method to robustly analyse the data represented in these records.

Results We found that 15% of all taxa in California have ranges that have shifted upward over the past century. There are significant differences between range shifts of taxa with different naturalization statuses: 12% of endemic taxa show significant upward range shifts, while a greater proportion (27%) of introduced taxa have shifted upward. We found significant differences between the proportion of significant range shifts across taxa with different seed sizes, but did not find evidence for differences in shift based on life-form (annual versus perennial, herbaceous versus woody).

Main conclusions Our analyses suggest that introduced species have disproportionately expanded their ranges upward in elevation over the past century when compared with native species. While these shifts in introduced species may not be exclusively driven by climate, they highlight the importance of considering the interacting factors of climate-driven range shifts and invasion to understand how floras are responding in the face of anthropogenic change.

Keywords
Climate change, Consortium of California Herbaria, endemism, invasive species, Markov chain Monte Carlo, sample bias correction, seed size.

INTRODUCTION

Recent climatic warming across the planet, which has been occurring more rapidly than during any other period in the past 65 million years (Diffenbaugh & Field, 2013), has led to shifts in species distributions. While a majority of studies reporting shifts document movement upward in elevation and poleward (Parmesan & Yohe, 2003; Chen *et al.*, 2011), recent findings suggest that range shifts often span multiple dimensions of niche space (Lenoir & Svenning, 2015). These modern shifts are

not entirely unexpected: late Pleistocene pollen records suggest that ranges of plant species have shifted repeatedly over time, tracking their temperature optima (Huntley & Webb, 1989; Jackson & Overpeck, 2000). However, it is not clear whether past rates of species movement will keep pace with the current rate of warming (Loarie *et al.*, 2009); the few studies done thus far suggest that biotic responses are lagging behind contemporary climatic shifts (Bertrand *et al.*, 2011; Devictor *et al.*, 2012). The pace of recent changes also poses a challenge to our process-level understanding of how species distributions shift in time and space. Hypothesized mechanisms mediating shifts in species distributions due to climate change are generally based on some form of niche conservatism. Evidence for niche conservatism, recent or historical, can be based on observations of leading edge expansion, trailing edge contraction, abundance shifts within a range or any combination of these that allow a species to track changes in climate (Glennon *et al.*, 2014).

While such recent distributional shifts have been observed in numerous floras around the world, the geographical distribution of studies has not been uniform – for example, we still know little about the extent of such shifts in much of the tropics (Lenoir & Svenning, 2015). Additionally, only a few studies have considered whether these changing distributions follow shifts in temperature versus shifts in other climate variables (Crimmins *et al.*, 2011), the extent to which range shifts are mediated by functional traits (Angert *et al.*, 2011) or the consistency of these changes across diverse ecoregions (Munson *et al.*, 2011). Understanding these factors is important for maintaining biodiversity, as the responses of species to climate change have the potential to influence their vulnerability to extinction (Thomas *et al.*, 2004; Lenoir & Svenning, 2015).

In addition to these rapid climatic shifts, present-day floras are also in flux due to the introduction of non-native species. Naturalized invasive species are important (if often undesired) constituents of many floras, and have manifest impacts on the success of the native flora. Although shifts of invasive species per se may not be directly linked to warming, it should be recognized that interactions between invasive and native species might condition the response of the latter to climate. Furthermore, these two factors, climate and the range expansions of introduced species, may interact: if changes in climate expand the potential niche space for several co-occurring species, then those species best able to move from their current realized niche and into this newly expanded niche space may preclude subsequent colonizations by taxa that shift more slowly. Alternatively, the converse could occur, with early colonizers (either native or invasive) facilitating subsequent colonization of harsher high-elevation sites (Cavieres *et al.*, 2005). Unfortunately, these types of interactions are difficult to predict; for example, even the extent to which species in their exotic ranges share the same realized niches as they do in their native ranges is not yet clear (Guisan *et al.*, 2014). In some cases, it may be that the realized niches of introduced species are constrained compared with the realized niches in their native ranges since these species are not yet in equilibrium with the new environment. Thus, empirical comparisons of shifts in introduced compared with native

species are a critical part of understanding how a given flora will respond to a changing environment.

Within this broad framework, the differential changes in the distribution of any given species may be mediated, *inter alia*, by: (1) the length of time a species has been present (i.e. native versus recently introduced), (2) the phenotype or set of traits that shapes the response of a given species to perturbations (Westoby & Wright, 2006), or (3) the speed of environmental change or the climate change velocity that is currently being experienced by a species (Mooney & Dunn, 1970; Pinsky *et al.*, 2013). These non-exclusive hypotheses lead to a set of predictions. Shifts driven primarily by expansion into an introduced range would occur more often than expected by chance, regardless of the functional traits that may be expected to mediate these expansions (e.g. small seed size). If range shifts are mediated primarily by some set of plant functional traits, then more vagile life-forms (e.g. grasses, annual plants), plants with shorter life spans or plants with higher dispersal ability should show larger shifts (Moorcroft *et al.*, 2006; Angert *et al.*, 2011), regardless of their native status. Finally, if local climate change velocity has a large influence on range shifts, then more pronounced shifts should primarily be observed where the magnitude of local climate change is large (Pinsky *et al.*, 2013). Each of these conceptual models have previously been employed to interpret species shifts in response to warming generally (Lenoir *et al.*, 2008; Willis *et al.*, 2008; Doak & Morris, 2010; Angert *et al.*, 2011; Chen *et al.*, 2011), but the relative importance of these factors, particularly across a large and diverse set of taxa, has remained ambiguous.

One of the reasons why it is difficult to conduct such all-encompassing analyses is that data sufficient to assess the impact of these rapid changes on floral distributions are difficult to come by—high-quality, detailed observational records are often sparse and short-term. Thus, many workers have recognized the value of using historical records in climate change studies (Parmesan, 2006), despite many potential pitfalls (Tingley & Beissinger, 2009). Herbarium collections, in particular, have been identified as especially rich datasets due to advantages in: (1) the diversity of taxa included, (2) the time span covered, which includes recent changes in climate, and (3) the rapidly increasing number of records that are digitally accessible. It is therefore not surprising that herbarium specimens are increasingly being used as major inputs into species distribution models (Feeley, 2012; Enquist *et al.*, 2013). Despite their utility, fundamental assumptions made with these types of data often remain unvalidated and examinations of potential biases have rarely been performed.

To better understand how climate and invasion are affecting the distribution of a diverse flora, we sought to quantify the impact of 20th-century climate change on the elevational distribution of the entire flora of California, a floristically rich region with diverse climates, topographies, and soils. Specifically, we used historical herbarium records to examine changes in the mean location of species relative abundances across elevational gradients over time. We tested the relationship between these shifts and the floristic origins (native versus intro-

duced), life-history traits (e.g. annual/perennial, seed size), and realized climate niches of each in relation to a null model. Aware of the complex challenges inherent in using herbarium data for this type of analysis, we first identify and quantify potential confounding factors, including collection bias, land-use change, and taxonomic uncertainty, that could otherwise complicate the interpretation of results from this dataset. We then address three questions in relation to species shifts in elevation across this large set of taxa.

1. What are the magnitudes of shifts in species mean elevation over this time period?

2. How are these shifts related to phenotypic or functional traits, climatic niches of species or floristic origins (native versus introduced)?

3. Are the observed shifts consistent with the conservation of thermal or precipitation niches?

METHODS

Data sources

To assess distributional changes across the California flora, as defined in the second edition of *The Jepson Manual* (TJM2; Baldwin & Goldman, 2012), we used the definitive source of historical information on these species, herbaria records of occurrence (Consortium of California Herbaria, 2010) (Fig. 1 and Fig. S1 in Supporting Information). Specimen data were downloaded from the Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/) on 18 June 2012. These data are the result of extraordinary efforts by thousands of collectors, taxonomists, and herbaria staff throughout California over more than a century; in recent years, the Consortium of California Herbaria has done much to make these data coherent and broadly available. The interests, activities, and priorities of these workers have shaped the data over time and could thus bias the distribution of specimen records in ways that could confound analyses such as ours (see Appendix S1 for further discussion of this challenge and approaches that can be taken to mitigate it).

While these biases could affect apparent range shifts over time, we argue that these biases are likely to be greater for narrower, more taxon-specific analyses. Here we focus on the entire flora and on broad plant groupings, and by comparing all shifts to null models, we are able to report trends that are statistically robust despite the intrinsic biases in the underlying dataset.

Below, we highlight our efforts to account for three potential sources of bias that we took particular care to address: taxonomic integrity, land-use change, and sample selection bias (with additional discussion in Appendix S1). First, to address the issue of taxonomic integrity, all taxon observations were resolved to one of the 8569 species recognized by TJM2 (Baldwin & Goldman, 2012; see the detailed discussion in Methods S4). Second, to address the impact of land-use change, we excluded different sets of species based on the likelihood that their ranges included significant shifts in land use over our study period and assessed the effect of these choices on our conclu-

sions. We concluded that land-use change is common enough in these data over our study period to warrant concern. Therefore, species with substantial changes in their distribution on lands now categorized as urban and agricultural (nearly 1000 species, or roughly 20% of the dataset) were flagged and removed prior to further analysis. We present here only shifts in elevation calculated as residuals after any changes related to land use have been accounted for (see a detailed discussion of these procedures in Methods S6; see also Fig. S6).

Testing for the presence of sample selection bias across an aggregated herbarium dataset is considered to be one of the most difficult issues confronted by researchers creating species range estimates (Elith *et al.*, 2006). To address this source of bias, we developed, validated (Wolf *et al.*, 2011), and employ here a robust statistical methodology to detect shifts in distributions over time. We also tested for bias in herbarium data introduced by collector behaviour—specifically collectors seeking ever-higher-elevation exemplars of particular taxa of interest (see Methods S5). We conclude that such collector behaviour does not confound our study.

For this analysis, we used specimens collected between 1895 and 2009 inclusive. We only included records for which geographical coordinates were available ($n = 681,609$). These coordinates exhibited varying levels of precision: we argue that our approach, which focuses on large groupings of species as opposed to single taxa, is a conservative approach to extracting trends. Our statistical method tests for changes in the mean of a distribution between two time periods, where the distribution of an individual taxon is conditioned on the distribution of all taxa collected in the same geographical range (see 'Statistical methods', Methods S7 and Wolf *et al.*, 2011). We chose 1970 to separate an early period (1895–1970) and a late period (1971–2009; Fig. S2) to be close to the median accession. All available data were used to estimate the background sampling intensity of all species, but mean elevation and climate niches were only estimated for taxa with more than 10 samples in each time period, yielding estimates of shifts for 4426 taxa. We conducted an extensive sensitivity study (Wolf *et al.*, 2011) and found that this number of samples (i.e. 10 per time period), given an environmental gradient discretized into four bins, was sufficient to minimize Type 1 errors (false positive) for change detection in the face of sample selection biases ranging from none to severe. In this study, we also examined shifts under more stringent sampling requirements for the case where at least 25 or 50 samples per species were present in each time period (results of this analysis are in Table S1).

Many specimen records included elevation data, but these data were often problematic, being either wildly inaccurate (Fig. S3a), different from expected based on latitude and longitude (Fig. S3b), or had values in exact multiples of 100 ft (Fig. S3c). For these reasons, 30-arcsec elevation data were assigned on the basis of geographical coordinates from the PRISM digital elevation model (DEM; described below). Using elevations assigned from the DEM is a conservative approach that potentially gives up accuracy for individual accessions in exchange for consistency across the entire dataset. Further, we
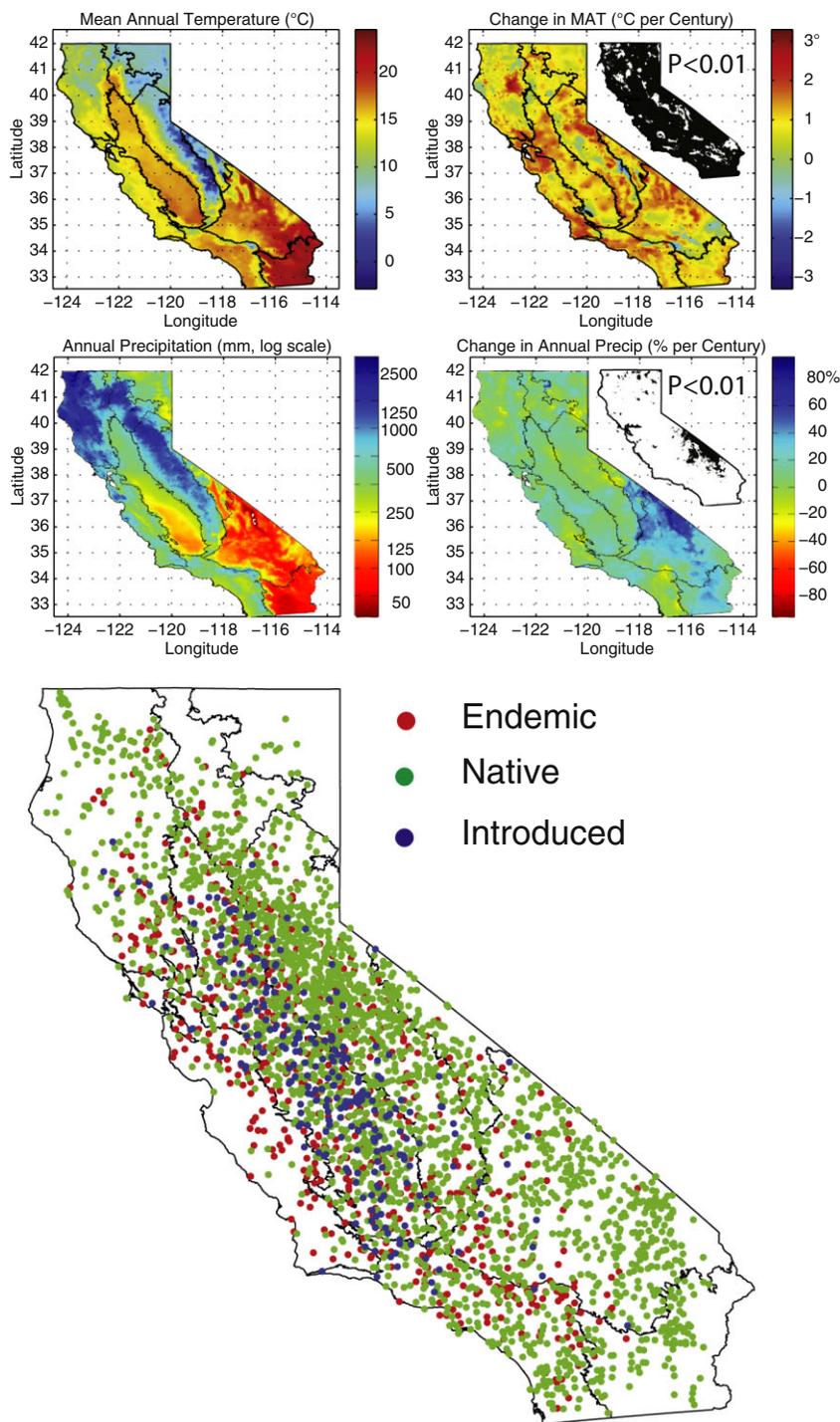
Figure 1 Mean climate in California at 2.5′ resolution, and its linear trends over the study period (1895–2009): (a) mean annual temperature; (b) trend in mean annual temperature; (c) annual precipitation; (d) trend in mean annual precipitation. Lower panels show annual precipitation. Insets to the trends show areas (in black) where the trend is significant ($\alpha = 0.01$). (e) Geographical mean of each taxon in the study, according to its endemic, native non-endemic or introduced status. The colour version of the figure is available in the online version only.

are interested here in shifts across broad groups of species, and acknowledge that this approach would be less appropriate if we were primarily interested in detecting shifts with high confidence for individual species.

Climate and elevation data were downloaded from the PRISM Climate Group, Oregon State University (http://prism.oregonstate.edu) in July 2010. Monthly precipitation and temperature grids at 2.5-arcmin resolution (Di Luzio *et al.*, 2008) were recalculated into annual sums, means, and other derived values, and associated with each herbarium record for

the year of its collection. This difference in grid cell size between elevation (0.5′) and climate data (2.5′) means that we are better able to detect small-scale shifts in elevation than in climate space. These climate grids covered the full extent of our accession records (1895–2009). The differences between early and late time periods in mean annual temperature (MAT) and annual precipitation (PPT) across the state are shown in Fig. 1. Climatic variables for calculating aridity represent the mean for each taxon (see below) for that variable using the PRISM data source (Di Luzio *et al.*, 2008). To allow qualitative characterization of

aridity across environments (and mindful of biases in this equation; Dobrowski *et al.*, 2011; Stephenson & Das, 2011) we used Holdridge's classification (Holdridge, 1947) of aridity as PET/PPT, where PET is potential evapotranspiration calculated using Thornthwaite's equation (Thornthwaite, 1948; Bonan, 2008).

Species categorizations—including naturalization status (invasive, non-endemic native or California endemic) and lifeform (woody, herbaceous, annual, perennial)—were collated from the Calflora species attribute table (The Calflora Database, 2009). Plant family and national distribution were gathered from the USDA PLANTS database (USDA NRCS, 2011). Seed sizes were obtained with permission from the Kew Seed Information Database (Royal Botanic Gardens Kew, 2008). While seed size is an imperfect proxy for dispersal ability, particularly to the extent that herbivores aid in dispersal, we believe it is a reasonable approximation on empirical (Flores-Moreno *et al.*, 2013) and theoretical grounds (Venable & Brown, 1988).

Statistical methods

We developed and applied stringent statistical procedures to detect change in geographical, climatic, and edaphic distribution for each species between two time periods (1895–1970 and 1971–2009), taking into account the potential presence of sample selection bias (Wolf *et al.*, 2011). For each of 4426 plant taxa, along multiple axes of geographical and climatic space, we used a Monte Carlo procedure to estimate distributions of relative abundance for each taxon, which we used in turn to calculate mean position along an elevational gradient, niche breadth (that is, the range of climatic or edaphic parameters encompassed within the range of a given species), and a probability distribution for each shift. Because the occurrence data cannot be used to estimate distributions of absolute abundance, shifts unfortunately cannot be interpreted in terms of expansion or contraction at range margins, but only as shifts within a given range. The estimation procedure follows Wolf *et al.* (2011), which describes in detail how to estimate the mean, variance, and estimated shift between sampling periods of a target species along an environmental gradient or geographical range. A concise overview of the approach is described in Methods S7.

We additionally made use of a null model in which elevation shifts were recalculated for identical data, albeit with the year of sampling shuffled. The null model provides an estimate of the statistical expectation for the flora (all taxa), for example the mean elevational shift or the fraction of taxa that would experience a significant shift, if there were no temporal pattern in the collection data (see Lenoir *et al.*, 2010, for a similar approach). Thus, the shuffled data represent a means to determine whether the patterns we observe could be an artefact of biases intrinsic to this dataset and that are not otherwise accounted for in our statistical estimation procedure. We are therefore quite confident that the shifts we detect after conducting Markov chain Monte Carlo (MCMC) significance tests, subtracting variation explained by covariates, and comparing the results to a null model are not artefactual or the result of collector biases.

RESULTS

Shifts in the mean elevation of native and introduced species ranges

We find evidence that around 15% of Californian plant taxa have ranges that increased in mean elevation over the past century (537 of 3479 species, including invasive, native, endemic and unclassified; null model, 234 of 3479 (6.7%); see also Data S1 and Fig. 2). This overall number is comparable to those upward shifts for both categories of non-introduced species: native species (361 of 2467, 14.6%, average change 9 m; null model, 171 of 2467, 7%) and endemic species (83 of 688, 12%, 3.9 m; null model 37 of 688, 5%) also exhibit significant upward shifts. However, by far the greatest shifts in elevation are seen in species considered naturalized invasive species, among which 27% shifted upward (73 of 269; 76.2 m; null model, 19 of 269, 7%), while only 5% shifted downward (Fig. 2, Table S1). This tendency for species varying in endemic status to differentially shift in elevation is significant ($F = 15.88$, $P < 0.001$).

Relationships between functional types and elevational shifts

Within these broad classifications, we also considered some of the plant functional differences that could explain the differences observed between groups. In particular, we looked at the differences between annual and perennial plants and seed size. We found that the tendency for annual plants to shift upward (193 of 1138, 17%; null model, 88 of 1138, 7.7%) was slightly greater than for perennials, especially woody perennials (93 of 688, 13.5%; null model, 47 of 688, 6.8%; Table 1). Despite this trend, the effects of life-form (annual versus perennial, woody versus herbaceous) on the magnitude of elevation shift was not significant in analyses of variance ($F = 1.04$, $P = 0.35$).

In contrast, seed size had a comparably large effect on the shift in mean elevation (Table S1, Fig. 2). Species with small seeds (1000-wt < 0.1 g) have a much greater propensity to shift upward (35 of 150, 23%, 49.5 m; null model, 13 of 150, 8.7%), with decreasing tendency to shift upward for medium (0.1 g ≤ 1000-wt < 10 g) sized seeds (190 of 1084, 18%, 28.7 m; null model, 67 of 1084, 6.2%) or large (1000-wt ≥ 10 g) sized seeds (27 of 222, 12%, 12.81 m; null model, 13 of 222, 5.9%). Despite no significant differences in the distribution of seed sizes among groups of species of different endemic status ($\chi^2 = 1.5$, $P = 0.8$) or in the mean elevation shifts for each seed size group ($F = 1.46$, $P = 0.23$), when compared with native or introduced species of a given seed size, we observed that fewer endemic species shifted upward (Table 1, Fig. 2).

Shifts in species realized climatic niches

Species occupying different climatic zones experience slight variations in their propensity to shift, with species in mesic zones moving up (304 of 1848, 16.5%, 20.9 m; null model, 126 of 1848, 6.8%) in greater numbers than those in arid zones,
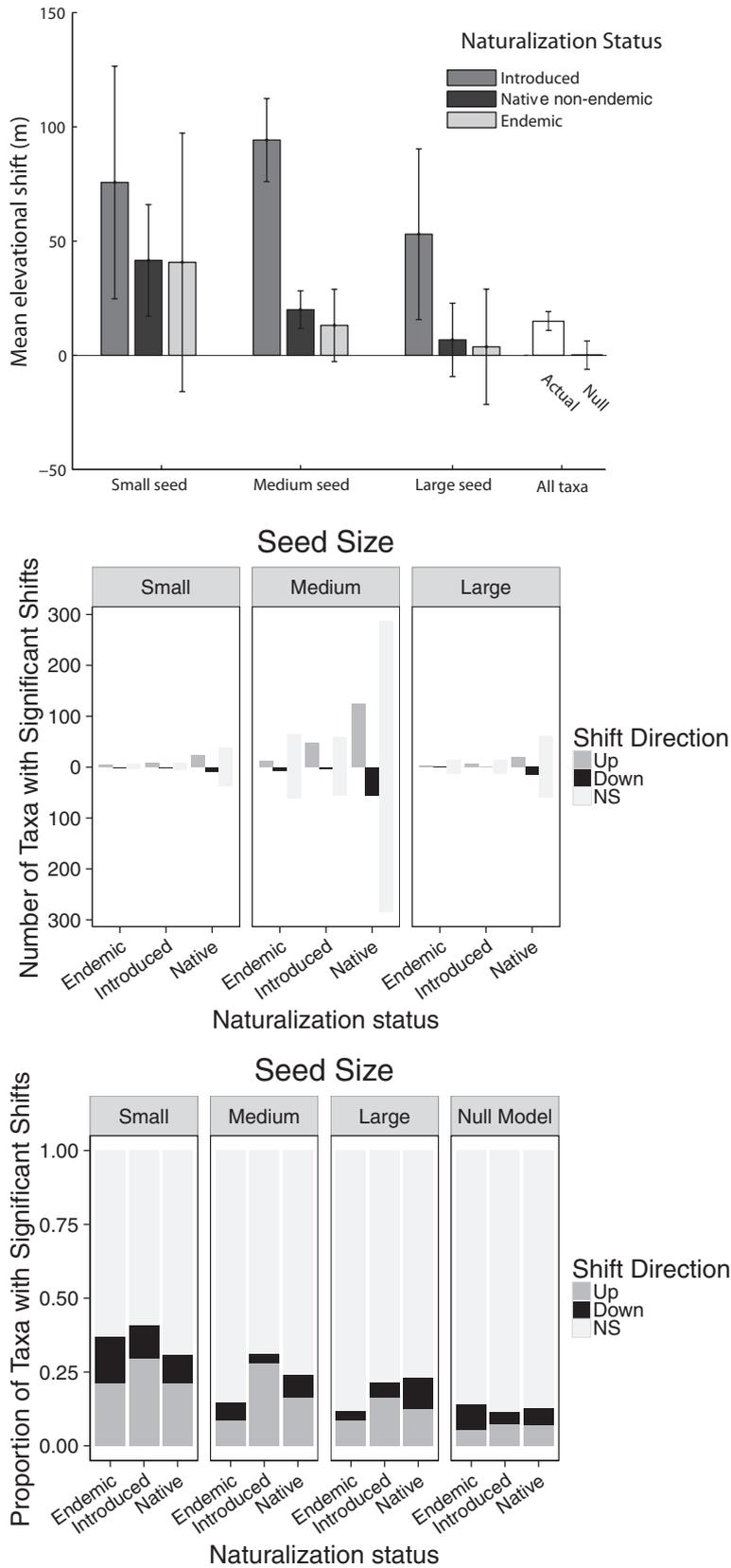
Figure 2 Shifts in elevation for species differing in seed size and naturalization status, relative to the entire flora, as well as a null model. Subpanels include: (a) mean elevational shifts for each plant functional type (PFT); (b) counts of each grouping moving significantly up or down, or not significantly moving ($\alpha = 0.01$); (c) proportion of each grouping moving significantly up or down, or not significantly moving ($\alpha = 0.01$), with reference to these same fractions for a null model.

Table 1 Number of significantly shifting taxa for different plant groupings. Not all taxa are defined for all plant groupings, and some taxa have multiple life-forms. Shifts for the same dataset but with the year shuffled are shown for comparison. Values are the number of taxa in each grouping; values in parentheses indicate the percentage of each grouping that exhibited significant shifts.

		Endemic status			Life-form			MAT niche breadth			Humid	Mesic	Arid
Observed	All	Introduced	Native	Endemic	Herb annual	Herb perennial	Woody perennial	σMAT < 1.5	1.5 < σMAT < 3	3 < σMAT	PET/PPT < 0.5	0.5 < PET/PPT < 2	PET/PPT > 2
Observed													
Number up (%)	537 (15.4)	73 (27.1)	361 (14.6)	83 (12.1)	193 (17.0)	249 (15.4)	93 (13.5)	81 (14.6)	245 (15.3)	211 (15.9)	175 (14.6)	304 (16.5)	58 (13.5)
Total no. of taxa	3479	269	2467	688	1138	1656	688	553	1598	1328	1201	1848	430
Number down (%)	299 (8.6)	14 (5.2)	215 (8.7)	66 (9.5)	101 (8.9)	127 (7.7)	64 (9.3)	71 (12.8)	141 (8.8)	87 (6.5)	102 (8.5)	151 (8.2)	46 (10.7)
Null (year shuffled)													
Number up (%)	234 (6.3)	19 (7.1)	171 (6.9)	37 (5.3)	88 (7.3)	106 (6.4)	47 (6.8)	28 (5.1)	127 (7.9)	79 (5.9)	74 (6.2)	126 (6.8)	34 (7.9)
Total no. of taxa	3479	269	2467	688	1138	1656	688	546	1598	1328	1201	1848	430
Number down (%)	215 (6.1)	10 (3.7)	146 (5.9)	58 (8.4)	67 (5.9)	100 (6.0)	41 (6.0)	35 (6.4)	118 (7.4)	61 (4.6)	81 (6.7)	114 (6.2)	20 (4.7)
Small-seeded													
Number up (%)	35 (23.3)	7 (30.4)	23 (21.1)	3 (20.0)	9 (15.0)	23 (28.8)	4 (22.2)	1 (8.3)	20 (29.0)	14 (20.3)	16 (23.5)	18 (25.4)	1 (9.1)
Total no. of taxa	150	23	109	15	60	80	18	12	69	69	68	71	11
Number down (%)	14 (9.3)	2 (8.7)	10 (9.2)	2 (13.3)	6 (10.0)	5 (6.3)	3 (16.7)	4 (33.3)	6 (8.7)	4 (5.8)	6 (8.8)	6 (8.5)	2 (18.2)
Medium-seeded													
Number up (%)	190 (17.5)	47 (28.1)	124 (16.5)	12 (8.2)	80 (19.4)	87 (16.4)	30 (16.7)	16 (13.2)	88 (18.5)	86 (17.6)	67 (17.8)	106 (17.7)	17 (15.6)
Total no. of taxa	1084	167	753	146	413	532	180	121	475	488	377	598	109
Number down (%)	71 (6.5)	4 (2.4)	57 (7.6)	8 (5.5)	21 (5.1)	28 (5.3)	18 (10.0)	9 (7.4)	33 (6.9)	29 (5.9)	27 (7.2)	35 (5.9)	9 (8.3)
Large-seeded													
Number up (%)	27 (12.2)	5 (15.2)	19 (12.2)	2 (6.7)	3 (11.5)	4 (6.5)	20 (13.0)	2 (6.1)	10 (9.2)	15 (18.8)	13 (17.1)	11 (8.9)	3 (13.6)
Total no. of taxa	222	33	156	30	26	62	154	33	109	80	76	124	22
Number down (%)	17 (7.7)	1 (3.0)	16 (10.3)	0 (0.0)	1 (3.8)	5 (8.1)	12 (7.8)	6 (18.2)	7 (6.4)	4 (5.0)	4 (5.3)	11 (8.9)	2 (9.1)

σMAT, variance in mean annual temperature across a species' range; PET/PPT, index of aridity based on potential evapotranspiration divided by annual precipitation.

Table 2 Relationship between the elevational shift of species groupings and associated shifts in mean annual temperature (dMAT) and precipitation (dPPT). Elevational shifts are classified as up (UP), down (DN), no significant shift (NS), and all shift types (All). We also report the standard error of the mean (SEM) for the changes in MAT and PPT. *P*-values quantify the significance of the MAT or PPT shift for each grouping between the two time periods assessed in this study. Finally, we report the counts of taxa exhibiting a change in MAT or PPT given a particular elevational shift.

Change type	Grouping	Elev. shift	Mean dMAT (°C)	SEM	*P*-value	MAT increase	MAT decrease	NS change	Sum
MAT	All	UP	−0.7	0.06	<0.001	53	152	334	539
	All	DN	1.23	0.08	<0.001	124	3	170	297
	All	NS	0.27	0.03	<0.001	444	135	2057	2636
	All	All	0.2	0.03	<0.001	621	290	2561	3472
	Endemic	UP	−0.84	0.17	<0.001	11	32	40	83
	Endemic	DN	0.75	0.14	<0.001	21	1	44	66
	Endemic	NS	0.22	0.05	<0.001	85	25	424	534
	Endemic	All	0.14	0.05	<0.001	117	58	508	683
	Native	UP	−0.77	0.07	<0.001	23	99	239	361
	Native	DN	1.36	0.09	<0.001	91	2	122	215
	Native	NS	0.25	0.03	<0.001	300	103	1486	1889
	Native	All	0.2	0.03	<0.001	414	204	1847	2465
	Introduced	UP	−0.42	0.18	<0.001	12	19	43	74
	Introduced	DN	1.43	0.41	<0.001	9	0	4	13
	Introduced	NS	0.56	0.1	<0.001	51	6	125	182
	Introduced	All	0.33	0.09	<0.001	72	25	172	269

Change type	Grouping	Elev. shift	Mean dPPT (mm)	SEM	*P*-value	PPT increase	PPT decrease	NS change	Sum
PPT	All	UP	76.55	9.61	<0.001	132	40	367	539
	All	DN	21.24	13.54	0.326	57	39	201	297
	All	NS	20.1	4.46	0.191	454	234	1948	2636
	All	All	28.96	3.89	<0.001	643	313	2516	3472
	Endemic	UP	66.59	25.34	0.022	23	7	53	83
	Endemic	DN	−3.99	27.08	0.245	15	9	42	66
	Endemic	NS	33.5	9.9	0.041	98	53	383	534
	Endemic	All	33.9	8.76	<0.001	136	69	478	683
	Native	UP	75.3	11.67	<0.001	89	27	245	361
	Native	DN	28.43	16.25	0.209	41	28	146	215
	Native	NS	17.33	5.26	0.356	327	161	1401	1889
	Native	All	26.79	4.62	<0.001	457	216	1792	2465
	Introduced	UP	88.29	26.48	0.003	16	4	54	74
	Introduced	DN	40.9	59.74	0.332	1	2	10	13
	Introduced	NS	5.35	16.79	0.29	22	18	142	182
	Introduced	All	29.89	13.98	<0.001	39	24	206	269

which overall exhibited a mean downward shift (58 of 430 shifting up, 13.5%, −25.1 m mean elevation change; null model, 34 of 430, 7.9%; Table 1).

While 15% of the taxa exhibit a significant increase in the mean of their elevational distribution, 17.9% experienced significant increases in MAT across their realized niche—averaging 0.2 °C between periods (Table 2). This includes the realized niche of 621 taxa becoming significantly warmer on average and that of 290 taxa becoming significantly cooler on average across their range. However, this increase was roughly equivalent to the null model (0.18 °C, 620 of 3472 increasing in MAT), suggesting that between our study periods the MAT for plants across their ranges *in aggregate* changed little. This aggregate trend occurs despite many individual examples of species that had elevational shifts of over several hundred metres (Data S1).

In addition to changes in MAT, the flora also experienced substantial changes in PPT: 18.5% of the flora experienced increases in PPT, averaging 29 mm between time periods (Table 2). Compared with elevation or MAT, there is much greater variance in the changes in PPT experienced by species, as is true with changes in PPT across the state itself (Figs 1 & S7).

DISCUSSION

Species in the Californian flora encompass a spectrum of geographical range sizes. This means that significant shifts in elevation may nevertheless be small in absolute value, and conversely large estimated shifts in elevation may be statistically insignificant. In addition, within a given grouping of species (e.g. invasive, native, annual, perennial), there are many individual

species that could, at the species level, exhibit significant shifts up or down in elevation. As we are interested in aggregate trends, and believe those to be the most robust considering the data, we focus on them here. However, we do include calculated shifts for individual species in Data S1.

We observed significant elevational shifts (both uphill and downhill) in comparatively fewer plant species (24%) than have been observed in other taxonomic groups in California, such as birds (84%; Tingley *et al.*, 2012) and mammals (*c.* 50%, Moritz *et al.*, 2008) in the Sierra Nevada. This fraction is, however, in agreement with significant shifts in the optimum elevation of 26% (41 of 171) of plant species in Europe (Lenoir *et al.*, 2008). Similarly, the average shift for all plant groups in this study was approximately 13 m upward in elevation over the whole period, which is less than the 127–1567 m documented in range boundary shifts in birds and *c.* 500 m in mammals over a similar time window (Moritz *et al.*, 2008; Tingley *et al.*, 2012), but our results come from a much broader geographical region that did not experience local climate changes as rapidly (*c.* 1 °C on average, as opposed to *c.* 3 °C in Moritz *et al.*, 2008) and represent much less vagile life-forms. Given increases in MAT of the order of 1 °C per century (Figs 1 & S7), our findings support the observations from many other studies in California (Kelly & Goulden, 2008; Moritz *et al.*, 2008; Tingley *et al.*, 2009, 2012), implying that numerous species have shifted their ranges upslope. These cross-kingdom differences in significant shifts and the magnitude of those shifts align well with expectations that plants should be less able than other taxa to shift ranges in response to changes in climate (e.g. Parmesan, 2006).

We note that the upward shift of naturalized invasive species (76.2 m) is nearly five times greater than for the flora overall (14.9 m). We suspect that these elevation shifts may not be due to climate warming but instead to the expansion of non-native species into new environments (Pauchard *et al.*, 2009), as these populations were likely not in equilibrium by the end of the early period in 1970. Those introduced species that did not significantly shift in elevation experienced a larger increase in MAT across their ranges (0.56 °C) than native or endemic species that have not shifted. These results evince a section of the flora that is still actively in flux. We speculate that even as introduced species expand into new habitats across the state they are chasing a moving target; as they seek their preferred climatic niches, changes in climate will effectively increase the extent and rate of their spread. This conclusion is in agreement with recent work suggesting that the invasion of higher-elevation ecosystems by non-native plant species will increase with climatic warming (Becker *et al.*, 2005; Pauchard *et al.*, 2009).

The broad scope of our analysis allows us to document a multiplicity of changes taking place across California's diverse flora; several of the diverse responses we observed warrant particular attention. It is notable that nearly three-quarters of species did not exhibit a significant shift in mean temperature over their realized niches, but of those that did have significantly different temperature means (911 taxa), 68% (621 taxa) experienced warmer temperatures (Table 2). Some of these species may be vulnerable to higher mortality rates due to climate stress,

loss of forest and shifts in dominant plant species, among other consequences (e.g. van Mantgem & Stephenson, 2007; Kelly & Goulden, 2008). The overall tendency in the flora is for more species to shift upward, instead of downward, in elevation. While we hypothesized that shorter-lived life-forms would have a greater propensity to change distribution under climatic forcing (Lenoir *et al.*, 2008), we found that the slightly higher rates of shift for annual grasses, as compared with woody perennials, were within the variation suggested by the null model.

The findings of an upward shift in the flora and patterns of shifts among different plant types were robust to our various efforts to control for confounding variation from the dataset (Table S1). Applications of methods to address intrinsic biases all acted to lower the mean elevational shift, with one exception: restricting the minimum threshold in each time period to larger sample sizes resulted in larger mean upward elevational shifts. This indicates that even though the effects of sampling and land use affected the distribution of specimen collections, the temporal effects of climate-associated elevation shifts were still detectable across the flora. The sorting between plant groupings is generally maintained for all bias removal efforts (Table S1), with minor exceptions. In addition to sources of bias that could be controlled for, we also tested for bias in collector behaviour that would have been directly at odds with the goal of examining elevation shifts. That is, we tested whether collectors systematically sought taxa that were consistently at the margins of the previously sampled range, but found no evidence for this phenomenon even in locations where there had been collection efforts explicitly with this intent (Appendix S1, Methods S5).

Our general observation is that taxa that shift upward generally experience a decrease in MAT and also have a tendency to experience increases in precipitation (Table 2, Fig. 3). Species that do not significantly shift upward (or shift downward) tend to have experienced increases in MAT. An exception to this finding is among the species found in arid climates, which tended to shift downward (−25.1 m) with little change in temperature but some slight gain in precipitation (Fig. 3). This tendency is consistent with the trend for these driest areas to be the only regions in California to experience significant increases in precipitation (Figs 1 & S5B), and is perhaps worth investigating further.

We note that the mean elevation shifts observed here are associated with climate warming in the direction expected by species physiology, but note that this observation falls short of demonstrating causality. Indeed, the flora is indisputably subject to a variety of pressures including changing land use, fire regime, invasive species pressures, air pollution levels, climate extremes and CO_2 levels, among other things. All of these factors undoubtedly shape the response of species to changes in mean climate, which is itself changing in geographically heterogeneous ways. Careful demographic observation of species across their ranges (e.g. Doak & Morris, 2010) can help to identify the diversity of mechanisms at work (Schwilk & Keeley, 2012). Definitive causal attribution of the species elevational shifts we observe to climatic warming is not feasible with
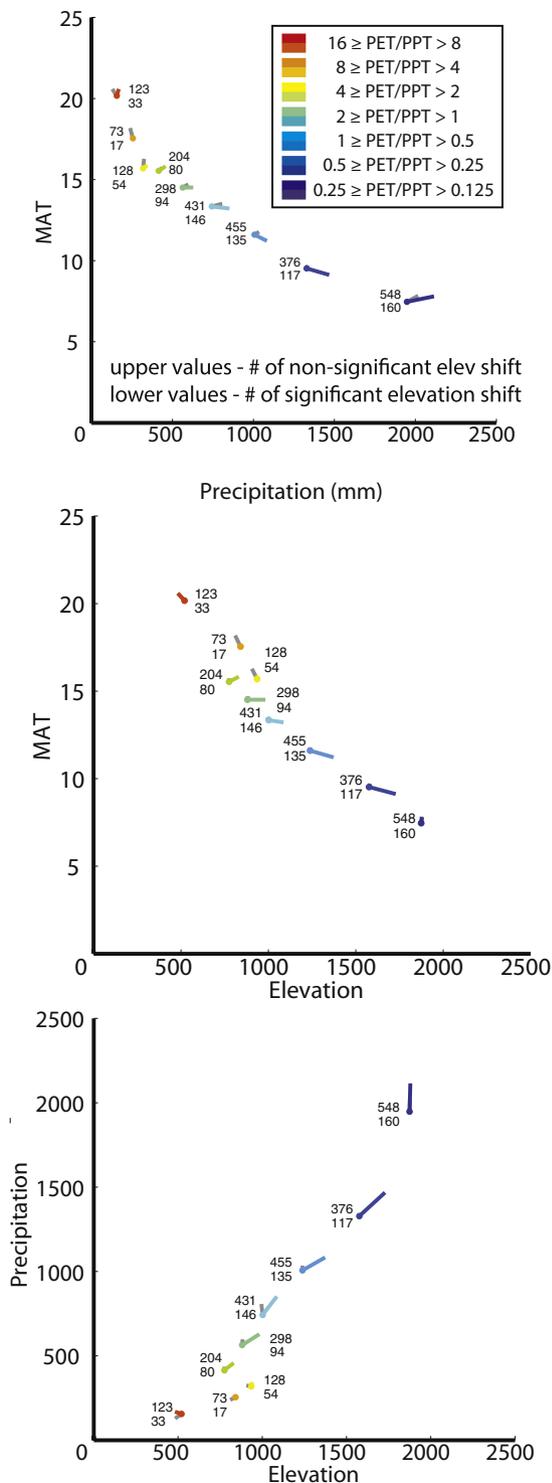
Figure 3 Shifts in elevation, mean annual temperature (MAT, °C), and annual precipitation (mm year⁻¹) for species spanning a gradient of climatic aridity PET/PPT (potential evapotranspiration/annual precipitation) based on Holdridge's (1947) life zone classification. Coloured arrows are the mean shift of species with significant elevational shift (legend in top panel); gray arrows are mean shifts of species without a significant elevational shift (the colour version of the figure is available in the online version only). Circles indicate the position in the earlier time period.

currently available data, but few other explanations are consistent with what we observe.

The findings presented here could have significant bearing on future conservation decisions, especially in light of projections of large decreases in the ranges of endemic species in this region (Loarie *et al.*, 2008). Endemic species in California have tended to move upward little in comparison with introduced or even with non-endemic native species (Fig. 2). Combined with the much more extensive movement of introduced species across the state, endemic species may face not just the ongoing challenge presented by a shifting climate, but two compounding challenges: climate and competition from introduced species. The diversity and rapidity of changes we describe across a large component of California's regional flora highlight the urgent need for continued research and conservation efforts.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 The use of herbarium data for studies of plant ranges.

Figure S1 Geographical and climatic distribution of species across California, and their relationships between mean annual temperature, annual precipitation, and elevation.

Figure S2 Collection intensity over time, 1895–2009.

Figure S3 Comparison of elevation from originally reported data for each specimen and from a DEM at the coordinates reported for each specimen.

Figure S4 Graphical explanation of estimation method.

Figure S5 Shift in elevation relative to shifts in latitude, longitude, and occupancy of lands now considered urban or agricultural.

Figure S6 Sampling intensity across an elevation gradient in each of two time periods, in three different locales.

Figure S7 Climate trends versus climate means in California from 1895–2009 based on PRISM reconstructions.

Table S1 Marginal impact of each bias correction method on the mean elevational shift, computed for different plant functional types.

Methods S4 Taxonomic categorization methods.

Methods S5 Test of collector tendency to seek higher-elevation specimens.

Methods S6 Addressing land-use change biases in Consortium of California Herbaria data.

Methods S7 Statistical methodology for estimating range shifts.

Data S1 Estimated shifts and other statistics for individual taxa.

BIOSKETCH

Adam Wolf earned a BS and MSc at the University of California, Davis, conducting his thesis research on environmental change in Central Asia. He went on to live in Moscow and St Petersburg as a US State Department Foreign Language and Area Studies fellow before studying for his PhD at Stanford under the mentorship of Joe Berry. His most recent academic appointment was an Associate Research Scholar at Princeton in the Steve Pacala Lab. At the time of this publication he has left academia to become CEO of Arable Labs, Inc (http://www.arable.com).

Statement of authorship: A.W. collated and prepared the data, developed methodologies to analyse the data, analysed the data, prepared figures and wrote the initial drafts of the manuscript; N.B.Z. contributed to data analysis and figure creation and led later revisions to the manuscript; W.R.L.A. and J.C. assembled the authors to develop the study; J.C. conceived the study; and all authors contributed substantially to conceptualizing the study and revising the paper.

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