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Impacts of a millennium drought on butterfly faunal dynamics

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21 **Abstract:**

22 Climate change is challenging plants and animals not only with increasing temperatures, but also
23 with shortened intervals between extreme weather events. Relatively little is known about
24 diverse assemblages of organisms responding to extreme weather, and even less is known about
25 landscape and life history properties that might mitigate effects of extreme weather. We find that
26 northern California butterflies were impacted by a millennium-scale drought differentially at low
27 and high elevations. At low elevations, phenological shifts facilitated persistence and even
28 recovery during drought, while at higher elevations a shortened flight season was associated with
29 decreases in species richness. Phenological and faunal dynamics are predicted by temperature
30 and precipitation, thus advancing the possibility of understanding and forecasting biological
31 responses to extreme weather.

32
33 **Main text:**

34 Extreme weather events have occurred with increasing severity and frequency in recent decades,
35 a trend that has been linked to anthropogenic climate change and shifts in atmospheric
36 circulation¹. Human societies are vulnerable to disruption by weather phenomena that include
37 hurricanes and heat waves, and these events add to and interact with other climate change
38 effects². Natural systems of plants and animals have been studied intensively from the
39 perspective of shifting average climatic conditions^{3,4}, but we know less about the impacts of
40 either elevated variation or extreme events on wild organisms^{5,6}. Here we take advantage of
41 decades of data on 163 butterfly species across an elevational gradient in Northern California
42 (Fig. 1a) to address knowledge gaps within the context of a severe, millennium-scale drought
43 that impacted the region from 2011 to 2015⁷. Specifically, we asked the following: 1) does an

44 extraordinary, multi-year drought elicit a faunal response that is extreme relative to faunal
45 behavior in previous dry years? 2) Are impacts on the fauna consistent or divergent across
46 elevations? A theoretical expectation is that organisms living in more heterogeneous
47 environments should be more resilient to extremes of temporal variation⁸. We predicted that
48 butterflies at montane sites would be robust relative to populations at lower elevations in
49 landscapes that are both less spatially variable and already impacted by a history of human
50 activity. 3) Finally, we asked if population-level responses to drought are mediated by
51 phenological shifts. Species that are able to begin activity earlier in the spring might reach
52 higher population densities⁹, potentially offsetting detrimental drought effects. Another
53 possibility is that ectotherms exposed to longer growing seasons could fall into a developmental
54 trap by which extra generations fail because of insufficient time¹⁰.

55 Investigations of butterflies at our focal sites have reported that a majority of populations
56 at the lowest elevations have been in decline since at least the mid-1990s¹¹, which has been
57 attributed to changes in land use and warming temperatures¹². Populations at higher elevations,
58 in contrast, have shown relatively less directional change over time, with the exception of a
59 decline in more dispersive, disturbance-associated species that rely on demographic connections
60 with lower-elevation source populations¹³. Previous analyses of abiotic effects, prior to the
61 2011-2015 drought, have noted responses to weather that were heterogeneous and idiosyncratic
62 among sites and species^{14,15}. In contrast to the previously-documented heterogeneity in
63 population response, we find here that the recent, extreme drought years resulted in a number of
64 faunal responses that were consistent across sites and elevational subsets of sites (montane
65 versus valley sites).

66

67 **Results**

68 A prolonged and consistent shift towards earlier spring flights can be seen in Fig. 1b. While the
69 shift in phenology is evident across elevations, the dynamics of the flight window diverge later in
70 the season: at higher elevations, the date of last flight shifted to an earlier time during the
71 drought, while at lower elevations the last flight dates from 2011 to 2015 are closer to the long-
72 term average (Fig. 1c). In other words, the total flight window expanded at lower elevations,
73 while in the mountains the flight window shifted and compressed towards the start of the season,
74 a change that is reflected in fewer overall flight days at higher sites (Fig. 1d).

75 Along with the recent reduction in the average number of days that butterflies were
76 observed flying at higher elevations during the drought years, there have been fewer butterfly
77 species observed per year at the same sites (Figs. 2a – 2e). In some cases, the millennium
78 drought was associated with a discrete downturn (e.g., Figs. 2b and 2c), while at other montane
79 sites the recent drought years contributed to ongoing, negative trends (Figs. 2d and 2e). A
80 downward trend in species richness is less evident at the highest site (CP, Fig. 2a), which
81 previous analyses have found to be receiving immigrants from lower elevations as populations
82 shift upslope in warmer years¹³. In a dramatic reversal of fortunes, the lowest elevation sites
83 during the millennium drought experienced some of their most productive years in nearly two
84 decades, as reflected both in numbers of species (Figs. 2g – 2j) and numbers of individuals
85 observed (Figs. 2l – 2o). Results shown in Fig. 2 are for simple richness (the number of species
86 observed per year). We repeated the analyses using alpha diversity Hill numbers that down
87 weight the importance of rare species (Fig. S1, S2), and found similar results for all sites except
88 for GC, where a long-term decline in the number of species becomes evident when rare, or
89 transient species have less influence.

90 Why did the low elevation sites apparently rebound during the drought years? Using the
91 lowest sites (RC, WS, NS and SM) and a span of years starting just before the millennium
92 drought, we discovered an effect of phenological plasticity. Specifically, species whose first
93 flight shifted to an earlier day were the species that became more abundant ($r = -0.50$, $P < 0.001$;
94 Fig. S3). Butterflies at the lowest elevations are almost entirely multivoltine, and an earlier start
95 for those species led to an extension of the flight season (Fig. 1d), and an increase in abundance
96 and richness (Fig. 2). To understand climatic drivers of phenology, at low and high elevations,
97 we modeled the dates of first flight as a function of maximum and minimum temperatures,
98 precipitation, and El Niño (ENSO) conditions. Models explained 60% of the inter-annual
99 variation at low elevations ($F_{6,138} = 35.17$, $P < 0.001$), and 72% at the higher elevation sites
100 ($F_{6,138} = 59.68$, $P < 0.001$) (Table S1). Minimum and maximum temperatures had negative
101 effects on first flight dates (warmer temperatures lead to earlier flights), and the effect of the
102 former was most noticeable at higher elevations (Figs. 3a and 3b). Precipitation, as reflected by
103 local weather and ENSO conditions, had a delaying effect on phenology (positive β coefficients
104 in Figs. 3c and 3d), which is expected as wetter conditions are associated with cooler, cloudy
105 days and delayed spring emergence.

106 Models of species richness revealed even more pronounced variation in weather effects
107 across elevations, including an increased importance of variation in minimum temperatures (Fig.
108 3e), maximum temperatures (Fig. 3f), and precipitation at higher elevations (Fig. 3g) (see Table
109 S2 for full details). The highest elevations are most negatively affected by dry years with
110 warmer nighttime temperatures. While daily maximum temperatures have risen everywhere
111 (Fig. 3j) and patterns of precipitation have fluctuated in concert across sites (Fig. 3k), minimum
112 temperatures have risen most steeply at the mountain sites (Fig. 3i). Models of species richness

113 also included phenology (date of first flight) as an explanatory variable, and we found an overall
114 negative association (Fig. 3h), such that earlier emergence is associated with elevated richness
115 (consistent with the effect of phenology on abundance at low elevations; Fig. S3). However, the
116 beneficial effects of earlier emergence at higher elevations might not be as consequential because
117 of a lack of multivoltine species, or they may simply be outweighed by the negative effects of
118 minimum temperatures. Negative effects of minimum temperatures at the higher elevation sites
119 range from 0.48 fewer species seen for every degree Celsius of warming at WA, to 6.46 fewer
120 species seen for every degree at DP (Table S3).

121

122 **Discussion**

123 In contrast to previous observations that extreme weather elicits species-specific responses¹⁶, the
124 millennium California drought produced consistent responses across many sites that included
125 advanced dates of first flight with elevation-specific changes in flight windows and species
126 richness. The resilience exhibited by the lowest elevations is associated with phenological
127 flexibility combined with multivoltine life histories and climatic associations that are less
128 detrimental (in the context of current climatic trends) than biotic-abiotic associations at higher
129 elevations. Many researchers have hypothesized an impending mismatch between trophic levels
130 as a result of climate change¹⁷. The results from low elevation butterflies in California perhaps
131 challenge that hypothesis, or at least suggest that a shift in phenology at the consumer trophic
132 level need not always have negative consequences. In addition to having multiple generations
133 each year, populations at the lowest elevations have access to agricultural lands. Although
134 association with irrigation does not appear to predict population dynamics during the drought
135 (Fig. S3), we cannot rule out the possibility that low elevation populations were buffered during

136 the drought by irrigated crops or agricultural margins. If true, a reliance on agriculture would be
137 interesting in the light of a recent hypothesis that long-term declines in low elevations butterfly
138 populations are associated with intensification of pesticide applications¹⁸. It is possible that the
139 rebound of the drought years could be followed by a more severe decline following concentrated
140 agriculture dependency and toxin exposure.

141 It has been known for some time that high latitude environments are warming faster than
142 the rest of the planet. It is only recently that climatologists have become aware that higher
143 elevations may also be experiencing a disproportionate share of warming¹⁹, which raises the
144 issue of how cold-adapted, montane ecosystems will respond. Contrary to the expectation that
145 mountains offer microclimatic refugia and preadapt species for climatic variation^{8,20}, we found
146 high elevation butterfly communities to be declining and especially sensitive to dry years with
147 warmer minimum temperatures. Warmer and drier years are associated with lower productivity
148 of mesic-adapted plant communities²¹, and shorter windows during which montane plants are
149 optimal for nectar and herbivory²². We did not model snowfall because it is highly correlated
150 with annual precipitation at our sites (see Methods), but reduced snowpack in dry, warm years
151 would have additional negative effects including higher overwinter mortality for life history
152 stages that typically spend the winter under a blanket of snow²³. The daily temperature range
153 (the difference between maximum and minimum temperatures) has been shrinking around the
154 globe²⁴, but the ecological consequences of this thermal homogenization are poorly understood
155 and not yet incorporated into theoretical expectations of global change biology²⁵. The results
156 reported here suggest that we have much yet to learn about organismal responses to extreme
157 weather at low and high elevations, but that powerful and simple models predicting faunal
158 dynamics are possible for ectotherms even in the face of unprecedented climatic variation.

159

160 **Methods**

161 **Butterfly data.** Ten study sites (Fig. 1a) were visited biweekly (every two weeks) by a one of us
162 (AMS) for between 45 and 29 years, depending on the site, and only during good “butterfly
163 weather” when conditions were suitable for insect flight (nearly year round at low elevations,
164 and during a more narrow period at higher elevations). At each site, a fixed route was walked
165 and the presence and absence of all butterfly species noted. Maps of survey routes and site-
166 specific details, as well as publically-archived data can be found at <http://butterfly.ucdavis.edu/>.

167 For most analyses, we restricted data to a common set of years, from 1988 to 2016, for
168 which we have data from all sites (the plots in Fig. 1 that go back to 1985 are exception, and do
169 not include all sites in the first few years). Plots and analyses (described below) primarily
170 involve species richness or phenological data, specifically dates of first flight (DFF) or dates of
171 last flight (DLF). The later two variables (DFF and DLF) involved filtering to avoid biases
172 associated with variation in the intensity or timing of site visits. Specifically, DFF values were
173 only used if they were preceded by an absence; in other words, there must be a negative
174 observation before a positive observation is taken as a DFF record. Similarly, DLF values were
175 not used if they were not followed by an absence; so any species observed on the last visit to a
176 site in a particular year did not have a record of DLF for that year. If a species was only
177 observed on a single day in a particular year, then that date was used as a DFF (and only if
178 preceded by an absence) but not as a DLF, in order to not use the same data point twice.

179 For a subset of years and sites, absolute counts of individual butterflies (by species) were
180 taken in addition to the presence/absence data; this was done at the 5 lowest elevation sites
181 starting in 1999. These data are used here to investigate the dynamics of the low elevation

182 butterflies during the drought years, specifically the relationship between phenological shifts,
183 changing abundance and dependence on irrigation. For the latter (dependence on irrigation), one
184 of us (AMS) ranked species *a priori* (without knowing the results of analyses) based on natural
185 history observations. Dependency on irrigated areas was categorized as follows: 1), butterfly
186 species that are essentially independent of irrigation; 2), species that use irrigated, non-native
187 hosts in some areas as well as native, non-irrigated hosts in other areas; 3), species that use
188 irrigated, non-native hosts in at least one of multiple generations; and 4), species that are
189 completely dependent on irrigated, non-native hosts.

190

191 **Weather variables.** Analyses included the following weather variables: maximum and
192 minimum daily temperatures, total precipitation, and a sea surface temperature variable
193 associated with regional conditions¹⁵. Following previous analyses¹³, maximum and minimum
194 temperatures were averaged and precipitation was totaled from the start of September of the
195 previous year through August of the current year. Previous fall through current summer is a
196 useful climatological time period in a Mediterranean climate and captures precipitation and
197 overwintering conditions that potentially affect butterflies through both direct effects on juvenile
198 and adult stages, and indirect effects through host and nectar plants. Data were generated as
199 monthly values using the PRISM system (Parameter-elevation Relationships on Independent
200 Slopes Model, PRISM Climate Group; <http://prism.oregonstate.edu>) for latitude and longitude
201 coordinates at the center of each survey route.

202 As a complement to the site-specific, PRISM-derived weather variables, we used an
203 index of sea-surface temperature associated with the El Niño Southern Oscillation (ENSO).
204 Specifically, we used the ONI (Oceanic Niño Index) values for December, January and February

205 (a single value is reported for those winter months; <http://cpc.ncep.noaa.gov>) from the winter
206 preceding butterfly observations for a given year. Higher values of this index correspond to
207 regionally warmer and wetter conditions. We also downloaded snowfall data from the Central
208 Sierra Snow Lab located near our Donner Pass site (station number 428, <http://wcc.sc.egov.usda.gov/nwcc>), but preliminary investigations found that annual snowfall totals were highly
209 correlated with annual precipitation totals. Correlation coefficients between snowfall and
210 precipitation were between 0.80 and 0.88, and the inclusion of snowfall caused variance inflation
211 factors from linear models (described below) to often exceed 10; thus snowfall was not included
212 in final models. In contrast, correlations among other weather variables (maximum
213 temperatures, minimum temperatures, precipitation, and ENSO values) were generally lower:
214 across sites and weather variables, the mean of the absolute value of correlation coefficients was
215 0.31 (standard deviation = 0.23).
216

217 Weather variables that were included in models were *z*-standardized within sites to be in
218 units of standard deviations. This allows variables from sites with different average conditions
219 (e.g., mountain and valley sites) to be readily compared and, more important, it allows for slopes
220 from multiple regression models to be compared among weather variables that are themselves
221 measured on different scales (as is the case with precipitation and temperature).
222

223 **Analyses.** Statistical investigations involved two phases. First, we used plots of *z*-standardized
224 data to visualize patterns in phenology (DFF and DLF) and flight days; the latter variable, the
225 number of days flying, was expressed as the fraction of days that a species is observed divided
226 by the number of visits to a site per year (this has been referred to as “day positives” in other
227 publications using these data¹⁵). DFF, DLF, and flight days were *z*-standardized within species

228 at individual sites and then averaged across species to facilitate comparisons of patterns across
229 sites and years. We also used plots of species richness to explore faunal changes over time at
230 each site. Plots of richness were accompanied by splines (with 5 degrees of freedom) and
231 predicted values from random forest analyses²⁶, which both allow for visualization of non-linear
232 relationships. The spline analysis has the advantage of producing smoothed relationships
233 (between richness and years), while the random forest analysis, performed with the
234 randomForest²⁷ package in R²⁸, has the complementary advantage of being able to incorporate
235 covariates (in this case the number of visits per year) as well as the advantage of making no
236 assumptions about the shape of the relationship (between richness and years, while controlling
237 for sampling effort). Patterns in species richness over time were also explored using diversity
238 indices and Hill numbers that weight rare and common species differently (at different levels of
239 q , which determines the sensitivity of the analysis to rare species)²⁹⁻³¹, using the vegetarian
240 (v1.2) package³² in R²⁸. In addition, we used the combination of spline and random forest
241 analyses to investigate changes in abundance (numbers of individuals observed per year) at the
242 low elevation sites where abundance data was available. As with other variables, abundance
243 values were z -standardized within species and sites, and z -scores were averaged across species.

244 Following the visualization phase of investigation, we developed simple linear models
245 that were focused on prediction of dates of first flight (DFF) and species richness. Independent
246 variables for both sets of models included average daily minimum temperatures, average daily
247 maximum temperatures, total precipitation, ENSO (ONI sea surface temperatures), sampling
248 effort (number of visits), and year. Models of species richness included date of first flight as an
249 additional variable because we were interested in the possibility that the timing of species
250 emergence affects butterfly populations and consequently observed species richness. These

251 models (for both DFF and richness) were estimated for each site individually and for high and
252 low sites as groups of sites (5 sites in each model). Additional model complexities were
253 explored that included interactions between weather variables, time lags (effects of previous
254 years on current year dynamics) and cumulative effects (sliding windows of averaged
255 precipitation values). Interactions were rare, but we report interactions between weather
256 variables that were significant (at $P < 0.05$). Lagged and cumulative weather variables did not
257 add to the explanatory power of models and the individual lagged and cumulative effects were
258 rarely significant and not discussed further.

259 As we have found elsewhere for analyses of phenology and richness with these data^{11,33},
260 linear models satisfied assumptions of normality and homogeneity of variance. To address
261 potential collinearity among predictor variables, variance inflation factors were investigated and
262 found generally to be between 0 and 5, and in a few cases between 5 and 10. For instances
263 where inflation factors approached 10, quality control was conducted by including and excluding
264 correlated variables to verify that estimated β coefficients were not affected. Linear models were
265 also used to test the hypothesis that phenological shifts at low elevations have demographic
266 consequences for individual species. For each species at the lowest sites (SM, WS, NS, and RC),
267 we separately regressed dates of first flight against years, and annual abundance against years.
268 Slopes from those regressions were then compared using correlation to ask if species that shifted
269 to an earlier flight (negative slopes for DFF versus years) were also species that become more
270 abundant (positive slopes of abundance versus years). This was done for the years 2008 – 2016
271 to capture the transition into the millennium drought years, and only included species that were
272 present in at least 6 of those years. As with other analyses, linear models were performed and
273 assumptions investigated using R^{28} .

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314

315 **Acknowledgements**

316 Research was funded by the National Science Foundation (DEB-1638773 to CCN, DEB-
317 1638922 to JAF, and DEB-1638793 to MLF), and MLF was supported by a Trevor James
318 McMinn professorship.

319

320 **Author contributions**

321 A.M.S. designed and carried out data collection. J.H.T. and D.P.W. managed data entry and
322 curation. M.L.F., J.A.F. and C.C.N. analyzed the data. All authors contributed to writing.

323

324 **Additional information**

325 Supplementary information is available in the online version of the paper.

326

327 **Competing financial interests**

328 The authors declare no competing financial interests.

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330 **Figure legends**

331 **Figure 1.** (a) Elevational profile of Northern California (left) and map of the same area (on the
332 right) with ten study sites indicated on both; site names as follows, from west to east: Suisun
333 Marsh (SM), Gates Canyon (GC), West Sacramento (WS), North Sacramento (NS), Rancho
334 Cordova (RC), Washington (WA), Lang Crossing (LC), Donner Pass (DP), Castle Peak (CP) and
335 Sierra Valley (SV). (b) Average dates of first flight and (c) last flight across species at each
336 location and year. (d) Average flight days, which are the average fraction of days individual
337 species are observed per year. In panels b, c, and d, color coding for individual lines
338 corresponds to sites as in panel a, and the data are shown as z-standardized values. Grey
339 rectangles in panels b, c, and d, indicate the major drought years from late 2011 into 2015.

340

341 **Figure 2.** Species richness (a through j) for all sites, and abundance (k through o) for low
342 elevation sites (abundance data was only collected at the low sites). Two letter site names and
343 colors follow Fig. 1A. In all panels, patterns are visualized with both a spline fit with five
344 degrees of freedom (thin black line) and predicted values from random forest analysis (thick gray
345 line) incorporating variation in sampling effort. In panels k through o, values plotted are z-
346 standardized values of total abundance (number of individuals) per year averaged across species.

347

348 **Figure 3.** Results from a model of phenology (a through d) and a model of species richness (e
349 through h), as well as plots of weather variables through time (i through l). In the model results
350 (a through h), the values shown are β coefficients (with standard errors) that summarize the
351 effect of a particular weather variable (while controlling for other variables) on either phenology
352 or richness for each site. Trend lines are only shown in plots where the effect of a particular

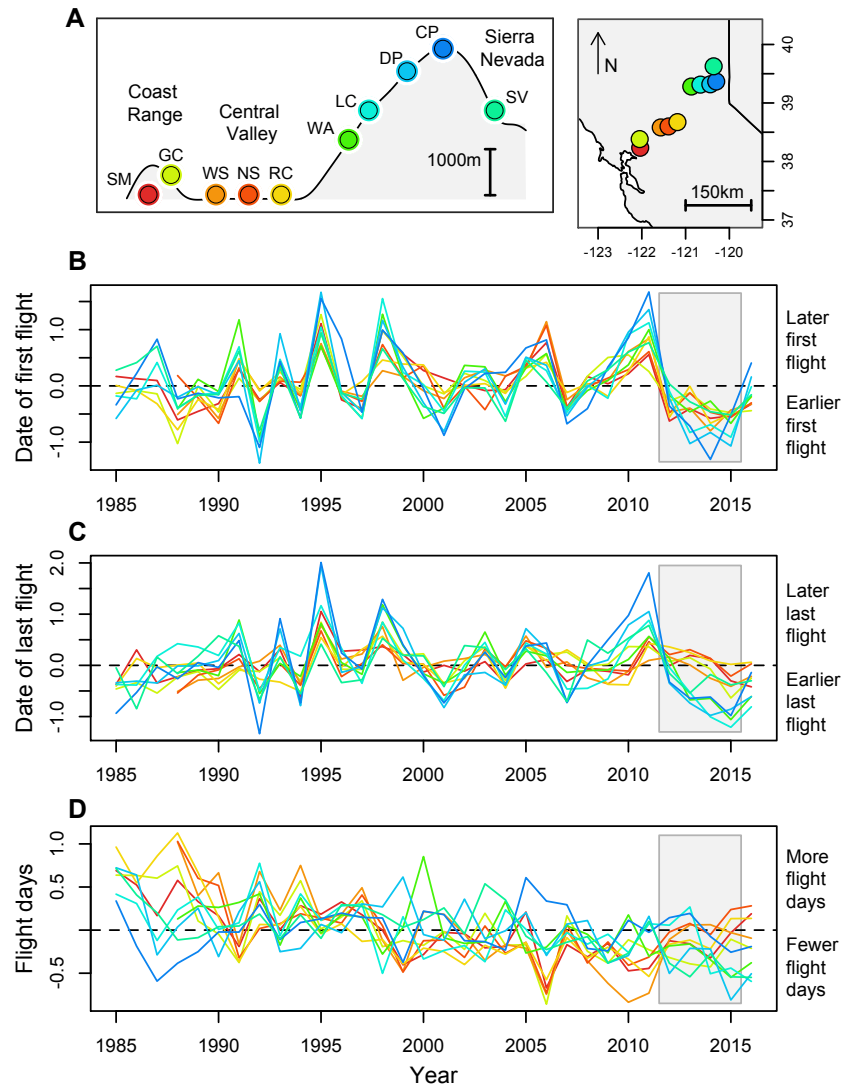
353 weather variable changes with elevation (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; see Table S4
354 for additional details). In panels **i** through **k**, weather patterns are visualized using splines with
355 five degrees of freedom; panel **l** is the El Niño index (ONI) for each year. Weather variables are
356 shown as z -standardized values in panels **i** through **k**, and site specific colors in all plots are the
357 same as in Fig. 1a.

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Fig. 1



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Fig. 2

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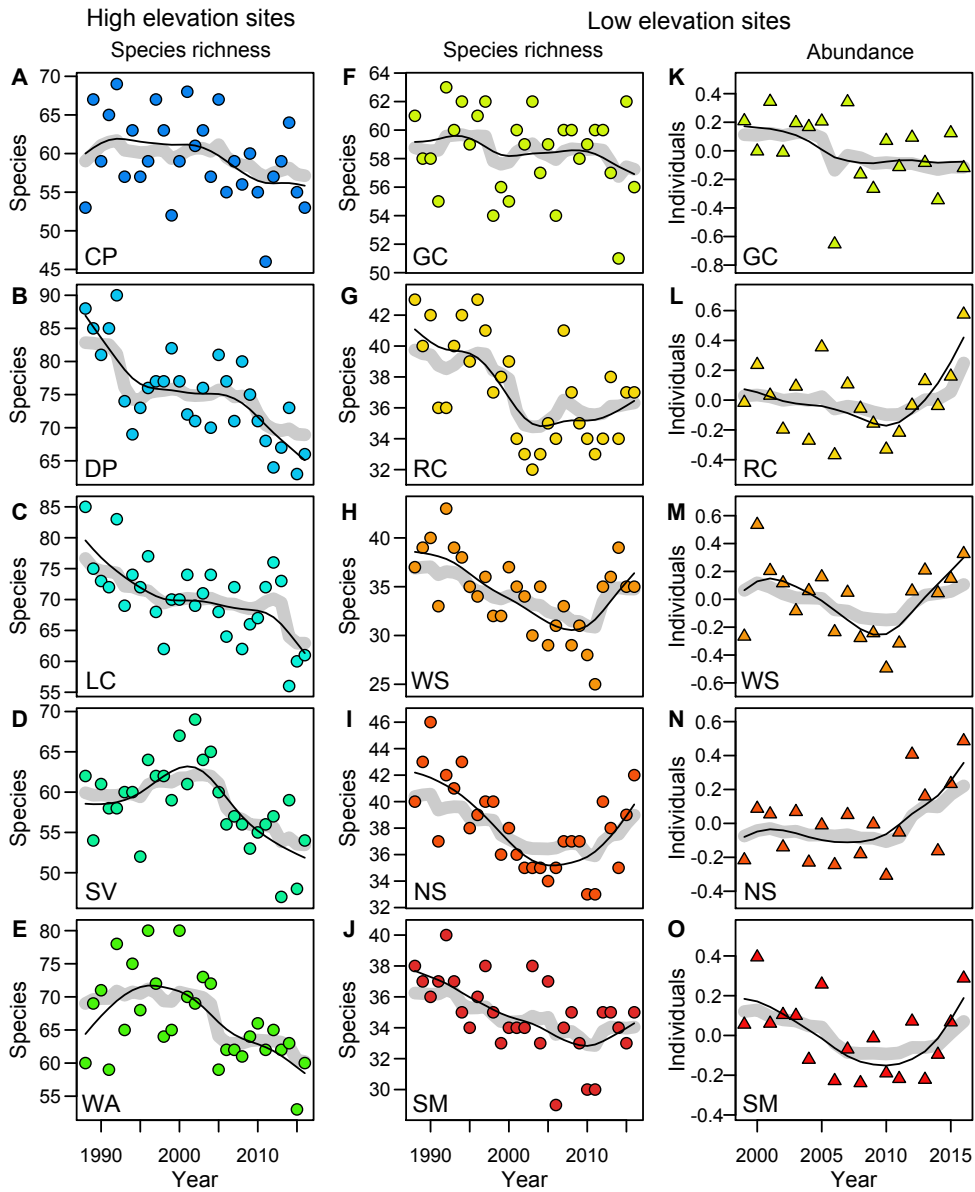


Fig. 3

