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**1Synchronous population dynamics explained by climatic forcing in California butterflies**

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## 25Abstract

26A long-standing challenge for population biology has been to understand why some species are  
27characterized by populations that fluctuate in size independently, while others display  
28synchronous fluctuations across space. An improved understanding of synchrony would advance  
29our predictive ability for a range of phenomena, including meta-population dynamics, pest  
30outbreaks, and biotic responses to climate change. We utilized 27-years of observations on 65  
31butterfly species at 10 sites that are 210 km apart and span 2750m of elevation, to investigate the  
32causes of interspecific variation in spatial synchrony. Specifically, we compared the relative  
33influence of two hypothesized drivers of spatial synchrony – climatic variation and dispersal  
34propensity. We report that sensitivity to climate explained 50% of interspecific variation in  
35synchrony, whereas dispersal propensity explained 23%. We also report that these two drivers  
36can interact to influence interspecific variation in synchrony. Sensitivity to large-scale climate  
37patterns, in particular the El Niño Southern Oscillation, was the best predictor of synchrony.  
38Additionally, we report a limited contribution of spatial synchrony to the ongoing decline of the  
39Northern California butterfly fauna. In summary, our results confirm the primacy of climatic  
40sensitivity for driving spatial synchrony in butterflies.

41Key Words: *butterfly, ENSO, elevational gradient, population decline, spatial synchrony*

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## 47Introduction

48 A primary goal of population ecologists is to understand the mechanisms that promote  
49fluctuations in density of natural populations of plants and animals through both time and space.  
50Early studies suggested the important roles that trophic interactions and exogenous forces, such  
51as climatic variability, might have in driving population fluctuations (Lotka 1925; Volterra 1926;  
52Davidson & Andrewartha 1948). More recently, population biology has made progress through  
53the integration of larger spatial and temporal datasets describing population dynamics. For  
54example, meta-population models can predict the persistence of spatially segregated populations  
55(Hanski *et al.* 1995; Keymer *et al.* 2000), and landscape genetic models can infer recent dispersal  
56among subpopulations on complex landscapes (Manel *et al.* 2003). A key parameter in many of  
57these areas of population biology is the extent to which subpopulations exhibit correlated  
58spatiotemporal dynamics (e.g., experience “good years” and “bad years” in parallel). Here we  
59take a multi-species approach using long term data to advance understanding of correlated  
60spatiotemporal dynamics in insect populations.

61 Three non-mutually exclusive mechanisms are often hypothesized to synchronize  
62population dynamics among populations: (1) dispersal of individuals among populations, which  
63links the dynamics of those populations; (2) synchronization due to density-independent factors  
64(e.g. climate) that are correlated across wide areas (i.e. the “Moran effect” (Moran 1953)); and  
65(3) interactions with other species (e.g. natural enemies and pathogens) that are themselves either  
66synchronous or highly mobile (Bjørnstad, Ims & Lambin 1999; Liebhold, Koenig & Bjørnstad  
672004; Korpimäki *et al.* 2005). Identifying the relative influences of each of these three  
68mechanisms is challenging because all three may cause similar patterns of synchrony among  
69populations (Ranta *et al.* 1995; Liebhold *et al.* 2004). Moreover, it is difficult to directly measure

70the contribution of dispersal, which is itself a complex trait, and the product of other interacting  
71biological characteristics (Clobert 2012). Furthermore, data describing natural enemy population  
72densities are not available for the majority of organisms, including our focal species; thus our  
73investigations focus on dispersal propensity and sensitivity to climatic variation, but not  
74interspecific interactions.

75       We use data from 27-years of observations of 65 butterfly species across ten sites that are  
76separated by 210 km and span an elevational gradient of 2750m (Fig. 1A) to compare the relative  
77influence of dispersal propensity and sensitivity to climatic variation on spatial synchrony. We  
78first characterized butterfly species in terms of their degree of spatial synchrony and a range of  
79species-specific properties that together acted as an index of dispersal propensity, including:  
80wingspan, geographic range, elevational range, and host breadth (see *Methods*). We then  
81characterized the sensitivity of each species to climatic variation (e.g. sensitivity to winter  
82precipitation, or summer temperature). Next, we used structural equation modeling (SEM) to  
83address the following questions: (1) Is interspecific variation in spatial synchrony better  
84predicted by dispersal propensity or sensitivity to climatic variation? (2) Can interspecific  
85variation in spatial synchrony be modeled through the combined or interacting effects of  
86dispersal propensity and climatic sensitivity? Finally, given that theory suggests that synchrony  
87can predispose meta-populations to collapse, we ask if an improved understanding of the drivers  
88of spatial synchrony can shed light on declines in focal butterfly populations, (Hanski & Woiwod  
891993; Heino *et al.* 1997; Keymer *et al.* 2000; Koenig & Liebhold 2016). The portion of Northern  
90California where our study sites are located has been characterized by dramatic declines and  
91local extirpations in recent years, particularly at low elevations (Forister *et al.* 2011). These  
92declines have been attributed to a combination of development, changing land use, and pesticides

93(Casner *et al.* 2014a; Forister *et al.* 2016), but the contribution of spatial synchrony to these  
94declines has not been studied.

## 95**Methods**

96**Study system and calculation of synchrony.** Butterfly data was collected by A. M. S. at ten  
97locations in Northern California from 1988-2013 (Fig. 1A). These sites include a variety of  
98habitat types, spanning a 2750 m elevational gradient, and are separated by 210 km from the  
99most western to the most eastern location. A fixed transect was walked every two weeks as per  
100Pollard (1988), and presence or absence of taxa noted (for maps of transects see  
101<http://butterfly.ucdavis.edu/>). Surveys were conducted in spring, summer, and fall on sunny days  
102with little wind, and thus suitable for butterfly flight. Previous analyses show that these  
103occurrence data are effective proxies for butterfly abundance (Casner *et al.* 2014b). In addition,  
104analyses were repeated using count data for the relatively limited subset of taxa and sites (those  
105in the central valley of California only) for which counts of individuals were available. In all  
106cases, results obtained were qualitatively similar, and are therefore not discussed further. The  
107number of presences in a given year was divided by visits for that year to account for differential  
108visitation across years and sites (henceforth referred to as fractional day positives [FDP]).

109 For each combination of site and taxon, the previous year's FDP was subtracted from the  
110current year's FDP to calculate a change in FDP between years ( $\Delta$ FDP). Correlation coefficients  
111were then calculated between  $\Delta$ FDPs from different sites in a pairwise fashion (Pearson's  $r$ ), as  
112has been done with a variety of taxa in studies of spatial synchrony (Bjørnstad *et al.* 1999;  
113Powney *et al.* 2010). For each pairwise correlation, data from the site with the longest history of  
114visitation was truncated to match the site with the shortest period of visitation. The resulting  
115correlation coefficients were averaged across all pairwise comparisons among sites to give a

116taxon-specific index of synchrony. If a species was absent for eight or more years at a site, then  
117that site was not included in the analysis for that species. Finally, for a species to be included in  
118this study it had to occur at three or more sites. In total, synchronicity indices for 65 butterfly  
119taxa were generated (Table S1).

120**Structural equation models (SEM).** To compare specific hypotheses for the drivers of  
121synchrony we used structural equation modeling (SEM). This method facilitates the testing of  
122causal relationships among variables, including comparison of direct and indirect causal  
123structures (Grace 2006). A total of six SEMs were constructed to compare *a priori* hypotheses  
124about potential drivers of spatial synchrony, based on insights gained from previous work with  
125these butterflies and sites (Forister *et al.* 2011; Nice *et al.* 2014; Harrison *et al.* 2015; Pardikes *et*  
126*al.* 2015). Two SEMs were generated to independently compare the influence of dispersal  
127propensity and sensitivity to climatic variation on synchrony, and a third SEM was assembled to  
128investigate the combined influence of both drivers. For all models, we also investigated the  
129influence of migratory behavior by removing nine butterfly species that undergo annual  
130migrations (including latitudinal and elevational migrations) and observed changes in model fit  
131and path coefficients (Table S1). We conducted these separate analyses because migratory taxa  
132represent a subset of extreme dispersers that could provide an informative contrast to more  
133sedentary butterflies. To understand how the removal of nine species from our analysis affected  
134the explained variance, each SEM was performed 1000 times with a random set of 56 butterfly  
135species (dropping 9 each time). The mean and standard error of variance explained were  
136calculated for each separate model (e.g., dispersal, climate, combined). Details of SEM  
137construction are provided below. Model fit was assessed using  $\chi^2$ , and model comparison  
138performed using the Akaike information criterion (AIC) (Akaike 1998). All SEM and path

139analyses were constructed using the lavaan package v0.5-17 (Rosseel 2012) in R v3.1.1 (R Core  
140Team 2014).

141**Modeling the influence of dispersal propensity on synchrony.** A maximum likelihood factor  
142analysis was used to reduce the dimensionality among correlated data that together characterize  
143variation in dispersal propensity among taxa (R package: psych v1.4.8.11; Revelle 2014). We  
144calculated two factors from an analysis of wingspan, geographic range, diet breadth (e.g.,  
145number of plant genera consumed), and elevational range. We choose these variables because  
146interspecific variation in butterfly dispersal ability has been linked to wingspan (e.g. Hughes,  
147Dytham & Hill 2007; Öckinger *et al.* 2010; Sekar 2012), geographical range and diet breadth  
148(Brändle, Öhlschläger & Brandl 2002; Komonen *et al.* 2004; Beck & Kitching 2007; Garcia-  
149Barros & Romo Benito 2010). Geographical range (km<sup>2</sup>) for each taxon was taken from Jahner et  
150al. (2011) and diet breadth was taken from Shapiro & Manolis (2007). Diet breadth included only  
151those larval hosts used in Northern California.

152 Two factors were calculated that respectively explained 30% (“Dispersal 1”) and 15%  
153(“Dispersal 2”) of the variance in underlying variables. “Dispersal 1” included all four variables,  
154but was most heavily weighted by geographical range, diet breadth, and elevational range.  
155“Dispersal 2” included all variables except diet breadth, and was primarily associated with  
156wingspan and geographic range (see Table S2 for loadings). These two factors were input into  
157SEMs and served as latent variables. Latent variables are used to model unobservable, or highly  
158multidimensional phenomena (e.g. dispersal propensity) using information from more easily  
159measurable phenomena (e.g. wingspan, geographical range). For each species, the average  
160number of sites occupied, the average FDP across sites (“Abundance”), and the average inter-  
161annual change in FDP (henceforth “Trend”, see Forister et al. 2010) were calculated, z-



162standardized, and included as covariates in the SEM to account for their influence on spatial  
163synchrony.

164**Modeling response to weather.** The response to climatic variation by each taxon was modeled  
165using a hierarchical Bayesian linear modeling framework. These responses were subsequently  
166used during calculation of factors characterizing variation in sensitivity to climate among taxa  
167(see below). Climate information was extracted from the PRISM dataset (Nice *et al.* 2014),  
168which interpolates data from weather stations with respect to site-specific topography. Data were  
169converted to seasonal values following a “water year” format, so that spring consisted of March,  
170April, and May; summer of June, July, and August; and, winter of December of the previous  
171year, and January and February of the current year. This “water year” corresponds to the post-  
172summer increase in precipitation typically observed beginning in September through much of  
173Northern California. Prior to model construction, all seasonal weather variables were converted  
174to z-scores. To identify responses to the El Niño Southern Oscillation (ENSO; the primary driver  
175of long-term weather patterns in Northern California (Schonher & Nicholson 1989) we used the  
176sea-surface temperature anomaly (SSTA) dataset from 1981-2010 in the “Niño 3.4” region of the  
177Pacific Ocean (Climate Prediction Center of the National Oceanographic and Atmospheric  
178Administration). The SSTA is defined as a departure from the long-term SST mean, and is a  
179commonly used index of the strength of ENSO. The mean values of SSTA of December, January,  
180and February from a given “water-year” were used in analyses because they correspond to the  
181peak of ENSO (Vandenbosch 2003). All weather variables were chosen because previous work  
182has shown the response to these weather conditions to be important drivers of butterfly  
183population dynamics in Northern California (Nice *et al.* 2014; Harrison *et al.* 2015; Pardikes *et*

184al. 2015). In addition, year was included as a covariate in each model to account for the impact  
185of variation in rate of decline among taxa (Forister *et al.* 2011).

186 For each taxon, a binomial response consisting of day positives and visits was modeled.  
187This response was linked to the output of a hierarchical linear model using an inverse logit link  
188function:  $p_{ij} = 1 / (1 + e^{-\alpha_{ij}})$  where  $p_{ij}$  is the number of presences in year  $i$  and at site  $j$ , and  $\alpha_{ij}$  is  
189the output of the linear model for year  $i$  at site  $j$ . The linear model was of the form:

$$190 \alpha_{ij} = \mu_j + \beta_{1j} \text{Winter temp}_{ij} + \beta_{2j} \text{Spring temp}_{ij} + \beta_{3j} \text{Winter precip}_{ij} + \beta_{4j} \text{Spring precip}_{ij} + \beta_{5j} \text{Summer precip}_{ij} + \beta_{6j} SS$$

191The mean estimate of FDPs for a given taxon at a given site is given by the intercept term  $\mu$ , and  
192regression coefficients for each model term by  $\beta_{1-6}$ . Normal distributions with means and  
193precisions equal to transect-wide parameters were used as sampling pools for site-specific  
194intercepts and beta coefficients:

$$195 \mu_j \sim N(\mu_\mu, \tau_\mu)$$

$$196 \beta_{kj} \sim N(\mu_{\beta_k}, \tau_{\beta_k})$$

197Where  $k$  is the number associated with each model term. We used uninformative hyperpriors for  
198these parameters defined by:

$$199 \mu_\mu \sim N(0, 1.0e^{-5})$$

$$200 \mu_{\beta_k} \sim N(0, 1.0e^{-5})$$

$$201 \tau_\mu \sim \text{Gamma}(0.1, 1.0e^{-3})$$

$$202 \tau_{\beta_k} \sim \text{Gamma}(0.1, 1.0e^{-3})$$

203Posterior probability distributions (PPDs) for the transect-wide impact of each model term were  
204approximated via Markov chain Monte Carlo sampling using *rjags* (v3.4.0, (Plummer 2013)).

205Two sampling chains were run for 30,000 iterations following a burn-in of 1,000 iterations.

206 Effective sample sizes and trace plots were examined to ensure adequate mixing and  
207 convergence on a suitable approximation of PPDs. The mean of the PPD for the transect-wide  
208 estimate of each regression coefficient was used as an estimate of the response to that term. The  
209 outputs of this approach were estimates of species-specific responses to weather variables that  
210 were informed by responses across all study sites (Table S1).

211 **Modeling the influence of climate on synchrony.** A maximum likelihood factor analysis was  
212 used to reduce the dimensionality of data describing how taxa respond to climatic variation as  
213 output from hierarchical linear modeling described above (Revelle 2014). We calculated two  
214 factors from the analysis of responses to temperature and precipitation in spring, summer, and  
215 winter, which explained 28% and 21% respectively of the variance in analyzed variables. We  
216 included ENSO (as measured by response to SSTA; see above) into our SEM as a standalone  
217 variable to compare the influence of regional climate versus local weather on synchrony, and  
218 therefore sensitivity to ENSO was not included in the factor analysis. Factor one (“Climate 1”)  
219 was composed of responses to all five climatic variables, but was most heavily weighted by  
220 spring temperature and to a lesser degree, spring precipitation. Factor two (“Climate 2”) included  
221 all climate variables except response to summer temperature, and was primarily weighted by  
222 responses to winter temperature (Table S3). Similar to the “dispersal” SEM, average number of  
223 sites occupied, average site abundance, and population trend were included as z-standardized  
224 covariates.

225 **Modeling the combined influence of natural history and sensitivity to weather on**  
226 **synchrony.** We also examined the combined influence of variation in dispersal propensity and  
227 sensitivity to weather on spatial synchrony via SEM. Both sets of latent variables used in the  
228 previous analyses were included in our “combined” model. This allowed us to compare the

229relative influence of sensitivity to weather and dispersal propensity on synchrony in the same  
230model. We hypothesized *a priori* that dispersal propensity and sensitivity to climate might  
231interact to influence spatial synchrony, therefore we generated models linking the latent variables  
232characterizing both of these drivers. We compared performance among models (using AIC and  
233 $\chi^2$ ) to determine which interactions between latent variables improved model fit.

## 234Results

235 Our index of spatial synchrony, which measures the correlation of changes in yearly  
236abundances across populations (Bjørnstad *et al.* 1999), identified 44 out of the 65 butterfly  
237species as being characterized by synchronous fluctuations (e.g., synchronicity index greater than  
2380.1); only 7 taxa had negative synchronicity indices, which indicated asynchronous fluctuations  
239(minimum index value was -0.11) (Fig. 1B). By visual inspection, index values greater than 0.2  
240represented fairly synchronized population dynamics, and values greater than 0.4 highly  
241synchronized dynamics (for examples see Fig. 1B-F). Only five species had indices over 0.4  
242(Table S1).

243 Our models successfully explained much of the variance associated with spatial  
244synchrony among Northern California butterflies (Fig. 2). We confirmed the contribution of  
245dispersal propensity to variation in spatial synchrony among butterfly species using structural  
246equation modeling (SEM) (Fig. 3A.  $\chi^2 = 1.41$ ,  $p = 0.84$ ,  $df = 4$ ,  $n = 65$ ; higher p-values signify  
247better fit; Table S4). This SEM explained 23% of the variance in spatial synchrony among taxa,  
248and 59% of the variation in the average number of sites occupied across the elevational gradient.  
249The latter result suggests that our latent variables captured meaningful biological variation  
250pertaining to dispersal ability. The influence of dispersal propensity on patterns of spatial  
251synchrony was restricted to the positive influence of a single latent variable (“Dispersal 1”),

252which was primarily weighted by diet breadth and geographic range. Removing migratory  
253species from the SEM reduced the explanatory power of the model (Fig. 3B,  $\chi^2 = 4.42$ ,  $p = 0.35$ ,  
254 $df = 4$ ,  $n = 56$ ; Table S5), which subsequently only explained 3% of the variance in spatial  
255synchrony.

256       Our “climate” SEM was well supported, and revealed that sensitivity to climate,  
257especially to large-scale climate patterns (e.g., ENSO), was strongly, positively associated with  
258variation in spatial synchrony among butterfly taxa (Fig. 3C,  $\chi^2 = 5.41$ ,  $p = 0.80$ ,  $df = 9$ ,  $n = 65$ ;  
259Table S6). This SEM explained 50% of the variation in spatial synchrony among butterflies.  
260ENSO drives regional climate patterns and was the strongest predictor of spatial synchrony for  
261the entire fauna, with butterflies more sensitive to ENSO exhibiting greater synchrony. We also  
262observed that those butterfly species most responsive to ENSO were negatively associated to  
263local climatic conditions, suggesting complex relationships between sensitivity to local and  
264regional climatic variation.

265       When excluding migratory butterflies, which are especially sensitive to ENSO  
266fluctuations (Vandenbosch 2003; Pardikes *et al.* 2015), SEM performance decreased (Fig. 3D.  $\chi^2$   
267= 16.36,  $p = 0.06$ ,  $df = 9$ ,  $n = 56$ ; Table S7) and the role of ENSO as a driver of spatial synchrony  
268was diminished, which is consistent with the previously-observed importance of regional  
269weather for the most dispersive and widespread species (Pardikes *et al.* 2015). However, model  
270performance was still high and explained 28% of the variance in spatial synchrony among  
271species. Sensitivity to local weather was the best predictor of variation in synchrony for non-  
272migratory butterflies. Species with the most asynchronous dynamics were also the most sensitive  
273to local weather, in particular spring and summer precipitation.

274 The “combined” SEM, which included both dispersal propensity and climatic sensitivity,  
275 was also strongly supported and explained 53% of the variance associated with spatial synchrony  
276 among species (Fig. 4A;  $\chi^2 = 15.19$ ,  $p = 0.65$ ,  $df = 18$ ,  $n = 65$ ; Table S8). In line with results from  
277 our climate SEM, sensitivity to climatic variation was the best predictor of spatial synchrony, and  
278 both sensitivity to local weather and ENSO resulted in more synchronous dynamics among  
279 butterflies; with sensitivity to ENSO being the strongest predictor of synchrony. A significant,  
280 direct influence of dispersal ability on spatial synchrony was not observed, but we did uncover  
281 several indirect effects of dispersal mediated by sensitivity to climate (Fig. 4A). Both indirect  
282 effects of dispersal propensity positively influenced spatial synchrony, and provide evidence that  
283 the role of dispersal propensity on synchrony is likely mediated by climate. Repeating the  
284 “combined” SEM without migratory butterflies resulted in an unsupported causal structure (Fig.  
285 4B;  $\chi^2 = 36.05$ ,  $p = 0.01$ ,  $df = 18$ ,  $n = 56$ ; Table S9). However, path coefficients were still  
286 informative because they represent the output of pairwise regression, and the model explained  
287 35% of the variation in synchrony associated with non-migratory butterflies. Without migratory  
288 species, the direct influence of ENSO on synchrony was lessened and an indirect influence of  
289 ENSO on synchrony, via local weather, became evident. In all models, the variance explained  
290 when nine random species was removed was equal to models that included migratory species,  
291 supporting the idea that the nine migratory species are biologically unique among this butterfly  
292 assemblage (Fig. 2).

293 Finally, we considered the effect of spatial synchrony on trends in inter-annual population  
294 change (Fig. 3 & Fig. 4; Tables S4-S9). For each SEM, synchrony explained only ~5% of the  
295 variation in inter-annual trend across taxa. However, in all three SEMs the direct path coefficient  
296 from spatial synchrony to population trend was significant ( $p < 0.05$ ). The strength and

297significance of this path depended on the presence of migratory species in the model. Removing  
298migratory species eliminated the path's significance and narrowly reduced the strength of the  
299coefficient in all three cases. In all three models, a negative coefficient was observed, suggesting  
300that higher levels of spatial synchrony are associated with population declines among the  
301butterfly assemblage, particularly for migratory species.

## 302**Discussion**

303        In this study we identified relationships between spatial synchrony and both dispersal  
304propensity and sensitivity to climatic variation among 65 butterfly species in a region  
305characterized by extreme habitat heterogeneity (Fig. 1). Our approach differs significantly from  
306previous investigations, in that we assessed climatic sensitivity directly for each species and  
307linked both climatic sensitivity and dispersal propensity to the degree of synchrony exhibited by  
308each species (Sutcliffe, Thomas & Moss 1996; Powney *et al.* 2010, Raimondo *et al.* 2004;  
309Koenig 2006). We have shown that the majority of interspecific variation in spatial synchrony  
310can be explained through sensitivity to climatic variation, especially large-scale climate patterns  
311such as ENSO, though the effect of ENSO is at least partially mediated by species traits related  
312to dispersal (Fig. 2).

313        The influence of a large-scale climate pattern, ENSO, on synchrony was particularly  
314prominent. In the portion of California where our transect is located, the ENSO may lead to  
315either increased, or reduced precipitation, but effects on precipitation are dramatic and region-  
316wide (Schonher & Nicholson 1989). Our results support previous efforts, which show that large-  
317scale climate patterns (e.g. ENSO) can act to synchronize population dynamics across large areas  
318(Post & Forchhammer 2002, 2004). Our ability to quantify a connection between ENSO  
319sensitivity and spatial synchrony was affected by the presence of migratory species in our model.

320A possible explanation for this is that the population dynamics of migratory species are shaped  
321by climate across a broader spatial scale than sedentary species. Accordingly, variation in spatial  
322synchrony among non-migratory species was best predicted by sensitivity to localized weather  
323conditions. Given the elevational range encompassed in this study and the corresponding breadth  
324of habitat types, local weather conditions often vary dramatically between sites, which can act to  
325desynchronize sub populations of conspecifics occurring across the transect. Indeed, previous  
326investigations have shown that butterfly species can respond to the same climatic variable (e.g.  
327winter precipitation) differently at different sites (Pardikes *et al.* 2015).

328         Interestingly, sensitivity to spring and summer precipitation was indicative of taxa with  
329asynchronous dynamics, and sensitivity to spring temperature and winter precipitation was  
330representative of taxa with synchronous dynamics. These results complement previous work  
331showing that volatile species are positively influenced by increased spring and summer  
332precipitation, and negatively influenced by increasing spring temperatures and winter  
333precipitation (Harrison *et al.* 2015). Moreover, winter precipitation has previously been linked to  
334earlier emergence time in California butterflies (Forister and Shapiro 2003) and increased winter  
335precipitation positively influences abundances of butterflies in the region (Nice *et al.* 2014).

336When taken together these results suggest that degree of spatial synchrony for non-migratory  
337taxa is facilitated by the ability for rapid changes in abundance under suitable climate conditions.

338         Dispersal is thought to be an important contributor to spatial synchrony (Ylikarjula *et al.*  
3392000; Vogwill, Fenton & Brockhurst 2009), yet species-specific dispersal propensity was not a  
340strong predictor of interspecific variation in spatial synchrony (Fig. 2). Work with other  
341Lepidoptera species has also suggested that dispersal plays a minor role in synchronizing  
342populations (Haynes *et al.* 2009, 2013; Liebhold, Haynes & Bjørnstad 2012). A possible



343 explanation for why increased dispersal propensity did not increase spatial synchrony is that  
344 most butterflies rarely move between sites. Our focal sites span 2750 m of elevation and many  
345 habitat types, thus habitat heterogeneity may limit the ability of butterflies to disperse between  
346 sites. This hypothesis is supported by decline in variance explained when migratory species,  
347 which are known to move between sites, were omitted from our model (from 23% to 3%  
348 variance explained). We acknowledge that interactions with natural enemies (de Roos, McCauley  
349 & Wilson 1998; Ims & Andreassen 2000; Vogwill *et al.* 2009) likely account for a portion of the  
350 unexplained variance in our models of spatial synchrony. However, we were unable to assay the  
351 influence of natural enemies because relevant information was unavailable for even a subset of  
352 our focal taxa.

353        Although populations of most butterfly species at lower elevations in our study area are  
354 in decline (Forister *et al.* 2011), interspecific variation in spatial synchrony appears to play a only  
355 minor role in explaining the current population declines. Theory predicts that synchrony within a  
356 meta-population can increase extinction propensity, because in this scenario recolonization of  
357 extirpated subpopulations is more difficult, thus predisposing the meta-population to eventual  
358 collapse (Harrison & Quinn 1989). Consistent with theory, we detected a significant negative  
359 influence of increased spatial synchrony on population trends, such that more synchronized  
360 species were characterized by more severe declines. However, that negative influence only  
361 explained ~5% of the variation in declines, and the low amount of variation explained may be  
362 due to the buffering influence of habitat and microclimatic diversity across all ten sites. Habitat  
363 heterogeneity likely reduces synchronous dynamics among spatially segregated populations  
364 because different axes of an organism's niche may vary asynchronously among subpopulations,  
365 thus buffering the negative consequences of synchrony. Consequently, homogenization of

366landscapes due to extensive invasion and human-induced environmental change could increase  
367patterns of spatial synchrony and strengthen the link between synchrony and decline (Olden *et*  
368*al.* 2004).

369

### *Conclusion*

370 We report that interspecific variation in spatial synchrony among the butterflies of  
371Northern California is best explained by sensitivity to climatic variation. The large-scale climate  
372pattern, the El Nino Southern Oscillation (ENSO), was highly predictive of spatial synchrony,  
373particularly so for the most mobile species (e.g., migratory). Dispersal propensity was less  
374predictive of spatial synchrony than climate, especially when migratory species were removed  
375from the analysis. However, our analyses revealed that interactions between both drivers  
376influenced the degree of synchrony exhibited by a species. Finally, spatial synchrony appears to  
377only weakly contribute to the ongoing declines in butterfly abundance in this assemblage. In a  
378world ever more characterized by habitat fragmentation, climate change, and consequent sub-  
379division of populations, understanding the forces that drive variation in spatial synchrony among  
380species is critical if we wish to understand shifting population dynamics and preserve fragile  
381meta-populations.

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## 521**Figure Legends**

522**Figure 1:** (A) Map of Northern California (inset) showing our ten study sites, along with a  
523portrayal of the elevational relief present. (B) Histogram displaying the frequency distribution of  
524synchrony indices for the 65-butterfly taxa included in this study. (C-F) Time series (1999-2014)  
525of four butterfly taxa representative of the variation in synchrony among species (C, *Vanessa*  
526*cardui* (synchrony index: 0.82); D, *Papilio zelicaon* (index: 0.07); E, *Junonia coenia* (index:  
5270.56); F; *Glaucopsyche lygdamus* (index: 0.09))

528**Figure 2:** Explained variance in spatial synchrony among Northern California butterfly species  
529by SEM: limited to dispersal propensity (“Dispersal”), sensitivity to climate (“Climate”), or the  
530combined influences of both drivers of spatial synchrony (e.g., dispersal and climate)  
531(“Combined”). Dark gray bars represent SEM models from which migrants were excluded  
532(leaving 56 species), while light gray bars represent variance explained when all species were  
533considered (65 species). The “Random” bar represents variance explained for each model when  
534nine species were randomly removed from the original 65 species. Models were permuted 1000  
535times and the mean and 95% confidence interval of variance explained is plotted (see Methods).

536**Figure 3:** Structural equation models (SEM) of synchrony as driven by taxon-specific responses  
537to climatic variation and natural history traits associated with dispersal. Circles represent “latent”  
538variables generated by factor analysis that together describe a taxon’s sensitivity to local weather  
539conditions and natural history traits associated with dispersal (see *Methods*). The variable  
540denoted “Abundance” is the average fraction of days a species was observed (out of the total  
541number of visits per year) across the study area over the 27 year long study period—a proxy for  
542abundance (Casner et al. 2014). The variable denoted “Avg. Sites Occupied” is the average  
543number of sites occupied by a taxon across the study area over the study period. “Population  
544Trend” refers to inter-annual trend in population density for a particular taxon. In all three  
545models, path coefficients were standardized and path widths scale with coefficient sizes (see  
546legend at top of figure). Arrows represent positive coefficients, while lines ending with a circle  
547represent negative coefficients. Paths in grey represent insignificant coefficients, while those in  
548black with an asterisk (\*) denote significance ( $p \leq 0.05$ ; see supplementary tables for exact p-  
549values). A) “Natural History” SEM modeling synchrony as driven by natural history traits with  
550all butterfly species included ( $\chi^2 = 1.41, p = 0.84, df = 4, n = 65$ ). B) “Natural History” SEM

551 modeling synchrony as driven by natural history with migratory butterfly species excluded ( $\chi^2 =$   
 552 4.42,  $p = 0.35$ ,  $df = 4$ ,  $n = 56$ ). C) “Climate” SEM to model synchrony as driven by sensitivity to  
 553 climate with all butterflies included ( $\chi^2 = 5.41$ ,  $p = 0.80$ ,  $df = 9$ ,  $n = 65$ ). ENSO refers to  
 554 sensitivity of a taxon to the sea surface temperature anomaly, a proxy for the severity of the El  
 555 Niño Southern Oscillation (ENSO). D) “Climate” SEM to model synchrony as driven by  
 556 sensitivity to climate with migratory butterflies excluded ( $\chi^2 = 16.36$ ,  $p = 0.06$ ,  $df = 9$ ,  $n = 56$ ;  
 557 see Table S1 for migratory species excluded).

558 **Figure 4:** Structural equation models (SEM) that describe the combined effects of natural  
 559 history traits and sensitivity to weather on spatial synchrony. Paths are represented similarly to  
 560 Figure 2. “Disp. 1” and “Disp. 2” refer to two factors extracted from a factor analysis of species-  
 561 specific dispersal propensity (see *Methods*). “Clim. 1” and “Clim. 2” refer to two factors  
 562 extracted from a factor analysis of sensitivity to local weather. A) An SEM constructed using  
 563 data from all focal species, which was well supported ( $\chi^2 = 15.2$ ,  $p = 0.65$ ,  $df = 18$ ,  $n = 65$ ). B)  
 564 An SEM calculated while omitting migratory taxa (Table S1). The overall model structure was

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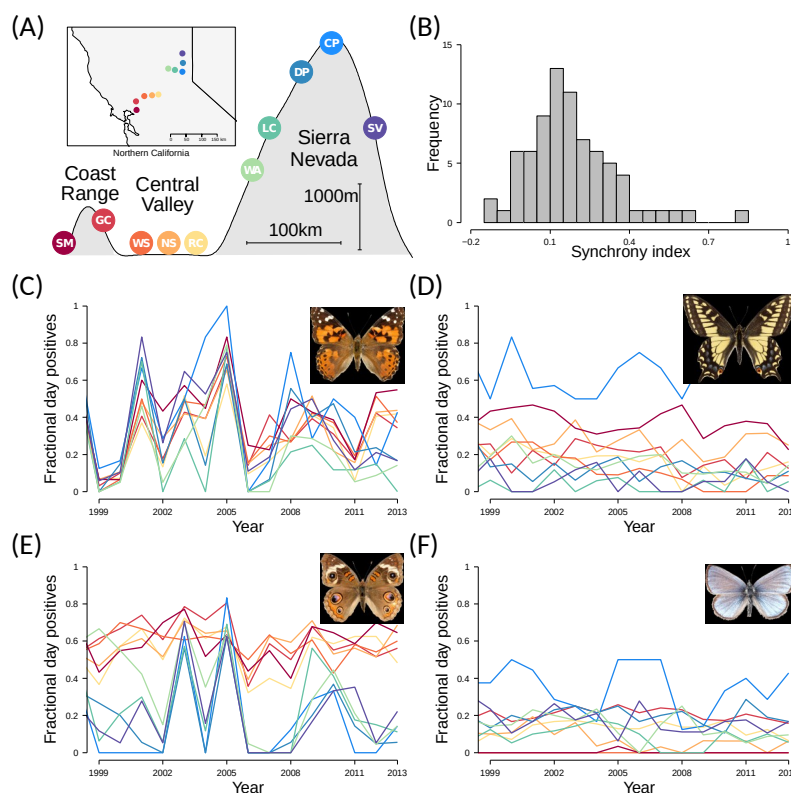
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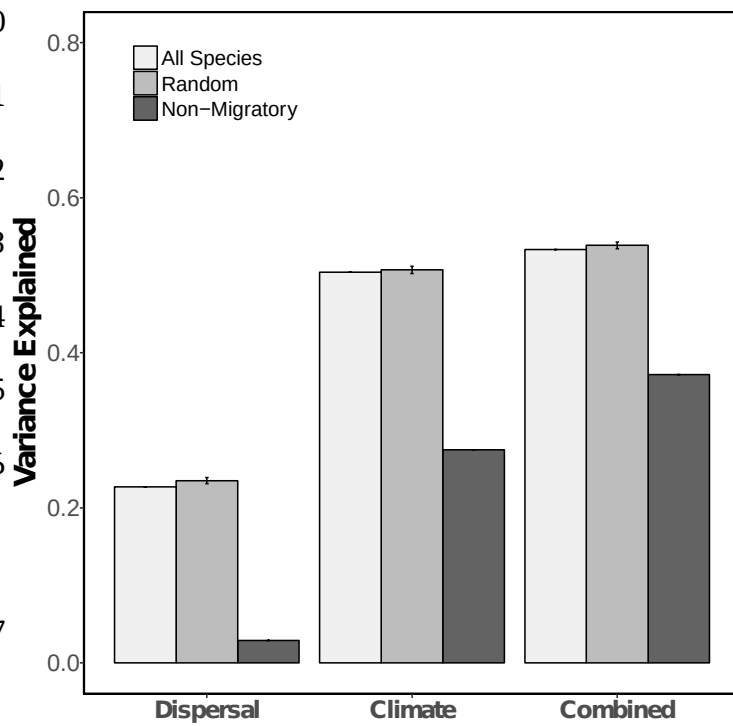
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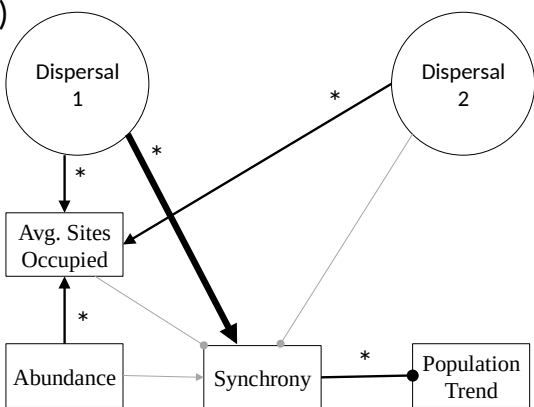
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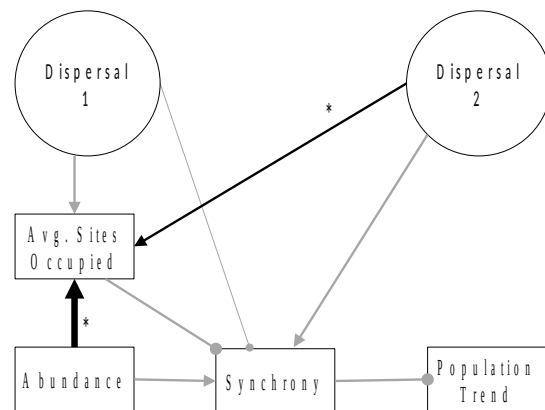
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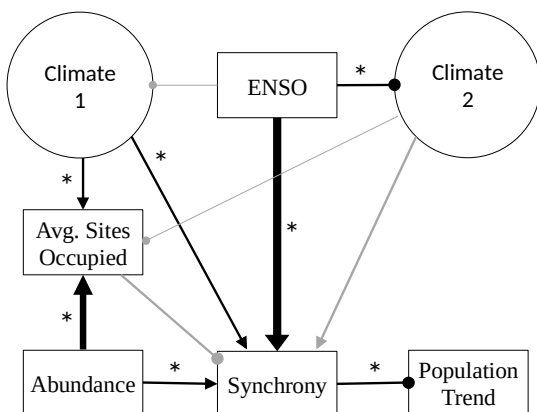
611 (A)



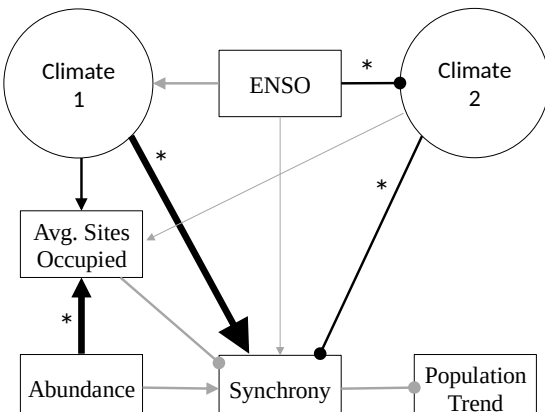
(B)



617 (C)



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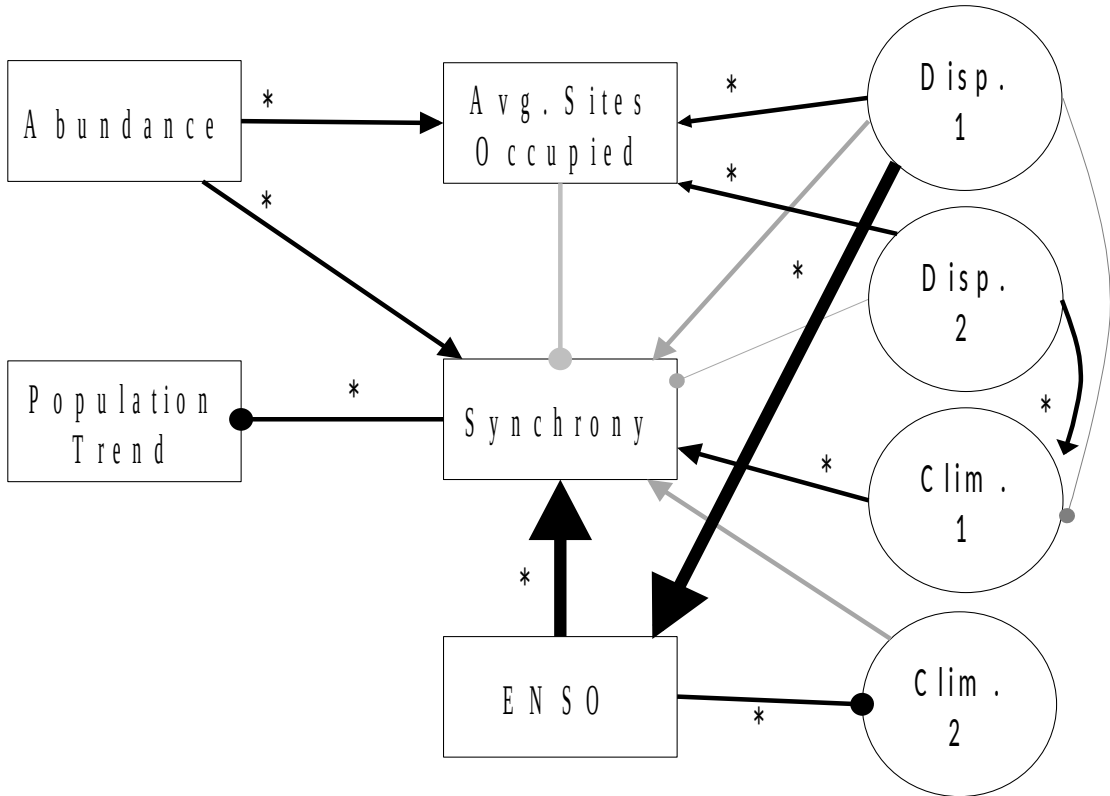
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635 B)

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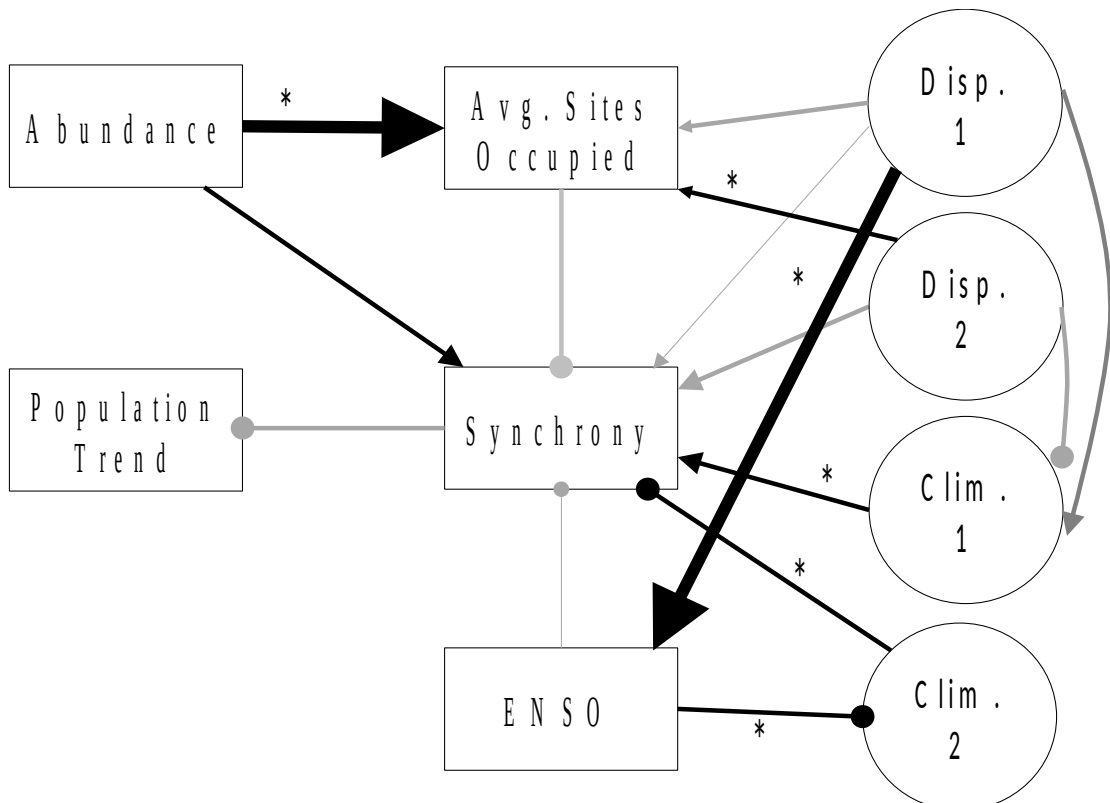
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