

Why are monarch butterflies declining in the West? Understanding the importance of multiple correlated drivers

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Abstract. Understanding the factors associated with declines of at-risk species is an important first step in setting management and recovery targets. This step can be challenging when multiple aspects of climate and land use are changing simultaneously, and any or all could be contributing to population declines. We analyzed population trends of monarch butterflies in western North America in relation to likely environmental drivers. Unlike the larger eastern monarch population, past analyses of western monarchs have only evaluated the importance of climate (i.e., not land use) factors as drivers of abundance. We used partial least squares regression (PLSR) to evaluate the potential importance of changes in land use and climate variables. Trends in western monarch abundance were more strongly associated with land use variables than climate variables. Conclusions about importance of climate and land use variables were robust to changes in PLSR model structure. However, individual variables were too collinear to unambiguously separate their effects. We compared these conclusions to the more widely used technique of multiple regression, followed by multi-model inference (MRMI). Naïve interpretation of MRMI results could be misleading, if collinearity were not taken into account. MRMI was also highly sensitive to variation in model construction. Our results suggest a two-pronged approach to monarch conservation, specifically, starting efforts now to restore habitat, while also using experiments to more clearly delineate separate effects of climate and land use factors. They also demonstrate the utility of PLSR, a technique that is growing in use but is still relatively under-appreciated in conservation biology.

Key words: climate change; endangered species; glyphosate; habitat loss; land use change; multimodel inference; multiple regression; neonicotinoids; partial least squares regression; pesticide; threats analysis.

INTRODUCTION

Conservation biologists often need to understand the factors causing declines of at-risk species, but cannot always isolate or experimentally manipulate hypothesized environmental drivers of population dynamics (Davidson et al. 2012, Earl et al. 2018). This issue has become particularly problematic in recent years because, in many parts of the world, both land use and climate are changing simultaneously in ways that might affect population viability of many species, and it is difficult to disentangle their effects (Didham et al. 2005, Fagan and Holmes 2006, Brook et al. 2008). Even in a carefully planned correlative study, many aspects of land use and climate are likely to be changing together in ways that may affect population viability of focal species (Selwood et al. 2015, Zeigler et al. 2017). An important challenge

for conservation biologists is to use such environmental data to evaluate hypothesized drivers of population declines in ways that neither overstate nor understate confidence in the causal relationships.

Understanding contributions of different factors to population declines is essential for mitigating declines and enacting protections. In the United States, this information can help to determine whether a species should be protected under the Endangered Species Act (Smith et al. 2018). Listing in some cases is contingent on whether current practices are deemed sufficient to recover the species without government protection. For example, in 2010, the U.S. Fish and Wildlife Service determined that the Greater Sage-grouse (*Centrocercus urophasianus*) warranted listing. The Service reversed this decision in 2015, determining that listing was precluded because primary threats had been ameliorated through conservation efforts by public and private landowners (USFWS 2015). In other words, it was deemed low priority for federal protection because private land management actions seemed adequate to make

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near-term extinction unlikely. Now, similar criteria may be applied to monarch butterflies (*Danaus plexippus plexippus*), a formerly widespread species that has been under consideration for listing under the U.S. Endangered Species Act (USFWS 2018). Public and private organizations have begun extensive programs to protect the breeding and migratory habitat (Pleasants 2017, Thogmartin et al. 2017a), some of which were initiated with the specific goal of preemptively preventing listing.

The monarch butterfly has two migratory populations, which winter in reproductive diapause at overwintering sites then spread northward over multiple generations for breeding. These populations differ morphologically in common garden experiments (Davis et al. 2005, Altizer and Davis 2010), in spite of admixture (Lyons et al. 2012). The western population primarily overwinters in coastal California and breeds west of the Rocky Mountains. The larger eastern population overwinters in central Mexico and breeds east of the Rocky Mountains. During the past half-century, the eastern monarch population has declined by ~80% (Semmens et al. 2016), and the western population has declined by ~95% (Schultz et al. 2017), with an additional drop in 2018 to <1% of historic size (Pelton et al. 2019). Several recent studies (Thogmartin et al. 2017b, Boyle et al. 2019) have evaluated the potential contributions of different factors to population dynamics of the eastern monarch population. Here, we evaluate the importance of different aspects of climate and land use change for the western monarch population, with special emphasis on how we make inferences about the importance of these correlated variables, and what actions might mitigate these threats in the short and long term.

Land use change has not previously been evaluated in relation to western monarchs, but is among the primary threats faced by eastern monarchs (Thogmartin et al. 2017b, Stenoien et al. 2018). Deforestation of overwintering forests was one of the earliest causes of concern for eastern monarch population viability (Vidal et al. 2013) and is a leading correlate of abundance (Thogmartin et al. 2017b). In the breeding range, agricultural intensification and associated decline in milkweed (*Asclepias* spp., monarch host plants), formerly common in agricultural landscapes, are also strongly associated with eastern monarch declines (Pleasants and Oberhauser 2013, Boyle et al. 2019). For instance, increased use of glyphosate explains 77% of annual variation in monarch abundance through time (Thogmartin et al. 2017b). More generally, use of herbicides, herbicide-resistant crops, and insecticides has increased throughout the United States in recent decades (Benbrook 2016). Although land use change has not been evaluated as a driver of western monarch declines, neonicotinoid insecticide use is correlated with declines in butterfly diversity in California (Forister et al. 2016).

Relative to land use change, relationships between monarch abundance and climate are more heterogeneous and less well understood. After accounting for overall

negative population trends, breeding season monarchs in central California from 1972 to 2014 tended to be more abundant in years with warmer and wetter springs (Espeset et al. 2016). Western monarch abundance is also negatively correlated with drought (Stevens and Frey 2010). Together, these results have been interpreted as an indication that the primary threat to western monarchs may be increasing frequency and intensity of drought (Mann and Gleick 2015), with the caveat that land use change in the West had not been evaluated as a possible competing driver (cf. Espeset et al. 2016, Malcolm 2018). Similar to the West, higher precipitation in the spring led to larger eastern monarch populations by the end of the breeding season (Zipkin et al. 2012). Warmer springs in the summer breeding grounds were also associated with higher abundance (Zipkin et al. 2012), although, after accounting for effects of land use change, hot temperatures in August correlated negatively with residual variation in eastern monarch abundance on overwintering grounds (Thogmartin et al. 2017b).

We evaluate land use and climate variables as potential drivers of western monarch abundance on overwintering grounds in California from 1982 to 2016. During this period, the population dropped from ~3 to 10 million butterflies in the 1980s to ~200–300 thousand butterflies in the 2000s, with substantial fluctuations in the 1990s (Schultz et al. 2017). We began with a set of seven environmental variables that are the most widely cited threats to monarch populations (Stevens and Frey 2010, Zipkin et al. 2012, Thogmartin et al. 2017b): temperature and precipitation in the overwintering and breeding grounds (four variables), land conversion of overwintering sites, and use of two common pesticides: glyphosate, an herbicide that incidentally kills host and nectar plants, and neonicotinoids, a class of insecticides. Hereafter, we refer to this as the *a priori* predictor analysis, which also includes an eighth predictor: monarch abundance in the previous year. Considering a limited number of well-understood causal variables is widely encouraged in wildlife biology to prevent spurious correlations (Burnham and Anderson 2002). However, although analyses that consider only *a priori* hypotheses are good at determining relative support for different predictor variables, they are inherently subject to the existing biases of expert opinion. Therefore, we also considered a more extended set of 29 predictors, which includes a number of additional weather and pesticide-use variables. Hereafter, we refer to this as the “kitchen sink” analysis, with the recognition that evaluating 29 possible predictor variables for a 36-yr time series is likely subject to spurious correlations, as well as new hypotheses.

For both analyses, we used partial least squares regression (PLSR) to investigate the influence of multiple correlated variables on monarch abundance (Carrascal et al. 2009, Thogmartin et al. 2017b). PLSR deals with collinearity by estimating linear combinations of the predictor variables (here, climate and land use variables)

that best explain variation in the response variable (here, monarch butterfly abundance; Carrascal et al. 2009). PLSR is similar to principle components analysis (PCA), a technique that is currently more widely used in population and community ecology (cf. Gotelli and Ellison 2013). However, PLSR is better suited to identifying environmental drivers because it is a “supervised” analysis that finds the components that best explain the response variable, whereas PCA is an “unsupervised” analysis that finds components that simply capture variation in the predictor variables (James et al. 2013). PLSR is also well-suited to identifying cases where there is ambiguity in the set of causal variables (see *Results*). Finally, for comparison, we include a multiple regression analysis of the eight a priori variables, with multi-model inference across all possible models (hereafter, MRMI). Because MRMI is widely used but performs poorly in this situation, we include a brief exploration of what features of the data cause MRMI to fail in our situation.

METHODS

Monarch butterfly abundance

Western monarchs breed throughout western North America, and primarily overwinter in forested groves in coastal California, though some migrate to Mexico (Jepsen and Black 2015, Morris et al. 2015; Fig. 1). In early spring, wintering butterflies leave roosting grounds and breed in California and adjacent Nevada and Arizona (Dingle et al. 2005; C. B. Schultz et al., *unpublished data*). The population expands to Oregon, Washington, Idaho, and British Columbia (as well as other western states) over two to three successive generations, the last of which migrates back to overwintering sites in the fall. Because there are no systematic efforts to assess western monarch abundance in the breeding range, we use monarchs in the wintering grounds as our metric of relative abundance through time. Monarchs have been counted in coastal California overwintering groves intermittently from 1981 to 1996, and systematically from 1997 to present as part of the Xerces Society Western Monarch Thanksgiving Count (information *available online*).⁵ We previously analyzed these data with state-space models to obtain an estimate of the total wintering population size in each year (Schultz et al. 2017: their Fig. 2a). Here, we use the estimates from Schultz et al. (2017) as our primary metric of abundance. Because this abundance index comes with uncertainty, we accounted for uncertainty in annual abundance estimates by repeating PLSR analyses (described in *Analyses: partial least squares regression*) using 5,000 bootstrapped time series of abundance, generated by sampling from the mean and standard error of the estimate of abundance for each year.

⁵ www.westernmonarchcount.org

Land use change

Overwintering habitat.—We assessed coastal development using data from the California Farmland Mapping and Monitoring Program (FMMP; information *available online*).⁶ FMMP reports changes in urban and other land cover types from 1984 to 2014 in 2-yr intervals. We extracted developed land in each year within a 500 m radius around the centroid of each Thanksgiving Count overwintering site. To estimate annual values, we interpolated between biannual records in the FMMP data set. We extrapolated data for 1982–1983 (prior to the start of FMMP) and 2015–2016 (which had not been published yet) using lag-1 autoregressive moving average models (implemented using the nlme function [Pinheiro et al. 2018], in R [R Core Team 2018]).

Breeding habitat.—Pesticide use is a general measure of overall agricultural intensification in breeding habitat, and use of glyphosate in particular has been linked to monarch habitat loss in the east (Stenoien et al. 2018). We compiled data on commonly used pesticide classes from the California Department of Pesticide Regulation (CDPR) Pesticide Use Reporting database (information *available online*).⁷ Data from 1990 to 2016 are maintained in a searchable database, and 1981–1989 are in CDPR archives. Other states in the West do not maintain comparable systematic annual records, but trends in California pesticide use are parallel to other parts of the West (Sleeter et al. 2013, USGS 2016). We compiled CDPR data on annual use of two herbicides (glyphosate and dicamba) and five classes of insecticides (neonicotinoids, carbamates, organophosphates, pyrethroids, and organochlorines). Neonicotinoids include the five nitroguanidine neonicotinoid insecticides that are most persistent and prevalent in the West: acetamiprid, clothianidin, dinotefuran, imidacloprid, and thiamethoxam (Forister et al. 2016, Mogren and Lundgren 2016). CDPR tracks agricultural and non-agricultural use separately, and we kept these differences in our database. The additional four classes of insecticides are the most widely used non-neonicotinoid insecticides and have been included in prior analyses investigating associations between butterfly abundance and pesticide use in California (Forister et al. 2016).

Climate variables

Overwintering grounds.—For each site in our analysis (Schultz et al. 2017), we averaged climate variables from December to February using data from the PRISM database (information *available online*).⁸ We extracted total monthly precipitation, minimum monthly temperature, mean monthly temperature, and maximum

⁶ <http://www.conservation.ca.gov/dlrp/fmmp>

⁷ <https://www.cdpr.ca.gov/docs/pur/purmain.htm>

⁸ <http://www.prism.oregonstate.edu>

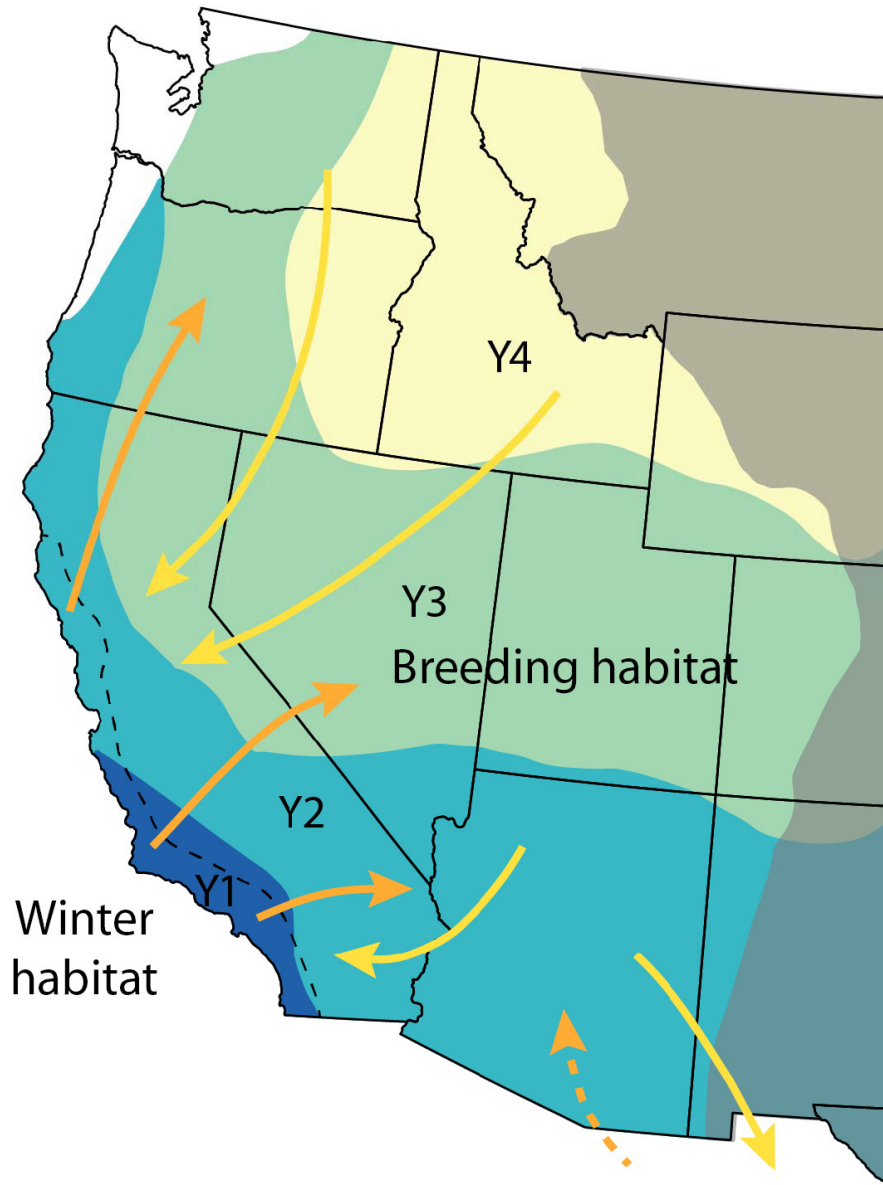


FIG. 1. Map of western monarch breeding and wintering in the West. The dotted line identifies the eastern limit of coastal winter habitat. Orange and yellow arrows identify hypothesized spring and fall migration routes. Colored bands (blue, green, and yellow) correspond to four regions of breeding habitat defined by Yang et al. (2016; Y1–Y4), based on isotopic differences in the birthplaces of overwintering monarch butterflies. Gray areas are outside the known range of western monarch breeding habitat, and white areas do not currently support milkweed.

monthly temperature. For each measure, we averaged the values across all overwintering sites each year.

Breeding habitat.—We compiled temperature and drought data averaged across the breeding range. We quantified drought using the Palmer Drought Severity Index (PDSI), averaged from January to September (Stevens and Frey 2010). We quantified temperature using average monthly maximum June–August temperature (T_{\max}) with temperature data from the NCDC, and

cooling degree days (days in which average temperature exceeds 18°C; CDD) in June–August. We first calculated temperature and drought indices separately for four regions defined by their contribution to the western breeding population (Fig. 1, corresponding to hydrogen isotope regions used by Yang et al. 2016, to identify sources of breeding monarchs). Hereafter, we refer to these four regions as: Y1, Y2, Y3, and Y4 (“Y” for Yang et al. [2016]). We also calculated the average of these metrics across the four regions, as a measure of overall

TABLE 1. Summary statistics from secondary analyses, including the “kitchen sink” partial least squares regression (PLSR) and multiple regression, followed by multimodel inference (MRMI).

Variable	Role in a priori PLSR	“Kitchen sink” PLSR				Multiple regression (MRMI)	
		VIP 1	VIP 2	Load 1	Load 2	w_i	β_i
Coastal development	included	1.65	1.45	−0.28	−0.14	0.50	−0.72
Glyphosate use, agricultural	summed	1.53	1.32	−0.28	−0.10	0.58	−0.97
Glyphosate use, non-agricultural	summed	1.69	1.56	−0.26	−0.23	0.58	−0.97
Dicamba use		0.83	0.75	0.13	0.07		
Neonicotinoid use, agricultural	summed	1.16	1.06	−0.25	−0.04	0.63	0.71
Neonicotinoid use, non-agricultural	summed	1.44	1.25	−0.26	−0.03	0.63	0.71
Carbamates		1.09	0.99	−0.24	0.01		
Organophosphates		0.49	0.68	0.15	−0.05		
Organochlorines (including DDT)		1.67	1.57	0.24	0.22		
Pyrethroids		1.51	1.31	−0.27	−0.09		
Coastal winter minimum temperature	included	0.16	0.44	−0.08	0.07	0.92	0.44
Coastal winter maximum temperature		0.07	0.62	−0.06	0.24		
Coastal winter average temperature		0.27	0.64	−0.02	0.33		
Coastal winter precipitation	included	0.05	0.52	0.07	−0.24	0.31	−0.20
Breeding season maximum temperature							
Y1	averaged	0.65	0.80	−0.18	0.26	0.22	−0.08
Y2	averaged	1.03	0.98	−0.24	0.18	0.22	−0.08
Y3	averaged	0.60	0.92	−0.20	0.36	0.22	−0.08
Y4	averaged	0.51	0.93	−0.19	0.36	0.22	−0.08
Breeding season cooling degree days (CDD)							
Y1		0.58	0.82	−0.18	0.27		
Y2		1.13	1.05	−0.25	0.17		
Y3		0.74	0.93	−0.21	0.34		
Y4		0.68	0.83	−0.19	0.32		
Breeding season Palmer Drought Severity Index (PDSI)							
Y1	averaged	0.33	0.64	0.13	−0.22	0.35	0.24
Y2	averaged	0.73	0.80	0.19	−0.20	0.35	0.24
Y3	averaged	0.85	0.76	0.14	−0.12	0.35	0.24
Y4	averaged	0.88	0.78	0.14	−0.07	0.35	0.24
SOI		0.25	0.33	−0.07	−0.07		
MEI		0.30	0.26	0.06	0.05		
Previous abundance	included	1.83	1.88	0.23	0.24	1.00	1.13

Notes: Related statistics for the a priori PLSR are shown in Fig. 4. Y1–Y4 are climate areas defined in Fig. 1. SOI, Southern Oscillation Index; MEI, Multivariate ENSO Index.

conditions (Table 1). We compiled data on two region-wide indices of the El Niño Southern Oscillation (ENSO) that may be associated with butterfly abundance, MEI (Multivariate ENSO Index) and SOI (Southern Oscillation Index; data available online).^{9,10}

Analyses

Univariate correlations.—To aid in interpretation of the multivariate analyses, we calculated all pairwise univariate correlations between the predictor variables used in each analysis, log-transformed monarch abundance in each year, log-transformed population growth rates

(change in abundance on a log scale), and year. We visualized and calculated these correlations using base functions in R and the *panel.cor* function.

Partial least squares regression.—We used PLSR to predict a single response variable (here, monarch abundance) from a number of predictor variables (here, land use and climate variables). PLSR generates orthogonal predictors that are weighted sums of the original predictor variables, selected to best explain variation in a response variable (see Chong and Jun 2005, Mehmood et al. 2012 for technical descriptions of PLSR and James et al. 2013 for a textbook-level introduction). The contributions of the input variables to each component are quantified by their loading, i.e., their correlations with each component, and their Variable Importance in the Projection (VIP), a cumulative measure of the relative

⁹ <https://www.esrl.noaa.gov/psd/enso/mei/>

¹⁰ <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>

contributions of each predictor variable to the first n components of the PLSR model. Because VIP is scaled to have an average value of 1, we use VIP as a qualitative measure of relative contribution, not a significance test. Unlike some model selection techniques that aim to identify a single best set of predictor variables, PLSR loadings should be interpreted as the potential importance of different factors. If a large number of correlated variables have high PLSR loadings, any or all could be the cause of abundance changes over time.

We implemented PLSR models using the `pls` package (Mevik et al. 2016) in R, and the `VIP.R` function. Models were evaluated using leave-one-out cross validation, and statistical significance of components was evaluated using the randomization test in the `selectNcomp` function. All models included natural-log-transformed monarch abundance as the dependent variable, and the log of abundance in the previous year as a predictor variable. Including previous abundance generalizes the model to include effects of environmental variables on growth rate as a nested model; if the slope coefficient for previous abundance were exactly one, and previous abundance was the only variable that determined the first PLSR component, then the second component would be an analysis of population growth rate, i.e., previous abundance would be equivalent to an offset in linear regression (recall that $\ln(A) - \ln(B) = \ln(A/B)$, so an offset is one way to estimate population growth rates from abundance data). For our data set, the first component was very highly correlated with previous abundance (*Results*), so the second, orthogonal, PLSR component approximates predictors of growth rate. In addition to previous abundance, the a priori model included seven environmental predictor variables: the proportion of developed lands near overwintering sites, glyphosate use, neonicotinoid use, average winter minimum temperature and winter precipitation at wintering sites, and average summer maximum temperature and summer drought severity (PDSI) in the breeding range (Table 1). In addition to previous abundance, the “kitchen sink” model included 28 environmental predictor variables, including additional weather and pesticide variables (Table 1).

Multiple regression (MRMI).—We report the results of multiple regression, followed by multimodel inference, for comparison with PLSR. In ecology, MRMI is currently one of the most widely used approaches for evaluating environmental correlates of ecological time series. The aim of this analysis is to illustrate how MRMI plays out for these data if implemented using typical off-the-shelf methods. Presenting this analysis is relevant to guiding management because MRMI is the most obvious analysis ecologists might apply to these kinds of multivariate data. For our data, this analysis violates a general rule of thumb in statistics texts, specifically, the rule that multiple regression models should not include highly correlated variables. One textbook solution to this issue (Zuur et al. 2010) is simply to use only an uncorrelated subset of variables in a

regression model, e.g., including glyphosate use only in our models, and stating verbally that glyphosate use is a surrogate for herbicide use, insecticide use, overwinter habitat development, temperature, and previous abundance. One problem with the reduced-variable solution is that we are explicitly interested in quantifying relative support for these different drivers of abundance. Another problem is that analyses of reduced-variable models are often interpreted as if the one variable included in the model were the primary driver of the response, as opposed to a surrogate for many correlated factors (cf. Thogmartin et al. 2017b). In part, our goal is to pre-empt future analyses that might lead to misleading inferences about causes of western monarch declines, and to add to the set of case studies showing when to use or not to use MRMI (see also Cade 2015, Banner and Higgs 2017).

We conducted MRMI using the a priori variable set. We fit a global model with all eight predictors and used the dredge function in the `MuMIn` package in R (Barton 2018) to search all possible variable combinations. Over this set of all possible models, we calculated importance values for each predictor variable (i.e., Akaike weights; Burnham and Anderson 2002) summed over all models including that predictor) and model-averaged standardized regression coefficients. To aid interpretation of results of variable importance and model-averaged coefficients, we explored selected subsets of the variable sets included in the global model. For these comparisons, we calculated importance values and model-weighted regression coefficients only over the appropriate subset of models, i.e., over new “global” models with five, six, or seven predictor variables (as appropriate), not the full eight variables. We did not apply MRMI to the larger “kitchen sink” parameter set because multiple regression is not meaningful when the number of predictor variables is approximately equal to the number of observations in a data set.

RESULTS

Univariate correlations

Nearly all of the variables included in the a priori analysis were changing through time, i.e., significantly correlated with year (Fig. 2, bottom row and right column). Coastal developed land area, glyphosate use, and neonicotinoid use increased through time (Pearson's $r = 0.99$, 0.98 , and 0.92 , respectively). Breeding season temperature and drought also increased through time, though not as strongly ($r = 0.48$ and -0.42 , noting that PDSI *decreases* with drought). Coastal winter minimum temperature and precipitation did not change significantly ($r = 0.28$ and -0.05). Monarch abundance also declined ($r = -0.76$), and was negatively correlated with coastal development, glyphosate use, neonicotinoid use, breeding season temperature and breeding season drought ($r = -0.77$, -0.75 , -0.59 , -0.33 , and 0.42 ; Fig. 2, top row and left column, noting that PDSI

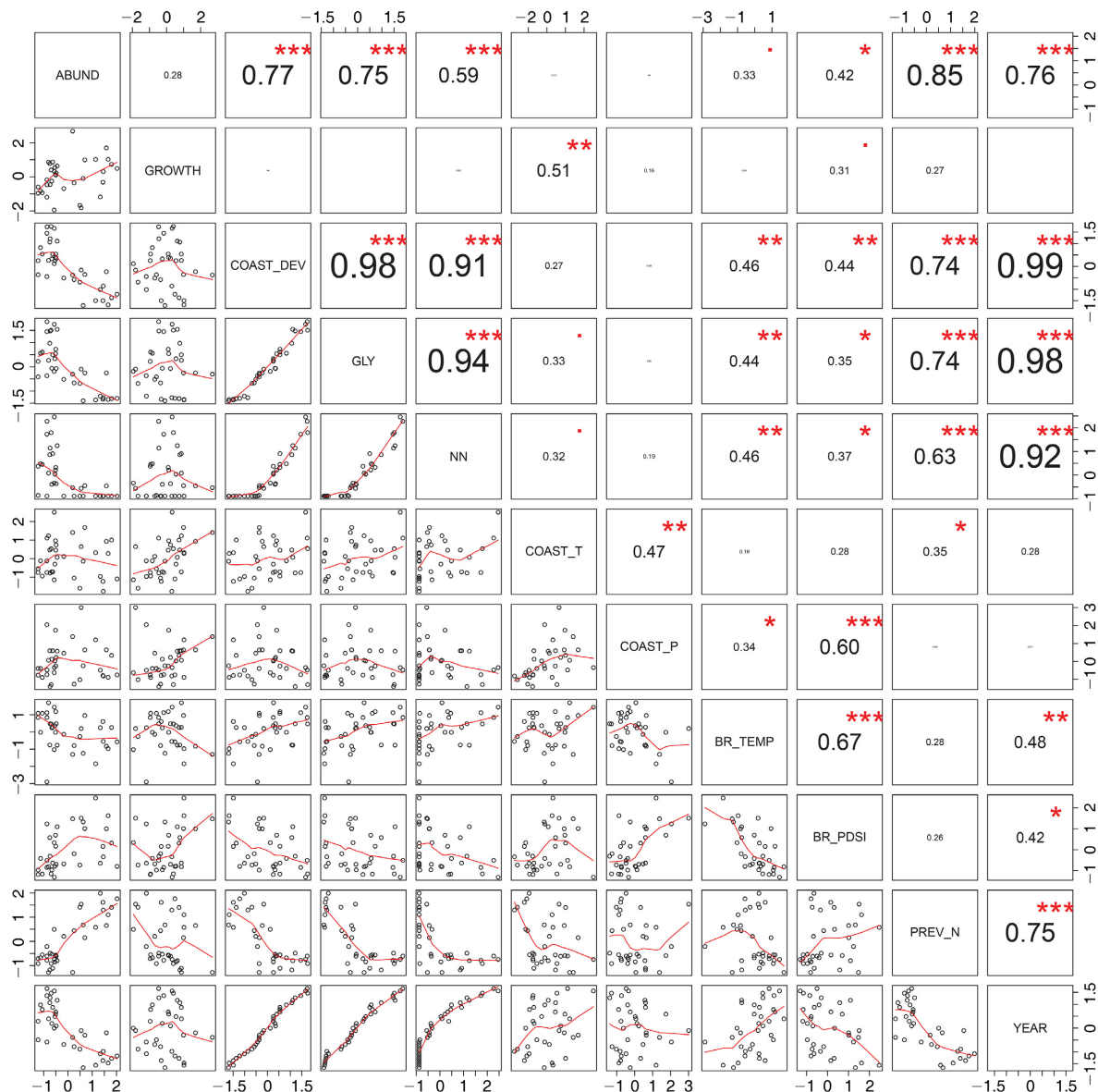


Fig. 2. Scatterplot matrix of standardized variables included in the a priori partial least squares regression (PLSR) and multi-model inference (MRMI) analyses. The first two variables are the log-scale abundance index in coastal wintering groves, and log-scale annual growth rate. Other variables follow the order of presentation in Table 1. For graphical presentation, all variables were scaled to have a mean of 0 and standard deviation of 1. Red lines in scatterplots (lower left) identify moving average values. Font size of correlation coefficients (shown as absolute values, upper right) is proportional to statistical significance of the correlation coefficient. Red dots and stars indicate statistical significance of correlations: “.” = $0.10 > P > 0.05$, * = $0.05 > P > 0.01$, ** = $0.01 > P > 0.001$, *** = $P < 0.001$.

decreases with drought). Annual population growth rates were higher following years with warmer winters ($r = 0.51$). Since the population was declining overall, monarch abundance in the current and previous years was positively correlated ($r = 0.85$). The set of a priori predictor variables was also highly collinear, with very strong correlations ($r > 0.9$) among coastal development, glyphosate use and neonicotinoid use, and weaker but statistically significant correlations among these variables and breeding temperature and drought

($0.70 > |r| > 0.35$). Coastal winter temperature was positively correlated with coastal winter precipitation ($r = 0.47$), but not with other variables. Coastal winter precipitation was negatively associated with breeding season temperature and drought ($r = -0.34$ and 0.60 , noting that PDSI decreases with drought).

The full set of variables in the “kitchen sink” analysis was also highly collinear, and strongly associated with monarch abundance (Appendix S1: Fig. S1). Seventeen of the 28 environmental predictor variables were

changing through time (Pearson correlation with year, $|r| > 0.34$, $P < 0.05$) and fifteen were correlated with monarch abundance (Pearson correlation with log-abundance, $|r| > 0.34$, $P < 0.05$). About half of the pairwise correlations among the predictor variables were statistically significant (Pearson correlation, $|r| > 0.34$, $P < 0.05$). The only significant correlations with annual growth rate were minimum and maximum coastal winter temperature ($r = 0.51$ and $r = 0.40$).

PLSR analysis

A priori analysis.—The first two components of the a priori PLSR model were statistically significant ($P < 0.001$ and $P = 0.007$, respectively, Appendix S1: Fig. S2). The first component explained 64% of variation in monarch abundance, and the second explained 18.5% (Fig. 3). None of the later components were statistically significant, and none explained $>3\%$ of variation in abundance. The first PLSR component was strongly negatively associated with land use variables (coastal development, glyphosate use, neonicotinoid use) and positively associated with previous abundance (VIP > 1 , $|\text{loadings}| > 0.35$, Fig. 4A, B), more weakly negatively associated with breeding season temperature and drought (VIP > 0.5 , $|\text{loadings}| = 0.3\text{--}0.35$, noting that PDSI decreases with drought), and not associated with coastal winter temperature or precipitation.

Because the first component was strongly associated with previous abundance, the second PLSR component approximates population growth rate, i.e., the annual difference between current and previous abundance (*Methods*). Coastal winter temperature and precipitation both had higher VIP values (0.67 and 0.44) when the first two components were considered (Fig. 4A, C), capturing the

positive association between population growth rate with warmer, and, to a weaker extent, drier winter conditions near overwintering sites (see univariate relationships in Fig. 2). Breeding season temperature was also significantly positively associated with the second PLSR component. This combination of a negative relationship between breeding season temperature and the first PLSR component and a positive relationship with the second PLSR component reflects a nonlinear, concave relationship between breeding season temperature and monarch abundance (see univariate relationship in Fig. 2). Conclusions were also broadly robust to estimation error in monarch abundance (shown as error bars in Fig. 4).

“Kitchen sink” model.—The kitchen sink PLSR, with 29 variables (28 environmental drivers + previous abundance) performed slightly worse than the a priori model. The first two components were statistically significant ($P < 0.001$ and $P = 0.016$, respectively, Appendix S1: Fig. S2), and explained slightly less variation in monarch abundance than the a priori model with eight variables (57.5% and 19.1% of variation in monarch abundance explained by the first and second components). The “kitchen sink” model also had noticeably higher prediction error than the a priori model (Appendix S1: Fig. S2). As in the a priori model, the first component was strongly positively associated with coastal development, glyphosate use, neonicotinoid use (both agricultural and non-agricultural), and previous abundance (Table 1). Breeding season temperature and drought were also generally negatively associated with monarch abundance, although the strength of this relationship varied among regions, with the strongest loadings of breeding conditions in Y2 on the first PLSR component (Table 1). As a measure of temperature, cooling degree days had slightly higher

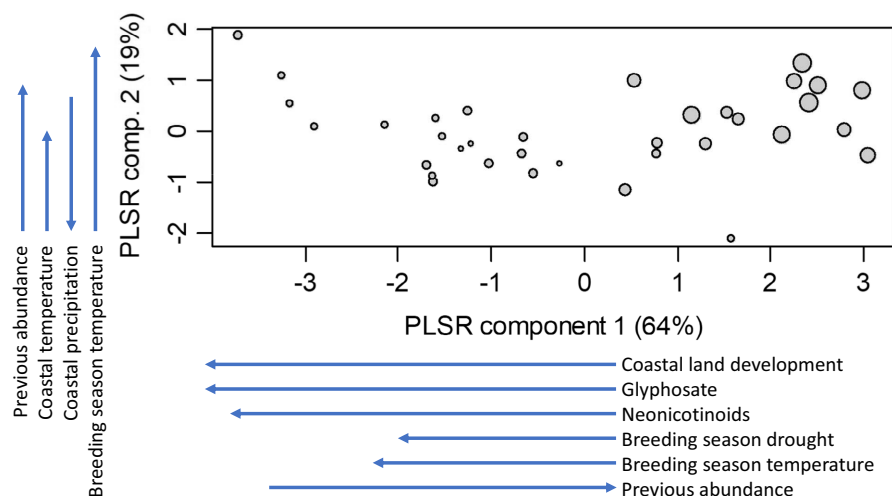


FIG. 3. Biplot of a priori PLSR. Length of arrows is proportional to loading and direction of arrows indicates the direction of each effect. (For visual clarity, the sign of the drought effect is reversed, to reflect smaller sizes with increasing drought, not increasing PDSI, which is inversely related to drought.) Size of points is proportional to log-abundance in each year. Axis length is proportional to the variation in monarch abundance explained by each component.

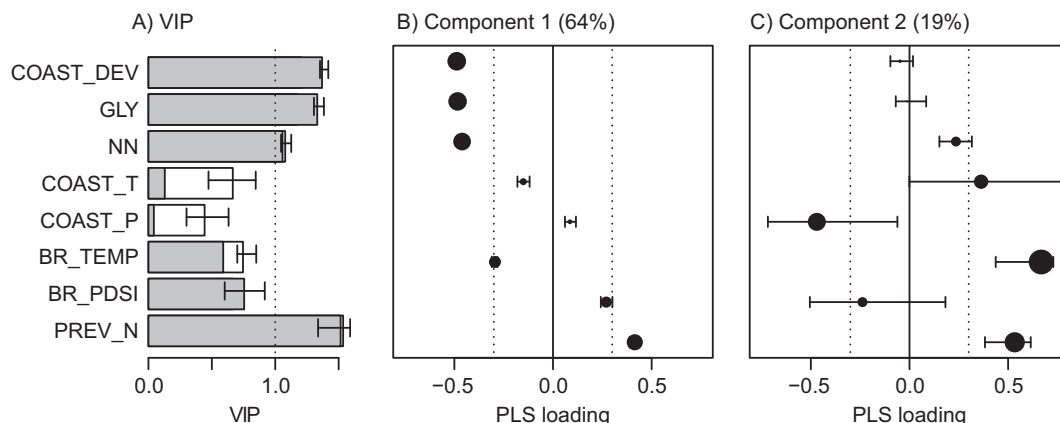


FIG. 4. Partial least squares regression (PLSR) results for a priori model. (A) Variable importance in the projection (VIP), with contributions to the first component in gray and contributions summed over the first and second components in white. (B) Loadings of each variable on the first PLSR component, with size of circles proportional to their loading. (C) Loadings of each variable on the second PLSR component, with size of circles proportional to their loading. Error bars on all three panels were calculated by repeating the analysis over 5,000 bootstrap time series, sampled from the mean and standard error of the abundance index estimate in each year. Variable names are abbreviated as in Fig. 1.

PLSR loadings than maximum temperature (the metric we chose for our a priori analysis, Table 1). Of the additional pesticide variables, pyrethroids also had strong negative loadings on the first PLSR component (Table 1). Organochlorines (the pesticide group that includes DDT), and dicamba use had positive loadings on the first component (Table 1). Use of both declined from the 1980's to the 2010's, so they are positively associated with trends in monarch abundance.

The second component in the “kitchen sink” model was nearly identical to the a priori model. It revealed positive association of annual population growth rates with warmer and drier conditions at winter roosting sites.

MRMI analysis

MRMI explained a slightly higher proportion of variance (85.9% in the global model and 84.3% in the model with the lowest AIC_c) than the first two a priori PLSR axes (82.5%). However, the MRMI variable weights and regression coefficients (Table 1) would be misleading if interpreted without accounting for the strong collinearity among predictor variables.

The variable with the highest importance was abundance in the previous year (Akaike weight, $w_i = 1.00$, standardized regression coefficient, averaged across the subset of models including this term, $\beta_i = 1.13$), followed by minimum temperature at overwintering sites ($w_i = 0.92$, $\beta_i = 0.43$). Glyphosate use and coastal development had very similar values ($w_i = 0.58$ and 0.50 and $\beta_i = -0.97$ and -0.72 , respectively). The contrast between the importance of winter temperature vs. glyphosate and coastal development occurs at least in part because trends in statewide glyphosate use and coastal development are so highly correlated ($r = 0.91$) that they

are effectively substitutable. For each, the relative importance across the subset of models including the other variable was small ($w_i = 0.21$ for coastal development across the subset of models constrained to include glyphosate, and $w_i = 0.24$ for glyphosate across the subset of models constrained to include coastal development), whereas the importance across the subset of models without the other variable was high ($w_i = 0.90$ for coastal development for the subset of models without glyphosate, and $w_i = 0.92$ for glyphosate use across the subset of models without coastal development; see Appendix S1: Table S1). In contrast, coastal winter temperature is only weakly correlated with any of the other predictor variables (Fig. 2), so its influence in statistical models cannot be substituted by other variables (Appendix S1: Table S1).

Neonicotinoid use had a high importance ($w_i = 0.92$), but the model-averaged regression coefficient was positive ($\beta_i = 0.40$), i.e., in the *opposite* direction of the univariate correlation and PLSR loading in relation to monarch abundance. This positive relationship is a statistical artefact of high collinearity among predictor variables included in the model; when neonicotinoids are considered only across the subset of models without any of the three highly collinear ($r > 0.9$, Fig. 1) variables (previous abundance, glyphosate use, and coastal development), i.e., only in the presence of climate variables, its importance was very high, $w_i = 0.99$, and the model-averaged regression coefficient was strongly negative, $\beta_i = -0.94$.

The least important variables in MRMI models were breeding season temperature, drought, and coastal winter precipitation ($w_i = 0.22$, 0.35 , and 0.31 and $\beta_i = 0.24$, -0.08 , -0.20). However, none of these effects are negligible; $w_i = 0.22$ can be loosely interpreted as a 22% chance that breeding season temperature is included in the best model. All three effects are consistent with

conclusions from the univariate correlations and PLSR models, i.e., negative association of monarch abundance with breeding season temperature, breeding season drought, and coastal winter precipitation.

DISCUSSION

Our results reveal many possible explanations for monarch declines in the West, and indicate that potential environmental drivers are too highly correlated to unambiguously discriminate their effects. Nonetheless, there is stronger support for land use change than climate change as the cause of declines. Past studies have investigated climate variables only as drivers of western monarch abundance (Dingle et al. 2005, Stevens and Frey 2010, Espeset et al. 2016). These past analyses, as well as naïve interpretation of our MRMI, could be interpreted as evidence that climate is the primary driver of western monarch populations. In contrast, our PLSR analysis suggests that habitat loss and pesticide use are more likely to be the primary drivers of declines in the West. We strongly encourage future experimental and fine-scale observational studies to disentangle effects of various climate and land-use drivers for western monarch population viability.

In spite of this contrast, our analysis reinforces previously found associations with environmental variables, including the general importance of central California for monarch abundance (compare Table 2 in Stevens and Frey 2010 to the importance of Y2 in our kitchen sink analysis). Similarly, the importance of overwintering habitat loss in the PLSR analysis corroborates speculation by Espeset et al. (2016), who proposed the overwintering stage as an important driver of monarch populations because, at a set of breeding sites in central California, declines in adult monarch abundance were stronger in spring than summer. Espeset et al. (2016) also showed higher abundance of monarchs at breeding sites in years with warmer winter and spring temperatures, and wetter springs. Combined with our results, these results suggest that warm winters and springs generally favor monarchs, but hot summers do not, similar to seasonal patterns shown by Zipkin et al. (2012) for eastern monarchs. Our results are also partly consistent with Forister et al. (2016), who found strong negative associations between annual neonicotinoid use and butterfly abundance across 67 species in California. Their data did not appear to reveal any association between butterfly abundance and carbamates or pyrethroids, both of which were negatively associated with monarch abundance in our “kitchen sink” analysis. This discrepancy may be due to differences in spatial and temporal scale of the two analyses, and it emphasizes that both results are correlational. Experimental investigation of nontarget effects of pesticides on butterflies is an important area for future research.

For this data set, PLSR is clearly a more robust tool than MRMI. Specifically, conclusions about which

variables were associated with declines were broadly consistent across the a priori and kitchen sink models, with only subtle qualitative differences. In contrast, variable weights and regression coefficients from MRMI differed radically, depending on which variables were included in the models. Simulation studies have shown that PLSR is more robust than MRMI, in the sense that it is better at identifying the correct causal variables, especially when sample sizes are low and/or predictor variables are correlated (Selwood et al. 2015). However, past comparisons of PLSR and MRMI (Carrascal et al. 2009, Hosseini et al. 2017) have emphasized smaller quantitative differences in predictive power, not the stark qualitative differences in variable importance and directions of effects we see here. In spite of calls for more careful consideration, MRMI continues to be used in an off-the-shelf manner by many ecologists, perhaps because tools such as PLSR that can be applied where MRMI is inappropriate, e.g., data sets with high collinearity, are still relatively unfamiliar. We hope that this example will reinforce the importance of carefully evaluating the right statistical tool for a particular question and data set. Of course, no statistical tool (including PLSR) is right for all situations. For example, it is tempting to include long lists of candidate predictor variables in PLSR models because PLSR is theoretically able to handle very large numbers of predictor variables. In such cases, however, models are subject to overfitting and begin to lose their ability to identify the correct variables, as evidenced by lower performance of our kitchen sink model compared to the a priori PLSR model (see also James et al. 2013).

A final important message from our analysis is that inference is ultimately limited by the available data. Our analysis is based on counts of monarch butterflies at overwintering sites because these are the only systematic data available for this population. Therefore, analyses of herbicides, insecticides, and breeding season climate conditions involve extrapolating environmental drivers during the growing season to counts at overwintering sites. Furthermore, even if detailed spatial data were available, effects of conditions in different places would be difficult to determine. For example, both insect behavior (Stoner 2016) and chemical persistence and movement (Simondelso et al. 2017) contribute to pesticide exposure risk. Even if the data existed (and they do not, at least not for our 1981–2016 study period), a simple overlay of pesticide use with habitat use would not determine exposure per se. Similarly, ecologists have long known that insects have multifaceted and nonlinear responses to temperature and drought (Mattson and Haack 1987, Huey and Berrigan 2001). The difficulties of disentangling these effects from monitoring data are further complicated by the fact that monarch butterflies are likely to experience different environments as larvae and adults. For monarch butterflies in particular, attention has been focused on inferring population trends and status from monitoring various indices of population abundance, which has at times led to conflicting interpretation of these data

(Inamine et al. 2016, Pleasants et al. 2017). We urge ecologists interested in monarch conservation to complement broad-scale monitoring studies with targeted observations and small-scale experiments to understand the demographic mechanisms behind landscape-scale patterns.

For insect populations in general, the list of at-risk species is growing, and previously widespread species are joining the ranks of at-risk species (Van Dyck et al. 2009, Cameron et al. 2011). In many cases, these declines represent some unknown combination of effects of land use and climate change (Casner et al. 2014). The strength of our PLSR analyses is that they deal with multiple correlated variables in a statistically robust way. In this case, because population declines are most strongly associated with land use change, habitat conservation and restoration are a good first management step that may go a long way toward population recovery. Such efforts are already underway in the East (MAFWA 2018) and being planned by many groups, including energy and transportation sectors and western state fish and wildlife agencies (WAFWA 2019), but much greater engagement is probably needed raise the likelihood of restoring monarch butterfly populations (Thogmartin et al. 2017a).

Ultimately, understanding how insect populations respond to environmental covariates across seasons and years, in relation to fine-scale as well as coarse-scale variation, may be necessary to understand the relative contribution of multiple factors to monarch declines. In other words, PLSR results are best interpreted as suggesting hypotheses for experimental testing (Alofs et al. 2014). The clear next steps are mechanistic experiments and targeted observations to test if habitat protection and restoration opportunities, which hinge on factors identified in analysis such as this, can reverse declines before we lose formerly widespread species like the monarch butterfly.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1975/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.b61q0c2>