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Roles of hostplant availability and quality for the distribution and climate change response of a dietary specialist herbivore

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15   A. Nalleli Carvajal Acosta[1*], and Kailen Mooney[1]

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20   [1] Department of Ecology and Evolutionary Biology, University of California-Irvine, Irvine,
21   California, United States of America

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27   * Corresponding Author
28   E-mail: ancarvaj@uci.edu (NC)

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Abstract

Species distributions are recognized to be driven by abiotic factors, but the importance of biotic interactions that provide critical resources is less well understood, especially with respect to variation in critical resource quality. Disentangling the relative importance of these factors – abiotic environment, presence of critical resources and their quality– may be critical to predicting species response to climate change. We used species distribution models (SDMs) to address these questions for the western monarch butterfly (*Danaus plexippus*), a species that obligately feeds upon plants in the genus *Asclepias,* and for which hostplant quality in this region varies among species by an order of magnitude. We modeled the distribution of 24 *Asclepias* species to develop and compare three monarch distribution models with increasing levels of ecological complexity: (i) a null model using only environmental factors (a climate envelope model), (ii) a model using environmental factors and *Asclepias* spp. distribution, (iii) and a model using environmental factors and *Asclepias* spp. distribution weighted by hostplant quality assessed through a greenhouse bioassays of larval performance. *Asclepias* models predicted that half of the *Asclepias* spp. will both expand their ranges and shift their distribution towards higher latitudes while half will contract within the study region. Our performance analysis of monarch models revealed that the climate envelope model was the poorest performing. Adding hostplant distribution produced the best performing model, while accounting for hostplant quality did not improved model performance. The climate envelope model estimated more restrictive contemporary and future monarch ranges compared to both hostplants models. Although all three models predicted future monarch range expansions, the projected future distributions varied among models. The climate envelope model predicted range expansions along the Pacific coast and

56   contractions inland while hostplants models predicted range expansions in both of these

57   regions and, as a result, estimated 14 and19% increases in distribution relative to the climate

58   envelope model, respectively. These results suggest that information on biotic interactions

59   that provide critical resources is needed to predict future species distributions, but that

60   variation in the quality of those critical resources may be of secondary importance.

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62   **Keywords:** *Danaus plexippus*; monarch, species distribution models; MaxEnt; climate change;

63   bioclimatic models; hostplant quality; Milkweeds; *Asclepias*; biotic interactions; specialized

64   herbivores

Introduction

66   Climate change is expected to alter the distribution of most species (Parmesan et al. 1999,

67   Crozier 2004, Bellard et al. 2012, Pauli et al. 2012) with many already experiencing range

68   contractions or facing extinctions (Sekercioglu et al. 2008, La Sorte and Jetz 2010, Bellard et al.

69   2012, Pauli et al. 2012). Understanding the underlying drivers is key to predicting such

70   distributional response and also critical if we are to mitigate these impacts. Species distributions

71   are presumed to be driven most strongly by abiotic factors, but biotic interactions can also play a

72   key role (Guisan and Thuiller 2005). Because species often respond differently to abiotic stress

73   (Schweiger et al. 2008, Van der Putten et al. 2010), producing accurate predictions necessitates

74   that we also account for climate change effects on interacting species. This is especially true for

75   species that engage in obligate interactions, as they depend on a few or even a single species to

76   survive, and such species may not be available in all areas that are otherwise climatically

77   suitable (Schweiger et al. 2008).

78   Herbivorous insects – the majority of multi-cellular species on earth (Lewinsohn et al.

79   2005) – are highly host-specific; thus, their response to climate change will likely depend

80   fundamentally on the responses of the plants upon which they are obligately dependent. Indeed,

81   most herbivorous insects feed on a single or a few plant families (Bernays 1989, Forister et al.

82   2015) with fewer than 10% feeding on plants belonging to more than three families (Price 1983).

83   Furthermore, it has long been recognized that hostplants demonstrate considerable intra- and

84   inter-specific variation in their resource quality to herbivores, and that resource quality is often

85   heterogeneously distributed across landscapes (Denno and McClurc 1983, Hunter et al. 1992).

86   Intra- and inter-specific variation in host-quality can have large effects on herbivore performance

87   (Singer et al. 2012) and may also play a significant role in determining the spatial distribution of

88   host-specific herbivorous insects at local scales (Memmott et al. 1995, Mcmillin and Wagner

89   1998, Egan and Ott 2007). However, the role of hostplant quality as a driver of species

90   distribution at large spatial scales, and its implications for herbivore's distributional response to

91   climate change, are largely unknown.

92   In this study we investigated the importance of hostplant distribution and quality as

93   drivers of herbivore contemporary distribution and response to projected future climate change.

94   We use Species Distribution Models (SDMs), statistical tools that combine observations of

95   species occurrences with environmental covariates to estimate species distributions. These

96   models identify the factors driving contemporary species ranges and can also infer species

97   response to climate change based on projections for how those driving factors will change in the

98   future (Elith and Leathwick 2009). SDMs have most often assumed that species distributions are

99   defined by environmental factors alone. This so-called "climate envelope approach" are based on

100   the Eltonian noise hypothesis, which posits that biotic interactions may be a major driver of

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101   abundance at smaller spatial resolutions, but at larger and coarser spatial resolutions the effects

102   of biotic interactions may average out, leaving abiotic factors as the principal drivers (Guisan

103   and Thuiller 2005, Soberon and Nakamura 2009, Elith and Leathwick 2009). Yet recent

104   modelling studies have identified biotic factors as important drivers of species distributions

105   (Dilts et al. n.d., Araújo and Luoto 2007, Preston et al. 2008, Schweiger et al. 2008, de Araújo et

106   al. 2014, Fraterrigo et al. 2014, Lemoine 2015, da Cunha et al. 2018) and SDMs predictions for

107   species response to climate change have yielded contrasting results based upon whether or not

108   biotic factors are included (Preston et al. 2008, Schweiger et al. 2008, Lemoine 2015).

109   Accordingly, climate envelope modeling may accurately define the potential niche of a species,

110   but the realized niche – defined in part by species interactions – may be substantially smaller.

111   Our aim in this study was to assess the importance of hostplant distribution and quality

112   for driving contemporary and future distributions of dietary specialist herbivores. To do so, we

113   studied the monarch butterfly (*Danaus plexippus*, Lepidoptera: Nymphalidae), the larvae of

114   which feed exclusively from plants in the *Asclepias* genus which varies greatly among species in

115   herbivore-defenses traits, nutrient content, and overall host quality (Agrawal and Fishbein 2006,

116   Pocius et al. 2017). Monarchs are well known for their migratory and overwintering behavior

117   (Pelton et al. 2019), and three previous studies have modelled their distribution. Lemoine

118   (Lemoine 2015) accounted for hostplant distribution in the eastern monarch population response

119   to climate change, predicting a poleward range expansion facilitated by *Asclepias* range

120   expansions. Steven and Frey (Stevens and Frey 2010), and more recently Dilts *et al* (Dilts et al.

121   n.d.), examined the role of hostplant availability and climate in determining the contemporary

122   western monarch distribution and their breeding grounds, again demonstrating the importance of

123   hostplants availability.

124   In the present study, we investigate the role of both hostplant distribution and quality in

125   driving contemporary and future distributions of the western monarch population. To do so, we

126   compared the performance of three species distribution models. In order of increasing

127   complexity, these three models were: (i) a model using only climatic variables as predictors

128   (hereafter, climate envelope model); (ii) a model using climatic variables and *Asclepias*

129   distribution as predictors (hereafter, hostplant-presence model); and (iii) a model that included

130   climatic variables, hostplants distribution and hostplant quality, which varied 10-fold among

131   species as assessed through bioassays of larval performance (hereafter, hostplant quality model).

132   We compared model performances and identified the variables determining the distribution of

133   the western monarch breeding ranges. These models were then used to project and estimate

134   changes in their distribution. Our study adds to past studies of this species and represents the first

135   to estimate the future breeding range of the western monarch population. More broadly, this

136   study is, to our knowledge, the first to explicitly test for the importance of hostplant quality of an

137   obligate resource in driving species contemporary and future distribution.

Materials and methods

Study System

140   Monarch butterflies occur world-wide and, in their larval stage, feed exclusively from

141   plants in the milkweed family (*Asclepias*, Apocyneceae: Asclepiadaceae). In North America,

142   there are two migratory populations that breed east and west of the Rocky Mountains, with each

143   of these regions being populated by multiple and largely unique sets of hostplant species (Ladner

144   and Altizer 2005). Despite its dramatic population decline (Pelton et al. 2019), the western

145   monarch population has been considerably understudied in comparison to the largest eastern

146   population and we know little about how this population will be affected by climate change.

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147   Western monarchs breed west of the Rocky Mountains and overwinter along the Pacific

148   coast from Bodega Bay in northern California and as far south as Ensenada, Baja California,

149   Mexico (Stevens and Frey 2010). During the spring, monarchs leave their overwintering sites

150   and disperse throughout the western U.S. where they breed continuously during the summer. In

151   the fall, adult monarchs return to their overwintering grounds (Pelton et al. 2019). Within North

152   America, monarchs have been recorded feeding on 27 different plant species in the genus

153   *Asclepias* (Ladner and Altizer 2005); however, adult females may oviposit in any available

154   *Asclepias* species. Thus, monarchs may utilize multiple *Asclepias* species throughout their

155   migratory paths.

156   The genus *Asclepias,* commonly known as milkweeds, consists of over 140 different

157   species of which 130 are endemic to North America (Agrawal and Konno 2009). Milkweeds

158   vary in their herbivore defensive strategies, which variously include combinations of

159   cardenolides, latex, and trichomes, among others traits (Agrawal and Fishbein 2006). Inter-

160   specific variation in the quantity of plant defenses (Agrawal and Fishbein 2006) and nutrient

161   content (Pocius et al. 2017) have been associated with monarch larval mass, developmental rate,

162   and early instar survival (Zalucki et al. 2001). In this sense, the quality of the *Asclepias* species

163   may be important in determining monarch distributions.

164   ## *Data Collection*

165   ***Occurrence data:*** We retrieved monarch and milkweed records for the United States

166   using R Studio (R Studio Team 2015) from multiple open source databases using the R

167   packages SPOCC, Ecoengine, rbison (Chamberlain et al. 2014, Karthik 2014, Chamberlain

168   2019) and by accessing species occurrences directly from GBIF and iNaturalist databases

169   ("GBIF Occurrence Download" 2019, "Naturalist [online]. Website" 2019). For monarchs,

170   we only selected eggs and larval records because they provide a direct index for the location

171   of the monarchs breeding grounds as opposed to adult records which may only indicate the

172   migratory path. Additional monarch larval records were provided by the Monarch Larvae

173   Monitor Program (MLMP) (Ries and Oberhauser 2015).

174   The occurrence data archived in open source databases originates mainly from citizen

175   scientist sightings and some from herbarium records. As opposed to formal survey methods, this

176   type of data has some limitations such as sampling biases, potential misidentification and

177   coordinate inaccuracies, and lack species absence records. We controlled for these limitations

178   whenever possible. For example, when permitted, we used filters that only retrieved records

179   confirmed by experts and/or records classified as of research quality and spatial filtering to

180   control for sampling biases.

181   To focus on the western monarch population, we selected Milkweeds and monarch larval

182   records from states corresponding to this region: California, Nevada, Colorado, Washington,

183   New Mexico, Arizona, Utah, Oregon, and Idaho. After removing duplicate records, incorrect (i.e.

184   over oceans) or inaccurate coordinates (>1000 meters uncertainty) and observations, the final

185   databases included 7,941 Milkweed records for 51 species (Data S1), and 904 monarch larval

186   records (Data S2). *A. fascicularis* and *A. speciosa* were the most common species with 22%

187   (2,541) and 12% (1,404) of total Milkweed records, respectively.

188   ***Environmental data and climate projections:*** Contemporary environmental

189   bioclimatic variables and projections for the year 2070 were downloaded in R from the

190   WorldClim website (Fick and Hijmans 2017) at 30-sec (approximately 1-km^2) grid cells, the

191   finest spatial resolution available. The current bioclimatic variables represent averages of a

192   50-year period from 1950 to 2000. Climate change projections for the year 2070 represent

193   averages of a 30-year period from 2061 to 2080 based on the Hadley Centre Global

194   Environmental Model, version 2, Earth System (HadGEM2-ES) model. The HadGEM2-ES

195   model is recommended for ecological modeling as it accounts for ecologically-meaningful

196   processes such as dynamic vegetation cover (The HadGEM2 Development Team: G. M.

197   Martin et al. 2011). These projections are based on Representative Concentration Pathway

198   (RCP) 8.5. The RCP 8.5 represents the worst-case scenario for greenhouse gas (GHG)

199   concentrations, assuming that GHG emissions will continue to increase after the 21st century

200   in contrast to other scenarios that assume GHG will remain stable or will decline after the

201   21st century (Collins et al. n.d.). While a comparison of different projections for future

202   climate would provide a more nuanced prediction for the future distributions of milkweeds

203   and monarchs, using this single scenario met our primary purpose of evaluating the

204   importance of host plant information in predicting specialist herbivore distributions.

205   Environmental layers were cropped to include the states corresponding to range of the

206   western monarch population. To reduce multicollinearity among variables, we removed highly

207   correlated variables based on their Pearson correlation coefficients using a pairwise correlations

208   approach following Dormann *et al.* (Dormann et al. 2013) but with a less restrictive threshold of

209   0.85 as in Elith *et al.* (Elith et al. 2006). We first removed variables that were correlated with

210   multiple variables and, when only two variables were correlated, we selected the variable that

211   was less statistically derived. This process yielded 11 environmental predictors (Table 1).

212   ### *Species distribution modeling*

213   Because species occurrences in these datasets are available in the form of presence-only

214   records, we used the maximum entropy method (hereafter MaxEnt) (Phillips et al. 2006) to

215   model the current and future distribution of *Asclepias* and monarch breeding ranges. The MaxEnt

216   algorithm is a presence-background modeling tool based on Bayesian and maximum likelihood

217   statistics (Elith et al. 2011). To estimate the probability of distribution of a species, MaxEnt uses

218   species presence records and a set of environmental predictors (e.g. precipitation, temperature)

219   across a pre-defined landscape that is divided into grid cells. From this landscape, background

220   points are randomly selected to represent the species environmental domain or background

221   environment. MaxEnt estimates the relative probability of occurrence for each grid cell by

222   maximizing the similarity between the environmental conditions of presence records and that of

223   the background environment, while constraining the prediction to have the same mean as the

224   presence records. The relative probabilities (raw output) are transformed to probability of

225   occurrence using post-logistic transformation (logistic output). Here we report the logistic output

226   which assigns a probability of presence between 0 and 1 to each grid cell, assuming that typical

227   presence localities have a probability of presence of 0.5. See Elith *et al.* (Elith et al. 2011) for a

228   comprehensive statistical explanation of MaxEnt.

229   Data collection, data processing, and modeling were performed in R studio (R Studio

230   Team 2015). Species distribution modeling was executed in MaxEnt using the 'dismo' package

231   (Hijmans et al. 2011).

232   ***Asclepias models:*** We developed models for individual *Asclepias* species and estimated

233   their distributions within an area restricted to the study region; therefore, our *Asclepias*

234   ranges do not represent their full distributions but only represent hostplant availability for the

235   western monarch. *Asclepias* species were modelled separately because their distributions

236   may be delimited by distinct environmental factors. We discarded records identified at the

237   genus level and species with fewer than 40 records as this limited number of observations

238   would not allow for an accurate estimation of their distributions. To correct for potential

239   sampling biases, we used a spatial filtering approach which consists on randomly selecting

240   one record per grid cell of a specified size (Kramer-Schadt et al. 2013). Spatial filtering was

241   performed individually for each *Asclepias* species. This allowed us to retain records for

242   multiple species co-occurring within a single grid cell as well as selecting the optimal spatial

243   resolution that maximizes sample size while correcting for sampling biases. For example,

244   species with a limited distribution (e.g. high-elevation species), were filtered at a finer spatial

245   resolution of 1 km^2 and more widely distributed *Asclepias* species were filtered at a 30-km^2

246   resolution. An additional two *Asclepias* species, *A. viridiflora* and *A. curassavica*, were

247   discarded because their records were clearly subject to sample biases and spatial thinning

248   decreased their number of records to less than 40. The process of removing incorrect records

249   and rare species, and spatial filtering, resulted in 24 *Asclepias* species databases each with a

250   minimum of 40 records, totaling 3,549 *Asclepias* records (Table 2).

251   Spatially filtered data were randomly split into training and test data by withholding 25%

252   of the occurrences and the remaining 75% was used for model training. To select background

253   points, we first determined the *Asclepias* environmental domain, corresponding to an area of 50

254   km^2 surrounding *Asclepias* occurrences. The environmental domain was then divided into 1 km^2

255   grid cells, and background points were randomly selected from within the monarch

256   environmental domain in a checkerboard fashion. Individual *Asclepias* species were modeled

257   using background points from the environmental domain represented by all *Asclepias* species.

258   This process yielded 9000 background points to model *Asclepias* species. The best-fitted models

259   for *Asclepias* with the highest AUC score were used to estimate their current and projected

260   distribution under climate change.

261   ***Monarch models:*** The monarch distribution was modeled using a similar approach to

262   *Asclepias*. As described above, we used spatial filtering to correct for sampling biases. Monarch

263   larval records were first filtered at a range of resolutions (1 to 55 km^2) and the spatial resolution

264   yielding the highest AUC was then selected. The final dataset used to model monarch breeding

265   range was thinned using 30 km^2 grid cells (the best-fitted model) and included 110 observations.

266   As with *Asclepias*, we withhold 25% of the data for model testing and the remaining 75% was

267   used for model training. To determined monarch larvae environmental domain, we selected

268   4,000 background points following the same procedure described in the *Asclepias* modeling

269   section, although the number of background points was lower due to the more restricted

270   distribution of monarchs.

271   To test for the importance of hostplant availability, we first summarized the resulting

272   individual *Asclepias* distribution layers into a single predictor layer representing overall

273   *Asclepias* distribution under current and projected environmental conditions (Fig 1, A and B).

274   The values assigned to grid cell in the genus-level hostplant distribution layer were determined

275   by:

276    $$P(Asc) = p(Asc1) + p(Asc2) + \cdots p(Asc24)$$

277   Where 'P' represents the summarized genus-level probability and 'p' probability of

278   distribution of individual *Asclepias* species numbered from 1 to 24. Because the ranges of many

279   *Asclepias* species overlapped, forming the *Asclepias* distribution layer by summing probabilities

280   captures not only the mean probability of distribution but also reflects species richness. We

281   choose this approach under the assumption that higher species richness is associated with

282   increased milkweed abundance and thus higher habitat quality for monarchs. Although a direct

283   assessment of milkweed abundance would be preferable, no such data is readily available. This

284   process is mathematically equivalent to averaging species probabilities and then multiplying by

285   species richness.

286   To assess hostplant quality, we used the average monarch larval weight supported by

287   each *Asclepias* species grown under greenhouse conditions (Table 2). These protocols are

288   described in detail by Petschenka and Agrawal (Petschenka and Agrawal 2015). Briefly,

289   *Asclepias* plants were grown from seed in a greenhouse and after a period of 4-7 weeks neonate

290   monarch caterpillars were placed individually upon the leaves of potted plants and weighed after

291   5 days. Assessing hostplant quality under controlled greenhouse conditions controls for

292   extraneous factors such as natural predator, competition with other herbivores, induced plant

293   defenses and environmental variation that are necessarily associated with a field bioassay.

294   We weighted each *Asclepias* species distribution layer according to its host quality. The

295   Milkweed with the greatest larval weight (*A. sololana*) was given a value of 1, and all other

296   species were assigned values as proportions of this value, with the lowest quality weight being

297   0.078 (*A. asperula*) (Table 2). Five species with no information on larval weight were weighted

298   by the average host quality weight of 0.55. Weighted layers were then summarized into a single

299   predictive layer representing the hostplant probability of distribution and species richness

300   weighted by hostplant quality (Fig 1, C and D). The values assigned to grid cells of the overall

301   hostplant quality layer were calculated as follow:

302         $$P_q(Asc) = [p(Asc1) * (q1)] + [p(Asc2) * (q2)] + \cdots [p(Asc24) * (q24)]$$

303   Where 'Pq' represents the summarized genus-level probability of distribution weighted

304   by hostplant quality, 'p' the probability of distribution of individual *Asclepias* species numbered

305   from 1 to 24, and 'q' the host-quality weight estimated for each *Asclepias* species. This approach

306   is parallel to that used for the *Asclepias* distribution layer (above), capturing the effects of both

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307   the mean probability of distribution and species richness for all co-existing *Asclepias* species, but

308   now weighting each species according to its relative hostplant quality.

309   Lastly, we used the summarized *Asclepias* layers as predictors to generate and compared

310   three models: a null model (climate envelope model) using only environmental factors as

311   predictors; a model using environmental factors and hostplant distribution represented by the

312   summarized *Asclepias* distribution (hostplant-presence model); and a second model using

313   environmental factors and *Asclepias* distribution weighted by host quality (hostplant-quality

314   model).

315   To identify the variables contributing more to each model, in addition to the "Analysis of

316   Variable Contribution" reported by MaxEnt, we performed a jackknife test of variable

317   importance. In a jackknife test, models are re-run using a single variable in isolation to identify

318   the variables that yield the highest model gain when used in isolation. This test also identifies

319   those variables that, when removed, decrease the model gain the most by re-running the models

320   excluding one variable at a time.

321   Since there is currently no consensus regarding a single most appropriate metric to

322   evaluate SDMs performance (Peterson et al. 2008, 2011, Warren and Seifert 2011), we evaluated

323   model performance based on several criteria. The area-under-the-curve (AUC) statistic provides

324   an estimate for the accuracy of predictions, with 0 indicating no predictive accuracy and 1

325   perfect predictive accuracy. An AUC score of 0.5 indicates that the model performs no better

326   than random. We also estimated performance metrics based on the Akaike Information Criterion

327   corrected for small sample sizes (AICc). The AICc metric have the advantage of balancing both,

328   model goodness-of-fit and model complexity. Furthermore, compared to AUC and BIC

329   (Bayesian-Information-Criterion) based methods, AICc evaluation methods have been shown to

330   favor models that more accurately estimate the relative importance of variables and habitat

331   suitability, both in the training region and when models are extrapolated to a different time

332   period (Warren and Seifert 2011). We calculated the AICc, delta AICc (ΔAICc), and Akaike

333   weights (wAICc) for each model using the ENMeval package (Muscarella et al. 2014). The

334   model with the lowest AICc value is considered the best model out of various candidate of

335   models. The ΔAICc is the difference between the best AICc and other candidate models. The

336   best candidate model has a ΔAICc of 0 and models with ΔAICc lower than 2 are generally

337   considered to have substantial support and should not be discarded (Muscarella et al. 2014).

338   Akaike weights (wAICc) represents the likelihood of a model given the data. The weights are

339   normalized to sum 1 and are interpreted as probabilities (Burnham and Anderson 2004).

340   Finally, we estimated suitable breeding area for monarchs and for *Asclepias* distribution

341   from polygons drawn around areas with grid cell values higher than 0.5 from the output logistic

342   layers projected from the final models.

Results

Asclepias models and estimated distribution

345   All *Asclepias* final models had AUC scores higher than 0.8, except for *A. speciosa* model

346   which yielded an AUC score of 0.74, indicating that these models are a good fit for the

347   observations (Table 2). The current estimated distributional ranges (Appendix S1, left panels.)

348   were consistent with *Asclepias* spp. distributions published by the Biota of North America

349   Program (BONAP) (Kartesz 2015).

350   Overall, within the study area, half of the *Asclepias* species are projected to expand their

351   ranges by a mean of 88% (i.e. nearly doubling their distributions) whereas the other half will

352   contract their ranges by a mean of 42% (i.e. more than halving their distributions) (Table 2 and

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353   Appendix S1). Of the 24 *Asclepias* species, 19 species are predicted to shift their distributions to

354   higher latitudes (79%) both along the Pacific coast and inland, with 11 of these also expanding

355   their distributions. Of the 4 species not shifting their distributions northward, 3 will contract their

356   ranges.

Monarch models and estimated distribution

358   The AUC scores did not differ considerably among the three models, but AUC values

359   were slightly higher for the hostplant-presence model (0.803) compared to both the hostplant-

360   quality (0.800) and climate envelope model (0.799). However, the AIC-based metrics preferred

361   the hostplant-presence model (ΔAICc=0, wAICc=1.00) over the hostplant-quality

362   (ΔAICc=123.50, wAICc=1.515^{-27}) and climate envelope models (ΔAICc=168.52, wAICc=2.545^{-37}

363   ^{37}). The ΔAICc for the competing climate envelope and hostplant quality model was much larger

364   than 2 indicating that these two models had limited support. Likewise, the wAICc of the

365   hostplant model was nearly 1 suggesting that the likelihood of this model being the best-fitted

366   model was high (Table 3).

367   The environmental variables that contributed the most to the climate envelope model

368   were the "minimum temperature of the coldest month" (43.4% contribution; (Fick and Hijmans

369   2017) and "precipitation seasonality" (25.2% contribution, Fig. 3 A ; (Fick and Hijmans 2017)).

370   For both hostplant-presence and hostplant quality models, the hostplants variable was the second

371   most important factor for predicting the western monarch breeding range. The hostplants

372   variable contributed most to the hostplant distribution model (22.5%), after the "minimum

373   temperature of the coldest month" (33.1%) (Fig. 3 B and C). Although the hostplant quality

374   model did not produce the best-fit model, weighting the hostplant layer by host-quality increased

375   the contribution of the hostplant variable by 3% and decreased "minimum temperature of the

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376   coldest month" variable contribution by 7% compared to the hostplant distribution model (Fig 3,

377   B and C). Both hostplants layers (weighted by host-quality and unweighted) exhibited the

378   highest gain (>0.40) in the jackknife test for variable importance in both hostplant models

379   (Appendix S2). This indicates that hostplants provided the most useful information for predicting

380   where monarch breeding grounds occur. For all three models the "average precipitation of the

381   warmest quarter" (Fick and Hijmans 2017) decreased model gain the most when omitted

382   suggesting that this environmental variable has the most information that is not present in other

383   variables (Appendix S2).

384   The process of weighting the *Asclepias* distribution layer by quality did not dramatically

385   altered the hostplant layer, and mainly rescaled the values of the layer (Fig 1, lower panels). This

386   was probably due to large range overlaps among *Asclepias* species as it can be observed by

387   overlaying the polygons corresponding to *Asclepias* suitable habitat (Appendix S3). Thus, a grid

388   cell occupied by multiple *Asclepias* with variable host-quality may have the same value as a grid

389   cell occupied by a few high-quality *Asclepias* species. The only area where weighting hostplants

390   by quality appeared to change the grid cell values of the hostplant quality layer was the

391   southwest region of Arizona and Utah which appeared to be occupied mostly by lower quality

392   species, predominantly by *A. asperula*, our lowest quality hostplant (Fig 1, lower panels and

393   Table 2).

394   The climate envelope model estimated more restricted ranges for the contemporary and

395   future monarch distributions. Both hostplants models estimated nearly identical contemporary

396   distributions for monarchs that were ~18% larger than the estimated by the climate envelope

397   model (Fig 2, left panels and Table 2). Although all three models predicted future range

398   expansions that nearly doubled their corresponding contemporary estimates, the hostplant-

399   presence and hostplant-quality models projected an increased in habitat suitability 14 and 19%

400   larger than that of the climate envelope model, respectively (Fig 2, right panels and Table 2).

401   This difference was primarily due to the fact that the climate envelope model predicted range

402   contractions inland whereas both hostplants models predicted range expansions in this region.

403   Finally, we detected some slight differences in the areas where hostplants models predicted that

404   such range expansions will occur. For example, the hostplant quality model predicted a smaller

405   range for monarchs in western New Mexico and a larger range in central Nevada, Utah and

406   western Colorado. (Fig 2, right panels).

Discussion

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408   Predicting herbivore response to climate change requires incorporating future hostplant

409   availability, but hostplant quality may play a secondary role. While climate envelope projected a

410   more restrictive current monarch distributions than hostplant models, model comparisons

411   suggested that hostplant information provided superior predictive power. Furthermore, the three

412   models differed in their future monarch projections under climate change with models including

413   hostplant information predicting an increased in habitat suitability 14-19% larger than that of the

414   climate envelope model. Despite the importance of hostplant information, models including

415   hostplant quality did not prove superior to the model based on hostplant presence. Our study

416   suggests that information on critical biotic interactions is essential to predict future species

417   distributions under climate change.

418   The hostplant model was preferred by AIC-based metrics over a traditional climate

419   envelope model and hostplant quality model. Hostplant availability, together with the minimum

420   temperature of the coldest month, contributed over fifty percent to the hostplant model and over

421   forty percent to the model gain when used in isolation. This suggests that the western monarch

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422   breeding ranges are co-limited by both cold temperatures and hostplant availability. These

423   findings are consistent with past work by Lemoine (Lemoine 2015) who found that models

424   incorporating hostplants and environmental factors most accurately estimated the eastern

425   monarch distribution. Additionally, our results are also supported by previous studies from

426   Steven and Frey (Stevens and Frey 2010) and Dilts *et al*. (Dilts et al. n.d.) who identified

427   *Asclepias* availability as well as climatic variables, including minimum temperature of the

428   coldest month, as key for structuring the western monarch breeding grounds. These findings add

429   to the increasing body of evidence suggesting that biotic interactions may govern species

430   distributions as strongly as environmental conditions (Dilts et al. n.d., Araújo and Luoto 2007,

431   Preston et al. 2008, Schweiger et al. 2008, de Araújo et al. 2014, Fraterrigo et al. 2014, Lemoine

432   2015, da Cunha et al. 2018).

433   Hostplant quality varied ten-fold among Milkweed species but did not have a large effect

434   on the overall estimates for the contemporary distribution of monarchs. We speculate this result

435   may be due to the fact that our genus-level distribution layer also reflected species richness.

436   *Asclepias* ranges exhibit substantial range overlaps in the American West (Appendix S3), thus,

437   adult monarchs may preferentially oviposit on higher quality milkweeds in areas with mixed

438   quality resources (Gripenberg et al. 2010), diminishing the influence of low-quality species.

439   Hostplants model projected similar monarch distributions under a climate change scenario;

440   however, their projections differed in some regions of the inland states of Utah, Nevada, New

441   Mexico and Colorado. This implies that the importance of hostplant quality in determining

442   herbivore distributions should not be discarded altogether as it may play a significant role in

443   instances where herbivores rely on hostplant with less geographic overlap, and therefore, fewer

444   food choices.

445   Our results demonstrate how climate envelope models that accurately represent current

446   distributions may provide poor prediction for the future. This can occur when critical

447   distributional drivers (e.g. hostplant distributions) correlate strongly with environmental factors

448   under contemporary conditions (Wharton and Kriticos 2004) but not under climate change.

449   These mechanistically-flawed models thus provide inaccurate predictions (Brewer and Gaston

450   2003, Soberon and Nakamura 2009). In our study, the climate envelope model– although more

451   restricted– estimated very similar monarch contemporary ranges than hostplant models (Fig 2,

452   left panels) but differed in their future projections (Fig 2, right panels). Specifically, the two

453   hostplant models predicted larger range expansions of monarchs than the climate envelope model

454   inland. This suggests that the climate envelope model over predicted monarch climatic

455   limitations due to contemporary correlations between climatic factors and milkweed

456   distributions, but that this correlation may not persist in the future. Accordingly, models based

457   solely on climatic factors may be adequate for estimating contemporary species distributions but

458   nevertheless produce misleading projections under novel circumstances where abiotic conditions

459   and biotic interactions do not respond in tandem to climate change.

460   The importance of incorporating the climatic response of hostplants into models is

461   underscore by the fact that only models including hostplant information predicted range

462   expansion inland while the climate-envelope model did not (Fig 2, right panels). The predicted

463   inland range expansions of the western monarch breeding range appeared to be driven by higher

464   hostplant availability in the regions of central Nevada, Utah and Colorado under future climatic

465   conditions, which was identified by our models as one of the most important factors delimiting

466   monarch distributions. Our results are congruent with previous findings by Lemoine (Lemoine

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467 2015) whose study predicted northern range expansion of the eastern monarch population

468 resulting from projected *Asclepias* range expansions under future climate change scenarios.

469   Lastly, it is worth noting that our model projections do not consider factors that were

470 beyond the scope of our study but that may significantly impact monarch future distributions.

471 For example, pesticide and land-use practices, specially overwintering habitat loss to housing

472 development, is an existing threat to monarchs habitat (Pelton et al. 2019) that is likely to persist

473 in the upcoming years. Furthermore, dams and human-facilitated invasions, may alter riparian

474 areas potentially disrupting monarch migration patterns and monarch breeding grounds. Autumn

475 migrants often follow riparian corridors (Dingle et al. 2005) and riparian vegetation has been

476 associated with habitat suitability for some western Milkweed species (*A. subulata*, and *A.*

477 *asperula*) (Dilts et al. n.d.).

Conclusions

479   In summary, this study shows that accounting for biotic interactions– and their

480 distributional response to climate change– is required to predict the future distributions of

481 species obligately dependent on such interactions. A climate-envelope approach may be effective

482 for estimating contemporary species distributions but may produce misleading future projections

483 as climate change may uncouple suitable climate from essential biotic interactions. Hostplant

484 quality did not play a significant role in delimiting monarch distribution in the American West

485 where *Asclepias* ranges overlapped substantially. However, there were slight differences in some

486 regions suggesting that host-quality may still be important for predicting distributions of species

487 dependent on a fewer number of resources. These results are relevant, not only for most

488 herbivorous insects which are highly host-specific, but also for all organisms incurring in

489 obligate biotic interactions (e.g. parasitic or mutualistic interactions). Ultimately, accurate

490   projections for the future will require better incorporating inter-specific dynamics into our

491   models.

Acknowledgements

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Literature Cited

509   Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. Ecology 87:S132–S149.

510   Agrawal, A. A., and K. Konno. 2009. Latex: A model for understanding mechanisms, ecology,

511   and evolution of plant defense against herbivory. Annual Review of Ecology, Evolution,

512   and Systematics 40:311–331.

513   de Araújo, C. B., L. O. Marcondes-Machado, and G. C. Costa. 2014. The importance of biotic

514   interactions in species distribution models: a test of the Eltonian noise hypothesis using

515   parrots. Journal of Biogeography 41:513–523.

516   Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species

517   distributions under climate change. Global Ecology and Biogeography 16:743–753.

518   Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of

519   climate change on the future of biodiversity: Biodiversity and climate change. Ecology

520   Letters 15:365–377.

521   Bernays, E. A. 1989. Host range in phytophagous insects: the potential role of generalist

522   predators. Evolutionary Ecology 3:299–311.

523   Brewer, A. M., and K. J. Gaston. 2003. The geographical range structure of the holly leaf-miner.

524   II. Demographic rates. Journal of Animal Ecology 72:82–93.

525   Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC

526   in model selection 33:261–304.

527   Chamberlain, S. 2019. rbison:Interface to the "USGS" "BISON" API.

528   Chamberlain, S., K. Ram, and T. Hart. 2014. spocc: R interface to many species occurrence data

529   sources.

530   Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, X. Gao, W. J. G. Jr, T. Johns, G.

531   Krinner, M. Shongwe, A. J. Weaver, M. Wehner, M. R. Allen, T. Andrews, U. Beyerle,

532   C. M. Bitz, S. Bony, B. B. B. Booth, H. E. Brooks, V. Brovkin, O. Browne, C. Brutel-

533   Vuilmet, M. Cane, R. Chadwick, E. Cook, K. H. Cook, M. Eby, J. Fasullo, C. E. Forest,

534   P. Forster, P. Good, H. Goosse, J. M. Gregory, G. C. Hegerl, P. J. Hezel, K. I. Hodges,

535   M. M. Holland, M. Huber, M. Joshi, V. Kharin, Y. Kushnir, D. M. Lawrence, R. W. Lee,

536   S. Liddicoat, C. Lucas, W. Lucht, J. Marotzke, F. Massonnet, H. D. Matthews, M.

537   Meinshausen, C. Morice, A. Otto, C. M. Patricola, G. Philippon, S. Rahmstorf, W. J.

538   Riley, O. Saenko, R. Seager, J. Sedláček, L. C. Shaffrey, D. Shindell, J. Sillmann, B.

539   Stevens, P. A. Stott, R. Webb, G. Zappa, K. Zickfeld, S. Joussaume, A. Mokssit, K.

540   Taylor, and S. Tett. (n.d.). Long-term climate change: projections, commitments and

541   irreversibility:108.

542   Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship.

543   Ecology 85:231–241.

544   da Cunha, H. F., É. D. Ferreira, G. Tessarolo, and J. C. Nabout. 2018. Host plant distributions

545   and climate interact to affect the predicted geographic distribution of a Neotropical

546   termite. Biotropica 50:625–632.

547   Denno, R. F., and M. S. McClurc. 1983. Variable plants and herbivores in natural and managed

548   systems. Academic Press, New York.

549   Dilts, T. E., M. O. Steele, J. E. Engler, E. M. Pelton, S. J. Jepsen, S. J. McKnight, A. R. Taylor,

550   C. A. Fallon, S. H. Black, E. E. Cruz, D. R. Cravier, and M. L. Forister. (n.d.). Host

551   plants and climate structure habitat associations of the western monarch butterfly.

552   Dingle, H., M. P. Zalucki, W. A. Rochester, and T. Armijo-Prewitt. 2005. Distribution of the

553   monarch butterfly, Danaus plexippus (L.) (Lepidoptera: Nymphalidae), in western North

554   America: Monarch Butterflies in Western North America. Biological Journal of the

555   Linnean Society 85:491–500.

556   Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B.

557   Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B.

558   Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013.

559   Collinearity: a review of methods to deal with it and a simulation study evaluating their

560   performance. Ecography 36:27–46.

561   Egan, S. P., and J. R. Ott. 2007. Host plant quality and local adaptation determine the distribution

562   of gall-forming herbivore. Ecology 88:2868–2879.

563   Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F.

564   Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G.

565   Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend

566   Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón,

567   S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve

568   prediction of species' distributions from occurrence data. Ecography 29:129–151.

569   Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and

570   Prediction Across Space and Time. Annual Review of Ecology, Evolution, and

571   Systematics 40:677–697.

572   Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical

573   explanation of MaxEnt for ecologists: Statistical explanation of MaxEnt. Diversity and

574   Distributions 17:43–57.

575   Fick, E. C., and R. J. Hijmans. 2017. WorldClim-Global Climate Data.

576   http://www.worldclim.org.

577   Forister, M. L., V. Novotny, A. K. Panorska, L. Baje, Y. Basset, P. T. Butterill, L. Cizek, P. D.

578   Coley, F. Dem, I. R. Diniz, P. Drozd, M. Fox, A. E. Glassmire, R. Hazen, J. Hrcek, J. P.

579   Jahner, O. Kaman, T. J. Kozubowski, T. A. Kursar, O. T. Lewis, J. Lill, R. J. Marquis, S.

580   E. Miller, H. C. Morais, M. Murakami, H. Nickel, N. A. Pardikes, R. E. Ricklefs, M. S.

581   Singer, A. M. Smilanich, J. O. Stireman, S. Villamarín-Cortez, S. Vodka, M. Volf, D. L.

582   Wagner, T. Walla, G. D. Weiblen, and L. A. Dyer. 2015. The global distribution of diet

583   breadth in insect herbivores. Proceedings of the National Academy of Sciences 112:442–

584   447.

585   Fraterrigo, J. M., S. Wagner, and R. J. Warren. 2014. Local-scale biotic interactions embedded in

586   macroscale climate drivers suggest Eltonian noise hypothesis distribution patterns for an

587   invasive grass. Ecology Letters 17:1447–1454.

588   GBIF.org. 2019. https://doi.org/10.15468/dl.sjg2d2.

589   Gripenberg, S., P. J. Mayhew, M. Parnell, and T. Roslin. 2010. A meta-analysis of preference-

590   performance relationships in phytophagous insects. Ecology Letters 13:383–393.

591   Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple

592   habitat models. Ecology Letters 8:993–1009.

593   Hijmans, R. J., S. Phillips, J. R. Leathwick, and J. Elith. 2011. Package 'dismo.'

594   Hunter, M. D., T. Ohgushi, and P. W. Price. 1992. Effects of resource distribution on animal-

595   plant interactions. Academic Press, San Diego, CA.

596   Kartesz, J. T. 2015. Floristic Synthesis of North America. Taxonomic Data Center, Chapel Hill,

597   N.C. [maps generated from Kartesz, J.T. 2015.

598   Karthik, R. 2014. ecoengine: Programmatic interface to the API serving UC Berkeley's Natural

599   History Data.

600   Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M.

601   Stillfried, I. Heckmann, A. K. Scharf, D. M. Augeri, S. M. Cheyne, A. J. Hearn, J. Ross,

602   D. W. Macdonald, J. Mathai, J. Eaton, A. J. Marshall, G. Semiadi, R. Rustam, H.

603   Bernard, R. Alfred, H. Samejima, J. W. Duckworth, C. Breitenmoser-Wuersten, J. L.

604   Belant, H. Hofer, and A. Wilting. 2013. The importance of correcting for sampling bias

605   in MaxEnt species distribution models. Diversity and Distributions 19:1366–1379.

606   La Sorte, F. A., and W. Jetz. 2010. Projected range contractions of montane biodiversity under

607   global warming. Proceedings of the Royal Society B: Biological Sciences 277:3401–

608   3410.

609   Ladner, D. T., and S. Altizer. 2005. Oviposition preference and larval performance of North

610   American monarch butterflies on four Asclepias species. Entomologia Experimentalis et

611   Applicata 116:9–20.

612   Lemoine, N. P. 2015. Climate change may alter breeding ground distributions of eastern

613   migratory Monarchs (Danaus plexippus) via range expansion of Asclepias host plants.

614   PLOS ONE 10:e0118614.

615   Lewinsohn, T., V. Novotny, and Y. Basset. 2005. Insects on plants: diversity of herbivore

616   assemblages revisited 36:597–620.

617   Mcmillin, Joel. D., and M. R. Wagner. 1998. Influence of host plant vs. natural enemies on the

618   spatial distribution of a pine sawfly, Neodiprion autumnalis. Ecological Entomology

619   23:397–408.

620   Memmott, J., R. K. Day, and H. C. J. Godfray. 1995. Intraspecific variation in host plant quality:

621   the aphid Cinara cupressi on the Mexican cypress, Cupressus lusitanica. Ecological

622   Entomology 20:153–158.

623   Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, M. Uriarte, and R. P.

624   Anderson. 2014. ENMeval: An R package for conducting spatially independent

625   evaluations and estimating optimal model complexity for MAXENT ecological niche

626   models. Methods in Ecology and Evolution 5:1198–1205.

627   Naturalist [online]. Website. 2019, January. . https://www.inaturalist.org.

628   Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L.

629   Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999.

630   Poleward shifts in geographical ranges of butterfly species associated with regional

631   warming. Nature 399:579–583.

632   Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J.

633   Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J.

634   Kollar, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L. Nagy, G. Pelino,

635   M. Puscas, G. Rossi, A. Stanisci, A. O. Syverhuset, J.-P. Theurillat, M. Tomaselli, P.

636   Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent plant diversity

637   changes on Europe's mountain summits. Science 336:353–355.

638   Pelton, E. M., C. B. Schultz, S. J. Jepsen, S. H. Black, and E. E. Crone. 2019. Western Monarch

639   population plummets: status, probable causes, and recommended conservation actions.

640   Frontiers in Ecology and Evolution 7:258.

641 Peterson, A., J. Soberon, R. G. Pearson, R. P. Anderson, E. Martinez-Meyer, M. Nakamura, and

642   M. Araújo. 2011. Ecological niches and geographic distributions. Princeton University,

643   Press.

644 Peterson, A. T., M. Papeș, and J. Soberón. 2008. Rethinking receiver operating characteristic

645   analysis applications in ecological niche modeling. Ecological Modelling 213:63–72.

646 Petschenka, G., and A. A. Agrawal. 2015. Milkweed butterfly resistance to plant toxins is linked

647   to sequestration, not coping with a toxic diet. Proceedings of the Royal Society B:

648   Biological Sciences 282:20151865.

649 Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species

650   geographic distributions. Ecological Modelling 190:231–259.

651 Pocius, V. M., D. M. Debinski, J. M. Pleasants, K. G. Bidne, R. L. Hellmich, and L. P. Brower.

652   2017. Milkweed matters: Monarch butterfly (Lepidoptera: Nymphalidae) survival and

653   development on nine midwestern Milkweed species. Environmental Entomology

654   46:1098–1105.

655 Preston, K. L., J. T. Rotenberry, R. A. Redak, and M. F. Allen. 2008. Habitat shifts of

656   endangered species under altered climate conditions: importance of biotic interactions.

657   Global Change Biology.

658 Price, P. W. 1983. Hypotheses on organization and evolution in herbivorous insect communities.

659   Pages 559–98 Variable Plants and Herbivores in Natural and Managed Systems.

660   Academic Press, New York.

661 R Studio Team. 2015. R Studio. Integrated Development for R. RStudio, Inc., Boston, MA.

662 Ries, L., and K. S. Oberhauser. 2015. A citizen army for science: quantifying the contributions of

663   citizen scientists to our understanding of monarch butterfly biology 65:419–430.

664   Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kühn. 2008. Climate change can cause

665   spatial mismatch of trophically interacting species. Ecology 89:3472–3479.

666   Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie. 2008. Climate change,

667   elevational range shifts, and bird extinctions: *Elevation, Climate Change, and Bird*

668   *Extinctions*. Conservation Biology 22:140–150.

669   Singer, M. S., T. E. Farkas, C. M. Skorik, and K. A. Mooney. 2012. Tritrophic interactions at a

670   community level: effects of host plant species quality on bird predation of caterpillars

671   179:363–374.

672   Soberon, J., and M. Nakamura. 2009. Niches and distributional areas: Concepts, methods, and

673   assumptions. Proceedings of the National Academy of Sciences 106:19644–19650.

674   Stevens, S. R., and D. F. Frey. 2010. Host plant pattern and variation in climate predict the

675   location of natal grounds for migratory monarch butterflies in western North America.

676   Journal of Insect Conservation 14:731–744.

677   The HadGEM2 Development Team: G. M. Martin, N. Bellouin, W. J. Collins, I. D. Culverwell,

678   P. R. Halloran, S. C. Hardiman, T. J. Hinton, C. D. Jones, R. E. McDonald, A. J.

679   McLaren, F. M. O&apos;Connor, M. J. Roberts, J. M. Rodriguez, S. Woodward, M.

680   J. Best, M. E. Brooks, A. R. Brown, N. Butchart, C. Dearden, S. H. Derbyshire, I.

681   Dharssi, M. Doutriaux-Boucher, J. M. Edwards, P. D. Falloon, N. Gedney, L. J. Gray, H.

682   T. Hewitt, M. Hobson, M. R. Huddleston, J. Hughes, S. Ineson, W. J. Ingram, P. M.

683   James, T. C. Johns, C. E. Johnson, A. Jones, C. P. Jones, M. M. Joshi, A. B. Keen, S.

684   Liddicoat, A. P. Lock, A. V. Maidens, J. C. Manners, S. F. Milton, J. G. L. Rae, J. K.

685   Ridley, A. Sellar, C. A. Senior, I. J. Totterdell, A. Verhoef, P. L. Vidale, and A.

686   Wiltshire. 2011. The HadGEM2 family of Met Office Unified Model climate

687   configurations. Geoscientific Model Development 4:723–757.

688   Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and

689   abundance responses to climate change: why it is essential to include biotic interactions

690   across trophic levels. Philosophical Transactions of the Royal Society B: Biological

691   Sciences 365:2025–2034.

692   Warren, D. L., and S. N. Seifert. 2011. Ecological niche modeling in Maxent: the importance of

693   model complexity and the performance of model selection criteria. Ecological

694   Applications 21:335–342.

695   Wharton, T. N., and D. J. Kriticos. 2004. Biodiversity: The fundamental and realized niche of the

696   Monterey Pine aphid, Essigella. Diversity and Distributions:10.

697   Zalucki, M., L. Brower, and A. Alonso. 2001. Detrimental effects of latex and cardiac glycosides

698   on survival and growth of frst-instar monarch butter ̄y larvae Danaus plexippus feeding

699   on the sandhill milkweed Asclepias humistrata 26:212–224.

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714 # Tables

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716 **Table 1. Selected environmental variables**

Worldclim Code	Environmental Variable*
Bio1	Annual Mean Temperature
Bio5	Max Temperature of Warmest Month
Bio6	Minimum Temperature of Coldest Month
Bio7	Temperature Annual Range
Bio8	Mean Temperature of Wettest Quarter
Bio9	Mean Temperature of Driest Quarter
Bio12	Annual Precipitation
Bio15	Precipitation Seasonality
Bio17	Precipitation of Driest Quarter
Bio18	Precipitation of Warmest Quarter
Bio19	Precipitation of Coldest Quarter

*Selected environmental variables with Pearson correlation coefficient of 0.85 or lower.

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733 **Table 2. Milkweeds models summary and estimated habitat suitability**

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Asclepias species	Spatial filtering (Km^2)	Records		AUC best model	Estimated Habitat (Km^2)		Host quality weight[1]
		Total	Filtered		Current	Projected	
A. albicans	1	434	209	0.977	37,937	28,444	**0.554**
A. asperula*	30	586	244	0.815	614,502	678,420	0.078
A. californica*	1	607	277	0.945	84,794	124,187	0.306
A. cordifolia*	30	683	173	0.848	230,690	215,368	0.621
A. cryptoceras	30	210	128	0.839	416,872	246,545	0.218
A. engelmanniana*	30	90	70	0.915	277,368	230,811	0.502
A. eriocarpa	30	878	145	0.888	147,561	235,229	0.541
A. erosa*	30	524	145	0.885	285,506	466,099	0.671
A. fascicularis*	30	2259	399	0.859	306,140	512,078	0.545
A. halli	1	48	48	0.915	197,755	2,896	0.898
A. incarnata*	1	144	94	0.805	113,426	64,869	0.823
A. labriformis	1	68	57	0.945	22,126	4,863	**0.554**
A. latifolia*	30	162	102	0.858	415,185	412,476	0.394
A. linaria*	1	127	75	0.962	376,557	382,289	0.427
A. macrosperma	1	71	62	0.965	624,888	124,259	**0.554**
A. macrotis*	1	46	44	0.925	196,251	151,159	**0.554**
A. nycatginifolia*	1	154	100	0.958	112,228	233,621	**0.554**
A. pumila*	1	89	73	0.985	69,502	5,581	0.660
A. soloanoana*	1	132	68	0.995	17,704	65,588	1.00
A. speciosa	30	1359	478	0.746	958,479	937,320	0.768
A. subulata*	30	627	114	0.927	114,507	379,000	0.606
A. subverticillata*	30	545	286	0.809	594,885	674,988	0.505
A. tuberosa*	30	184	88	0.831	305,144	470,641	0.681
A. vestita*	1	159	70	0.983	34,449	80,731	0.286

735 *Species marked with an asterisk are projected to shift their distribution to higher latitudes (S1
736 File.)
737 [1]Hostplant quality weight determined by the average weight of monarch larvae reared on 24
738 *Asclepias* species within a 5-day period. Bold numbers indicate the average weight assigned to
739 species with missing hostplant quality information.

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749 **Table. 3 Monarch model performance comparison and estimated habitat suitability**

Model	n^1	AUC	AICc	ΔAICc	wAICc	Estimated habitat (km^2) * Current	Projected (2070)
Climate envelope	60	0.799	25,694.99	168.52	2.545^{-37}	214,245	409,091
Hostplant-presence	61	0.803	25,526.46	0.000	1.00	252,464	466,306
Hostplant-quality	61	0.800	25,649.97	123.50	1.515^{-27}	252,465	486,200

750 *Estimated habitat was calculated by summarizing areas with probability of distribution higher
751 than 0.5 from the logistic output layers produced by each model. [1] n gives the number of
752 parameters of each model.

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Figures

Figure 1. Contemporary and projected genus-level milkweeds distribution
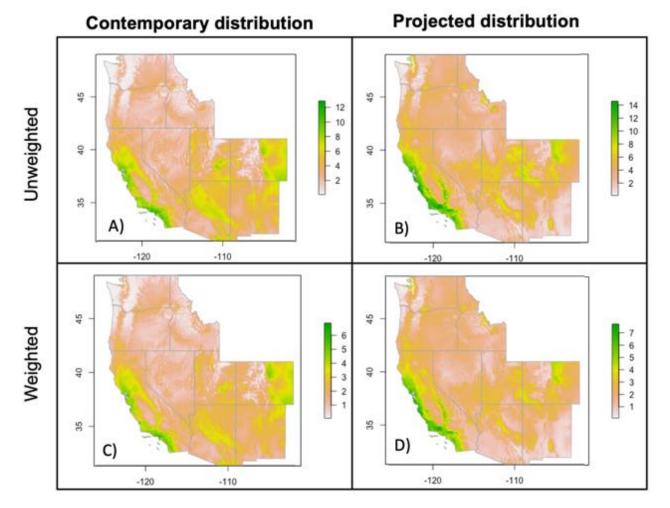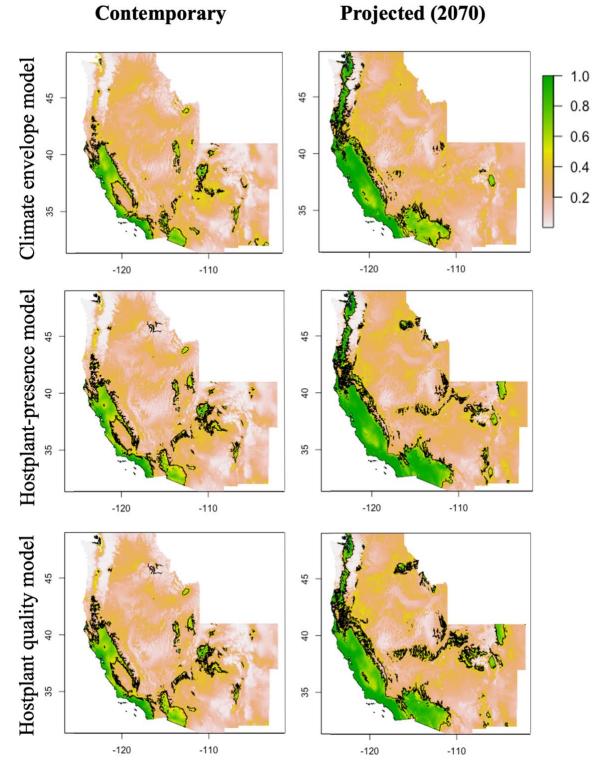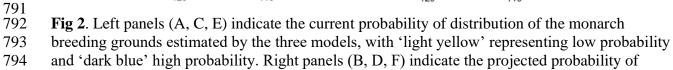

Fig 1. Genus-level *Asclepias* predictor and projection layers used in the monarch hostplant
distribution and quality models. The unweighted layers reflect the summed probability of
occurrence of all *Asclepias* species, thus reflecting mean probability of occurrence and species
richness, while the weighted layer additionally weighs each species by hostplant quality. 'Green'
indicate high probability of distribution, species richness and/or host-quality, and 'white' low
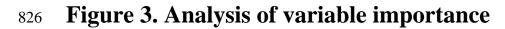probability of distribution, species richness and/or low quality.

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790   **Figure 2. Monarch contemporary and projected future breeding ranges**

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792   **Fig 2**. Left panels (A, C, E) indicate the current probability of distribution of the monarch

793   breeding grounds estimated by the three models, with 'light yellow' representing low probability

794   and 'dark blue' high probability. Right panels (B, D, F) indicate the projected probability of
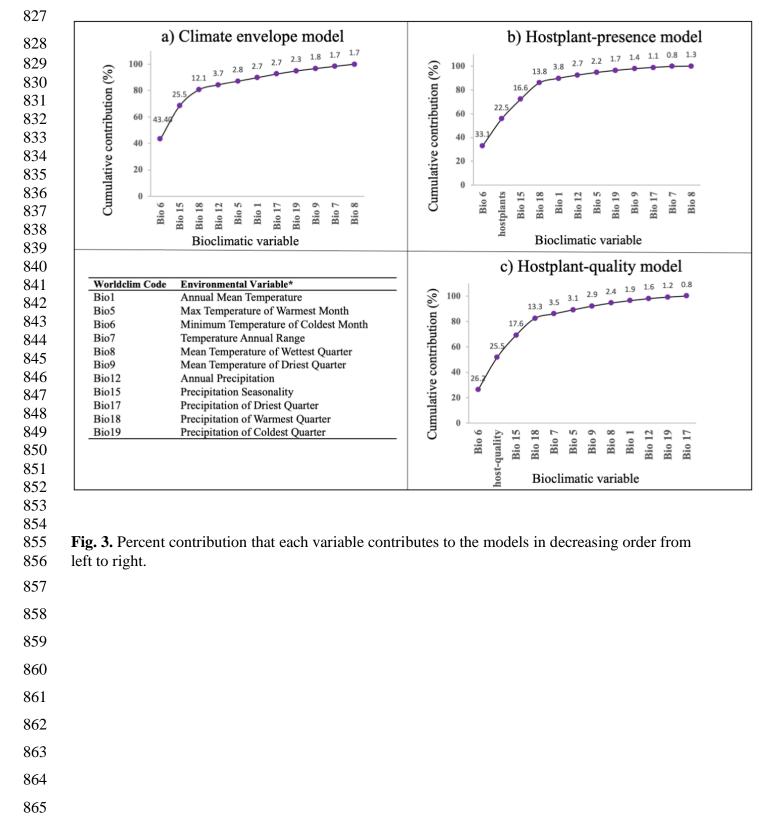
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795   distribution of the monarch breeding grounds for the year 2070 estimated by the three models.
796   Suitable habitat for monarch breeding is delineated in black and represent areas with a
797   probability of distribution greater than 0.5.

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Figure 3. Analysis of variable importance

Fig. 3. Percent contribution that each variable contributes to the models in decreasing order from left to right.

Appendices

Appendix S1. Milkweeds species contemporary and projected distributions. Estimated contemporary distribution of 24 species of *Asclepias* (left panels) and projections under a climate change scenario for 2070 (right panels), with 'green' indicating high probability of distribution and 'white' low probability. Suitable habitat for each *Asclepias* spp. is delineated in black and represent areas with a probability of distribution greater than 0.5.

Appendix S2. Jackknife Test of Variable Importance. Jackknife test of variable importance. Blue bars indicate model gain when each variable is used in isolation, turquoise bars represent model gain when a single variable is excluded, and red bars represent model gain when all variables are included.

Appendix S3. Milkweeds range overlaps in the Western United States. Each overlaid layer represents the range of individual *Asclepias* species estimated by drawing a polygon around areas with areas with a probability of distribution greater than 0.5. Regions in white represent areas with no Milkweeds, 'light green' represent low range overlap, and 'dark green' high range overlap.

Metadata S1. R code for monarch and milkweed species distributions modeling.

Data S1. Milkweed species records retrieved from various open source databases within the study region.

Data S2. Monarch larval records retrieved from open source databases and the MLMP (Monarch Larvae Monitoring Project) within the study region.