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Species distribution models for natural enemies of monarch butterfly (*Danaus plexippus*) larvae and pupae: distribution patterns and implications for conservation

Shaun M. McCoshum[1,2] · Shannon L. Andreoli[2] · Carl M. Stenoien[3] ·
Karen S. Oberhauser[3] · Kristen A. Baum[2]

Abstract Prey populations can be strongly influenced by predators and parasitoids, and migratory prey whose distributions vary geographically throughout their breeding seasons encounter different combinations of predators and parasitoids throughout their range. North American monarch butterflies (*Danaus plexippus*) are susceptible to a wide variety of natural enemies, but the distribution of these natural enemies has not been quantified. We developed ecological niche models using environmental data to identify areas with suitable abiotic conditions for eight known natural enemies of monarchs, including six predators: *Arilus cristatus, Harmonia axyridis, Monomorium minimum, Podisus maculiventris, Polistes* spp., and *Solenopsis geminata*; and two parasitoids: *Lespesia archippivora* and *Pteromalus cassotis*. We combined correlated suitable areas for individual predators and parasitoids to identify regions with the most predator and parasitoid species potential. The Gulf Coast, West Coast, Florida, and parts of the eastern United States are predicted to have the most natural enemy species. We suggest that future research should assess monarch mortality rates in these areas, and that monarch conservation strategies consider pressure from natural enemies.

Keywords Monarch · Natural enemies · Niche model · Conservation · Parasitoid · Predator · *Danaus plexippus*

✉ Shaun M. McCoshum
mccoshsm@gmail.com

1 Cornell University, Ithaca, NY, USA

2 Oklahoma State University, Stillwater, Oklahoma, USA

3 University of Minnesota, Minneapolis, Minnesota, USA

Introduction

Predators, parasitoids, and parasites can strongly influence prey populations, often causing oscillations in prey abundance (Huffaker et al. 1963; Hudson et al. 1998; Redpath et al. 2006) and local extinctions (Lei and Hanski 1997; Van Nouhuys and Hanski 1999, 2002). Interactions between prey and their natural enemies are influenced by numerous factors, including habitat preferences, landscape and patch connectivity (Pimentel et al. 1963; Kareiva 1987), predator and parasitoid specificity (Van Nouhuys and Hanski 2002), and interactions with other species (Huffaker et al. 1963), all of which require an overlap of climatically suitable areas for both species. Natural enemies of herbivorous insects, including invertebrate predators and parasitoids, are often considered beneficial because they are used as biological control against agricultural pests (Dosdall and Mason 2010; Cronin and Reeve 2014); however, natural enemies are of concern when prey species include beneficial or endangered insects (Van Nouhuys and Hanski 1999, 2002; Gomes et al. 2013). Furthermore, the effects of natural enemies on host fitness vary across space and time, making it difficult to predict the effects natural enemies may have on host populations (McCallum and Dobson 1995). Thus, understanding the interactions between prey and their natural enemies requires understanding the spatial and temporal distribution of prey and natural enemy populations.

Although generalist natural enemies can negatively impact prey populations, specialized predators and parasitoids can reduce prey populations even more, sometimes creating localized extinctions. These population reductions have led to the use of parasitoids and certain predators in biocontrol of crop pests (Dixon 2000; Dosdall and Mason 2010; Diehl et al. 2013). For example, significant aphid

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population reduction by two generalists, lacewings (Chrysopidae) and lady bird beetles (Coccinellidae) has been documented, but even stronger reductions occur when specialized natural enemies, such as parasitoid wasps, were also present (Dixon 2000; Diehl et al. 2013). Even though specialist natural enemies are better biocontrol agents, many generalists have been released, including *Pteromalus puparum* (Pteromalidae), a gregarious parasitoid with more than a hundred wasps emerging per gram from a single host (Takagi 1985), to control *Pieris rapae* populations (Dweck 2009) and *Lespesia archippivora* (Tachinidae) to control armyworm (Etchegaray and Nishida 1975). Although neither of these generalist parasitoids have been released for biocontrol recently both are known to cause mortality in native, non-pest species like monarchs (Oberhauser et al. 2007, CMS personal observation). The economic implications of agriculturally beneficial natural enemies have led researchers to focus on agricultural settings, but the spillover effects on native non-pest fauna from biocontrol introductions as well as native, non-pest predating natural enemies are less well studied.

Natural enemies strongly influence larval survival rates of the monarch butterfly (*Danaus plexippus* (Lepidoptera: Nymphalidae)) (Borkin 1982; Prysby 2004; Nail et al. 2015, reviewed in Oberhauser et al. 2015). Mortality is especially high (ranging from 88 to 98 %) during the egg and early larval instar stages (Borkin 1982, Zalucki and Kitching 1982; Prysby 2004; Nail et al. 2015). Eggs and larvae are susceptible to predation by generalist predators such as mantids (Mantodea) (Rafter et al. 2013), paper wasps (*Polistes* spp.: Vespidae) (Rayor 2004), ants (Formicidae) (Calvert 1996; Prysby 2004), wheelbugs (*Arilus cristatus*: Reduviidae) (SMM, SLA, personal observation), lacewings (Chrysopidae) (Oberhauser et al. 2015), multicolored Asian lady beetles (*Harmonia axyridis*: Coccinellidae) (Koch et al. 2003, 2006), spiny soldier bugs (*Podisus maculiventris*: Pentatomidae), various ant species including *Solenopsis geminate* (Calvert 2004, SMM, SLA personal observation) and spiders (Aranae) (Oberhauser et al. 2015) as well as parasitoids (e.g. *L. archippivora*: Tachinidae (Oberhauser et al. 2007)). The spatial and temporal distributions of monarch natural enemies are largely unknown (Rafter et al. 2013), and identifying these spatial distributions will help us to identify areas in which to observe interactions between monarchs and their natural enemies. Furthermore, the rate of mortality due to parasitoids (*L. archippivora* and *P. cassotis*) varies at small local scales (Oberhauser et al. 2007; Mueller and Baum 2014; Stenoien et al. 2015), but regional populations may have different levels of mortality risk based on the likelihood that parasitoids inhabit different areas.

Predation and parasitism during the pupal stage are more difficult to study in the wild due to larvae moving away from host plants and cryptic chrysalisids. Pupal mortality

due to the specialist parasitoid wasp *Pteromalus cassotis*: Pteromalidae (Oberhauser et al. 2015; Stenoien et al. 2015) and paper wasps (Oberhauser et al. 2015) have been documented but not extensively studied, and the locations in which these interactions are most likely to occur is not yet known. Monarchs are also affected by an obligate protozoan parasite, *Ophryocystis elektroscirrha* (OE) (Leong et al. 1997) that has been documented to occur in all major populations of monarchs, which is transmitted from adults to their offspring when larvae consume parasite spores.

Two main populations of monarch butterflies exist within the USA: the eastern population that breeds east of the Rocky Mountains and overwinters in Mexico, and the western population that overwinters in California (USA) and breeds in the western United States and Canada. Some authors distinguish a year-round breeding population that occurs in southern Florida (Brower and Jeansonne 2004), but others question whether this is really a separate population (Knight and Brower 2009). All of these populations have some crossover (summarized by Pyle 2015) and do not differ genetically (Brower and Boyce 1991; Lyons et al. 2012; Pierce et al. 2015). The long-distance migration of the eastern population from breeding grounds as far north as Canada to overwintering sites in the Transvolcanic Mountains in Mexico (Urquhart 1976, Urquhart & Urquhart 1978) is threatened by numerous factors, including habitat loss and loss of host plants (Brower et al. 2012; Pleasants and Oberhauser 2013; Crouch 2014; Pleasants 2015). Because of monarch conservation concerns (Center for Biological Diversity et al. 2014), many individuals and groups are maintaining, enhancing, or creating breeding habitat for monarchs with host plants and nectar sources, and these areas are known to support monarch larvae (Cutting and Tallamy 2015; Nail et al. 2015). Areas with resources for monarchs can also support their natural enemies, and a better understanding of the distribution of natural enemies can help to inform habitat design and placement.

Overwintering adults in both the western and eastern populations re-colonize their breeding grounds over multiple generations (Malcolm et al. 1993; Wassenaar and Hobson 1998; Flockhart et al. 2015), and overlap between monarchs and their natural enemies varies both spatially and temporally. Some of the early spring breeding areas, such as the southern Great Plains, can become unsuitable for monarchs in the hotter summer months when high temperatures (>29 °C) increase larval mortality rates and delay larval development (Rawlins and Lederhouse 1981; Zalucki and Kitching 1982; Zalucki 1982; Malcolm et al. 1987; York and Oberhauser 2002; Nail et al. 2015). Natural enemies of monarchs, however, persist in these areas throughout this time period.

Environmental factors also influence monarch host plants, which occur in a wide range of habitats (Wilbur 1976). For example, *Asclepias syriaca* is often used by monarchs and is common in the northern breeding grounds.

It grows in moist to dry soils, sand dunes and prairies, fence rows, lakeshores, roadsides, croplands, and woodland borders (Bhowmik and Bandeen 1976; Hartzler and Buhler 2000; Hartzler 2010), and re-grows after being cut back or mowed (Fischer et al. 2015). Other milkweed species, like *A. viridis*, which is more common during the spring in the southern breeding grounds of North America, senesce if no disturbance or rainfall occur. Disturbances such as fire or mowing will cause *A. viridis* to re-grow, as will sufficient precipitation (Baum and Sharber 2012; Baum and Mueller 2015). These factors create different habitats that vary in milkweed and floral resource density and diversity. Cumulatively, host plants and associated plant communities create a network of patches in a variety of habitats in which monarchs can reproduce; these habitats also vary in suitability for natural enemies.

With recent declines in monarch overwintering populations (Brower et al. 2012; Vidal and Rendón-Salinas 2014) and the petition to the U. S. Fish and Wildlife Service to gain legal protection for monarchs under the Endangered Species Act (Center for Biological Diversity et al. 2014), it is important to evaluate the distribution of monarch predator and parasitoid species to understand the potential implications for monarch butterfly populations. To elucidate where predation pressure might be the greatest, we modeled environmental suitability based on distributions of some documented monarch egg, larval, and pupal predators and parasitoids, using occurrence data within North America. These models identify areas which may support predator and parasitoid populations that in turn may negatively affect local monarch populations. We modeled the distribution of the larval and pupal parasitoids *L. archippivora* and *P. cassotis* because both have wide geographic ranges and are important mortality sources. We also modeled the generalist predators *A. cristatus, H. axyridis, M. minimum, P. maculiventris, Polistes* spp., and *S. geminata* based on previous research and observations documenting their impact on monarch eggs, larvae, and pupae. Because OE infections are likely to depend more on localized activity of infected adults (Altizer et al. 2000; Bartel et al. 2011; McCoshum and Baum 2014) than on the average environmental parameters, we did not include OE in our study.

Methods

Selected study species

Parasitoids

The best-studied larval parasitoid of monarchs is *L. archippivora*, which is in a family consisting of over 8000 species of dipteran parasitoids whose main hosts are Lepidoptera (Stireman et al. 2006; Oberhuaser 2012). While *L. archippivora* has been reported to parasitize larvae of 25 lepidopteran species in 14 families, and one hymenopteran species (Beneway 1963; Arnaud 1978), it has only been extensively studied in monarch butterflies (e.g., Oberhuaser 2012) and the beet armyworm (*Spodoptera exigua*: Noctuidae) (Stapel et al. 1997). While parasitism is most likely to occur in late second to fourth instar monarch larvae, it is possible at all instars (Etchegaray and Nishida 1975; Oberhuaser 2012). By the fifth instar, parasitism rates average about 13 % across years, but can reach up to 90 % in some local populations and vary a great deal from year to year (Oberhauser et al. 2007; Oberhuaser 2012). There is a higher rate of parasitism by *L. archippivora* in years following high monarch density, which may indicate that monarchs are the primary host (Oberhuaser 2012). The range of *L. archippivora* may be constrained by winter conditions; late instar maggots emerge from their host during late larval or early pupal stages, pupate in the leaf litter and eclose after about 2 weeks (Oberhauser et al. 2007). While their overwintering strategy is not fully understood, it is likely that they overwinter as pupae and emerge the following spring.

Monarch pupae are susceptible to parasitism by the gregarious parasitoid wasp, *Pteromalus cassotis*: Pteromalidae (Walker 1847; Stenoien et al. 2015). Recent observations of experimentally placed and wild collected pupae found parasitism rates varied, with one site of wild pupae having 100 % of the collected and observed pupae parasitized by *P. cassotis* (Stenoien et al. 2015). While it has been documented in 16 states across the United States, many of these reports are from one to a few sites and the geographic range of *P. cassotis* is unknown.

Predators

Few studies document the impact of generalist predators on monarch larvae (summarized in Oberhauser et al. 2015), so our selection of predators was restricted to published studies and observations from authors and citizen scientists. Studies concerning predation by *A. cristatus* (wheelbugs) on monarchs have not been published; however we have observed *A. cristatus* predating larvae in the field, multiple times in different years (SMM, SLA personal observation; citizen scientist photo submissions to SMM). Third instar to adult *H. axyridis* (multicolored Asian lady beetle) consume monarch larvae and eggs in the laboratory (Koch et al. 2003, 2006), but their impacts on field populations are unknown. Ongoing studies in Oklahoma have documented *M. minimum* (little black ants) predating experimentally-placed chrysalids (SMM, SLA, KAB unpublished data), but mortality during the chrysalid stage of wild monarchs is poorly studied. Similarly, predation by

P. maculiventris (spiny soldier bug) on monarchs is poorly studied, but we have received photographic reports of this generalist consuming monarch larvae (Monarch Larva Monitoring Project). *Polistes* spp. wasp predation of both larvae and pupae is documented (Rayor 2004; Oberhauser et al. 2015) and these wasps occur worldwide. The more restricted and introduced *S. geminata* (fire ant) is thought to have strong negative impacts on egg and larval survival (Calvert 1996, 2004). Although lacewing and mantid predation has also been documented, we did not model these groups due to the large number of species and habitats in which they occur.

Data collection

Environmental data selection

Environmental data (30 s resolution) were downloaded from WorldClim (www.worldclim.org) (Hijmans et al. 2005) and clipped to latitude 19°–52.5° N and longitude 52.0°–129.5° W, encompassing the most northern extent of monarch larvae reported from Journey North (www.learner.org), and the southern region of the Mexican overwintering sites. To account for collinearity among variables we performed a correlation analysis using ArcGIS. Starting with the most relevant environmental data (see next paragraph), we did not include environmental data layers that were strongly correlated ($r \geq |0.7|$) with other layers (Boria et al. 2014).

Because many insects are physiologically constrained by thermal extremes (Sunday et al. 2011), we began selecting data based on the minimum temperature of the coldest month, and the maximum temperature for the warmest month ($r < |0.7|$). We then added annual precipitation and precipitation seasonality because of their likely influence on plant communities. Finally, we included the two remaining ecologically informative layers that had correlation values less than our threshold: mean diurnal temperature and precipitation of the warmest quarter (WorldClim). We also modeled the distribution of monarch larvae so that we could identify areas within North America where they may be at most risk. Since monarchs migrate and are thus not exposed to annual maximum and minimum temperatures at many locations within their breeding range, we removed these data layers from the monarch models and used mean temperature of the warmest quarter instead because temperature can influence larval development and survival, and because these data did not correlate with the other four data layers.

Occurrence data were compiled from numerous sources. *Lespesia archippivora* occurrences were obtained through the Monarch Larva Monitoring Project (MLMP) (Prysby and Oberhauser 1999, 2004; Monarch Larva Monitoring Project 2015). Data from MLMP that documented fly parasitism of monarch larvae were assumed to be *L. archippivora* (Oberhauser et al. 2007). Egg and larval data for *D. plexippus* were obtained through Journey North (Howard and Davis 2004); although the MLMP also records egg and larval data, we chose not to use them so that our models of monarchs and their natural enemies were based on different data sets. The Global Biodiversity Information Facility (GBIF: an online database for field survey data and natural history museum records) was used for all generalist predator data and for some *P. cassotis* points. We also used data from the California Academy of Science, the Chalcidoidea Database, and the authors and citizen scientists for *P. cassotis* occurrences, which collectively contributed a total of 18 occurrence points. Personal observations from authors and photographs from citizen scientists (Monarch Larva Monitoring Project) were also used for poorly-represented areas.

Test models were run using *L. archippivora* because these data were the most spatially concentrated and observations occurred in most of the known North American range. To create test models, occurrence data were spatially rarefied by 10 km to reduce sampling bias (N = 88 observations) and 100 km (N = 41 observations) to further reduce training data bias (Boria et al. 2014; Radosavljevic and Anderson 2014). Rarefaction at 10 km produced models which favored areas in the upper Midwest where the majority of data reports occurred; this finding is likely to reflect survey intensity bias, and not a true distribution of the species. Models with 100 km rarefaction included more known areas for *L. archippivora* in their outputs. Final models for all species were then run using occurrence data filtered by 100 km, due to the large geographic range of each species, differences in survey intensities within the ranges, and the number of areas with poor sampling.

Observation points remaining after data were rarefied were used to create a training file using "Sample by Buffered MCP" (Brown 2014). We applied a 100 km buffer to the minimum convex polygon around rarefied occurrence points, and used this to delineate the background area which was used to train the Maximum Entropy algorithm (MaxEnt v. 3.3.3k) models. MaxEnt uses covariates at occurrence points to calculate the conditional probability for an organism to exist at these locations (Elith et al. 2011). We created models for each species using the spatially rarefied occurrence data and the environmental data layers specified above.

The models were run in MaxEnt with the following settings: MCP file used, projected onto the area we defined including the conterminous United States for all organisms; ten replications with averages reported, with 10,000 maximum number of background points; regularization

multiplier at 1; minimum training value, and cross-validate were also turned on. We converted each output raster into a binary layer, counting model outcome values of 0.5 and higher as suitable. Once converted to binary data, rasters were added together to identify areas where parasitoids and predators may be abundant.

Results

Monarch egg and larva distribution

Our models predict areas along the Gulf Coast, portions of the West Coast and throughout the eastern US as highly suitable environmental habitat for monarch reproduction. Low environmental suitability was predicted in the western plains, Rocky Mountains, and north into Idaho and Montana (Fig. 1). Mean diurnal temperature range contributed the most to the model output (38 %) while precipitation seasonality (5.7 %) and precipitation in the warmest quarter (1 %) contributed the least (Table 1). Note that our model did not include milkweed distribution, which will limit monarch distribution, but rather identifies areas where abiotic features of the environment are suitable for monarchs.

Parasitoid distributions

Our predictions of where suitable habitat for *L. archippivora* may occur show high suitability over much of the monarch range, with lower likelihood of interaction in areas just north of the central Gulf Coast (Fig. 2). This model was most influenced by the mean diurnal range and least by the maximum temperature (Table 1).

Predictions for occurrence of suitable habitat for *P. cassotis* are highest in Florida, the Gulf Coast, and Canada; with medium levels throughout much of the rest of the North American range; and with lowest levels in the Rocky Mountains and surrounding ranges (Fig. 3). This model was most influenced by mean diurnal range and was not affected by the maximum temperature of the warmest month.

Cumulatively, the models for *L. archippivora* and *P. cassotis* indicate that the Gulf Coast, areas of the west, and the Upper Midwest to southern Canada have high environmental suitability potential for parasitoid interactions with monarch larvae and pupae (Fig. 4).

Predator distributions

The generalist predator *A. cristatus* has the most habitat suitability from the Great Lakes south to Florida and into northeast Mexico (Fig. 5). Minimum temperature and annual precipitation had the most influence in our model and mean diurnal range had the least (Table 1).

Our model for the invasive *H. axyridis* predicts highly suitable habitat south of eastern Canada through Mexico, and the Pacific Coast. The Rocky Mountains west to the Cascades and south through the Sierra Madres are the least likely areas to have suitable habitat (Fig. 6). Annual precipitation contributed the most, and precipitation of the warmest quarter the least in this model (Table 1).

The ant species *M. minimum*, a generalist omnivore, is predicted to have suitable habitat throughout most of the study region, except for the south central portion of Canada and areas north of the Gulf of California (Fig. 7). Minimum temperature of the coldest month had the most, and maximum temperature of the warmest month the least contribution to the model (Table 1).

Our model for *P. maculiventris* shows high habitat suitability in the Gulf Coast, central United States, and British Columbia (Fig. 8). These predictions were most influenced by annual precipitation and least by maximum temperature of the warmest month (Table 1).

Polistes wasps are predicted to have suitable habitat throughout most of the United States and Mexico, with much of Canada predicted to have low habitat suitability (Fig. 9). Minimum temperature of the coldest month had the highest and precipitation in the warmest quarter the lowest contribution to the model predictions (Table 1).

The invasive ant *S. geminata* is predicted to have highly suitable habitat on the Gulf Coast and parts of California, as well as the northwest Pacific Coast, and the southern areas of Newfoundland (Fig. 10). Mean diurnal range had the most contribution to the model, and precipitation of the warmest quarter had the least (Table 1).

Using all of the predator models cumulatively, areas of the Gulf Coast north to the Great Lakes and parts of the upper northwest Pacific Coast are predicted to have the most predator species. The Rocky Mountains, northern Great Plains, and north into Canada are predicted to have the lowest numbers of predator species (Fig. 11).

Discussion

Our models show that monarch eggs, larvae, and pupae are at risk from parasitoids and predators throughout their North American range, and that predation pressure, based on the number of species potentially present, varies across regions. There are more predator species from the Gulf Coast north to the Great Lakes and on the northwestern edge of the western population, assuming suitable environmental habitat is occupied (Fig. 11). Although milkweed does not naturally grow in some extents of the northwestern range where our model indicates environmental suitability for monarch

Fig. 1 Model of environmental suitability for *D. plexippus* eggs and larvae, based on occurrence data from Journey North. Most areas appear to overlap with known native host plant ranges; however, areas for the western population indicate some areas where hostplants are not native but may occur in gardens
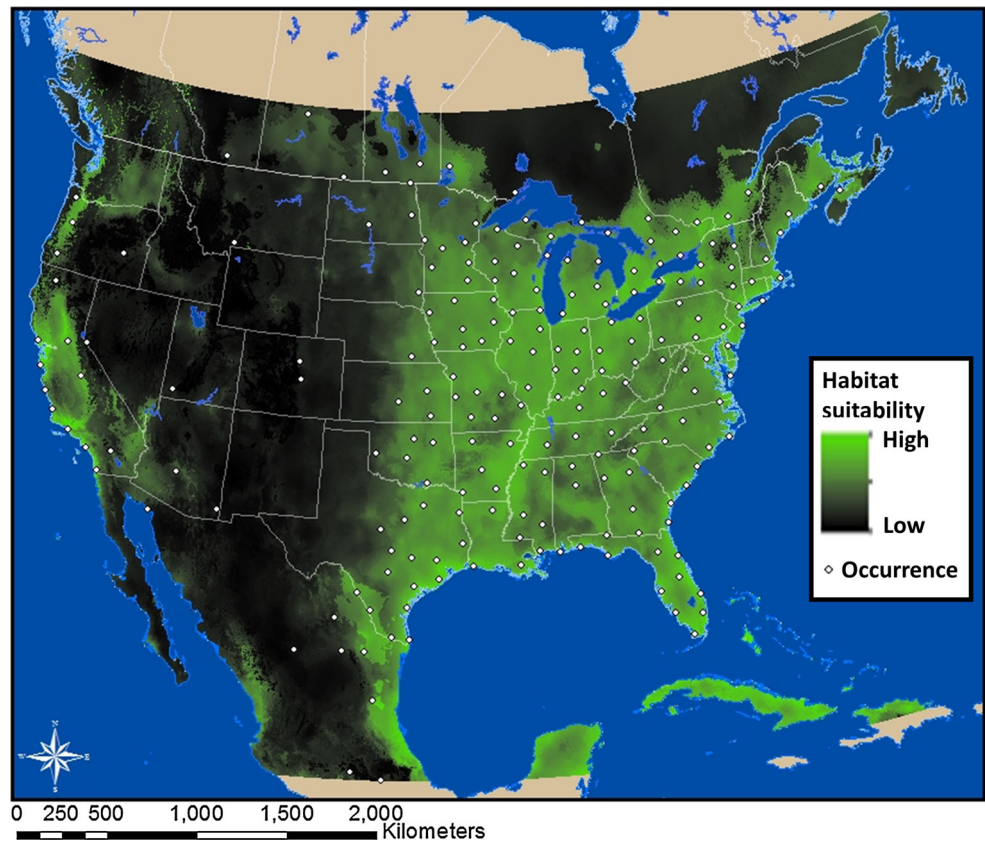
Table 1 Relative contribution power of each data layer in creating the final species distribution model

Organism	Mean diurnal temp range	Max temp of warmest month	Min temp of coldest month	Mean temp of warmest quart	Annual precip	Precip seasonality	Precip of warmest quart
Danaus plexippus	38.0	N/A	N/A	28.8	26.5	1.0	5.7
Predators							
Arilus cristatus	0.2	11.5	40.2	N/A	36.4	6.1	5.7
Harmonia axyridis	16.9	2.4	32.3	N/A	43.8	2.6	2.0
Monomorium minimum	35.9	0.6	39.2	N/A	12.9	6.7	4.8
Podisus maculiventris	21.8	5.4	9.8	N/A	41.2	8.6	13.2
Polistes spp.	21.9	7.0	58.3	N/A	7.4	3.5	2.0
Solenopsis geminata	59.6	1.3	26.2	N/A	11.9	0.5	0.4
Parasitoids							
Lespesia archippivora	61.8	3.5	0.8	N/A	26.4	3.1	4.3
Pteromalus cassotis	48.9	0	30.1	N/A	10.8	6.9	3.3

larvae, citizens and organizations which plant milkweed in these regions may create plots that experience higher natural enemy pressure compared to other regions. The Eastern population (including monarchs that are year-round residents in South Florida) is more likely than the Western population to overlap with suitable habitat for the two generalist hemipteran predators (*A. cristatus* and *P. maculiventris*). Coastal California, the Gulf Coast, and northern portions of the Eastern population breeding grounds are

predicted to have more environmentally suitable areas for the two parasitoids.

Escape from parasitoids and predators is suggested to occur with metapopulations of the Glanville Fritillary (*Melitaea cinxia*: Nymphalidae) (Van Nouhuys and Hanski 2002). Parasitoids of *M. cinxia* are restricted to areas that are most favorable to their host, and the butterfly could escape by using less favorable areas (Van Nouhuys and Hanski 2002), or by migrating to favorable habitat where

Fig. 2 Model of environmental suitability for the parasitoid fly *L. archippivora*, based on observations reported to MLMP and by the authors
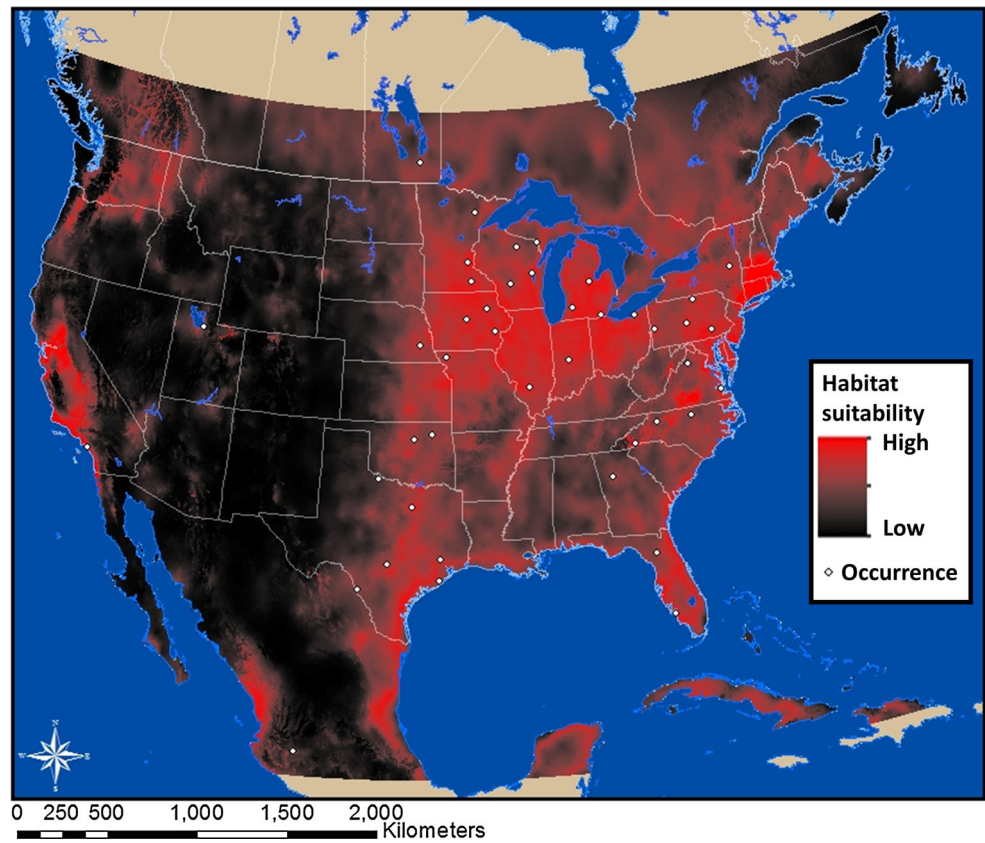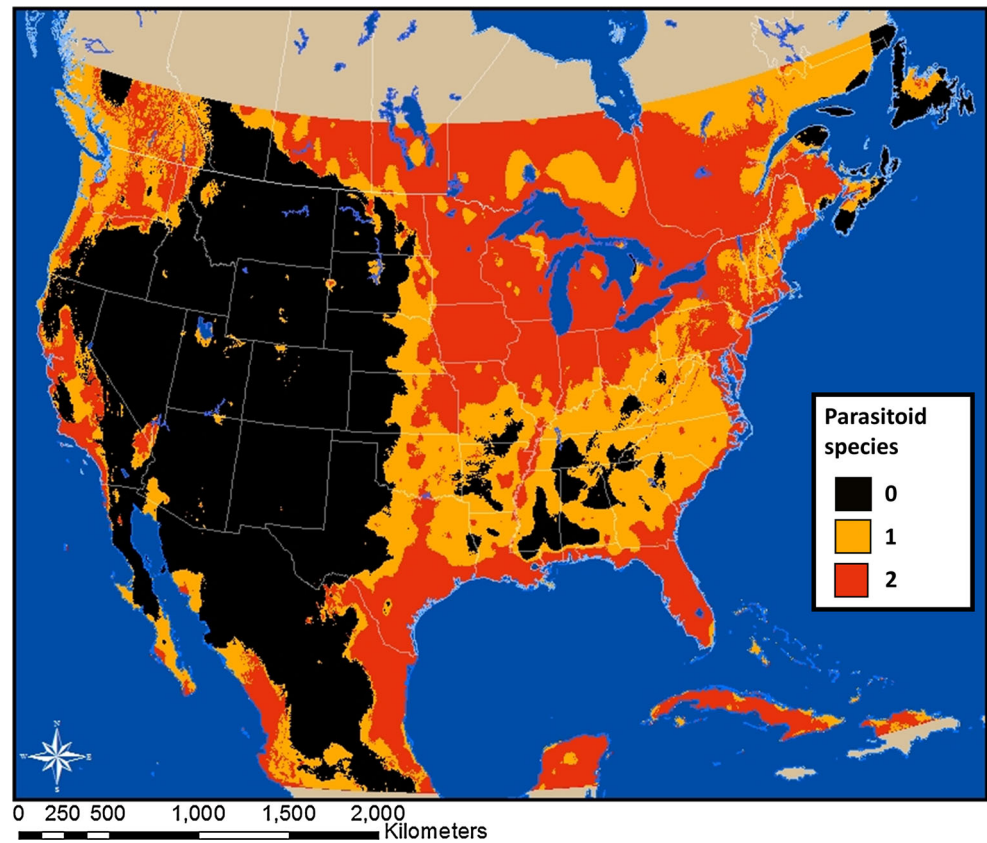

Fig. 3 Model of environmental suitability for the parasitoid wasp, *P. cassotis*, which attacks *D. plexippus* chrysalids, within the North American monarch range. Occurrence data were based on GBIF (2015f), data reported to MLMP, authors' observations and two records from Walker deposited in the California Academy of Sciences
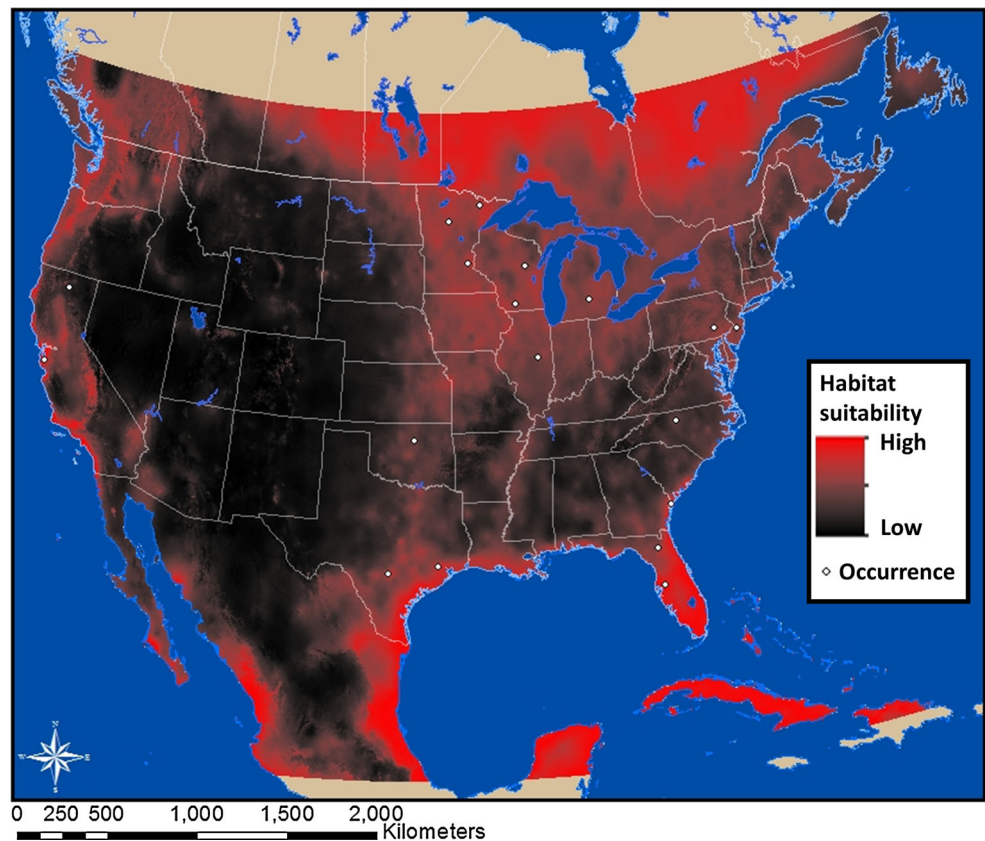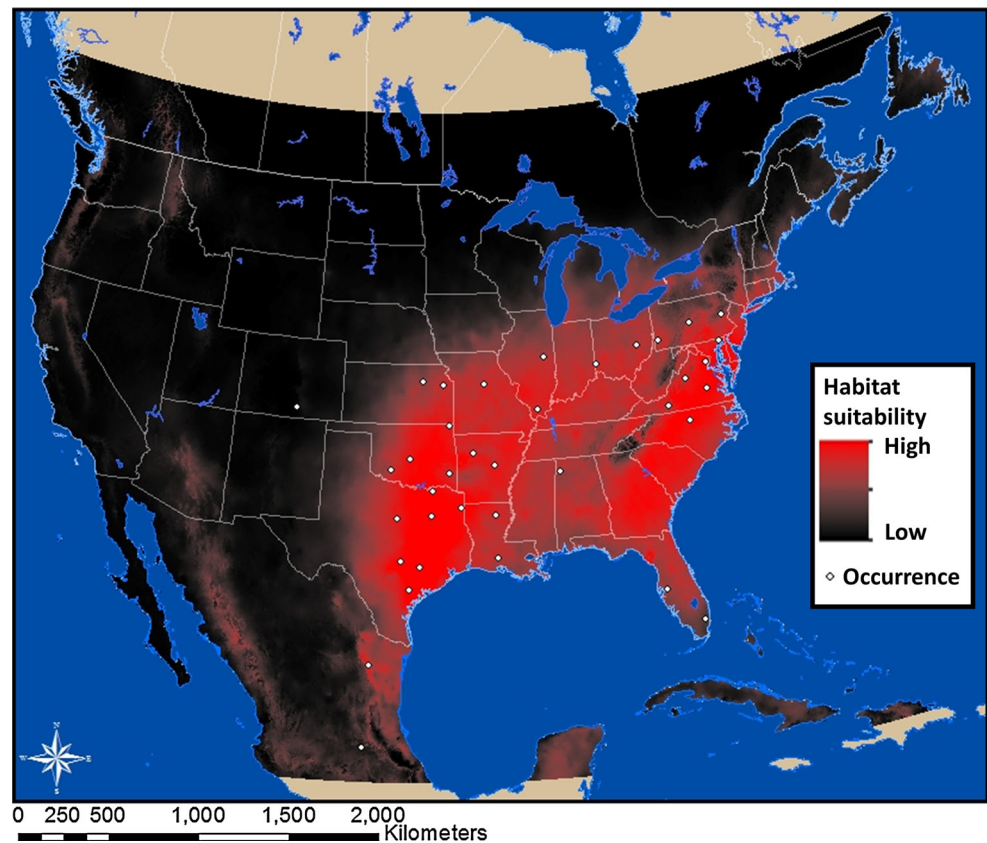
Fig. 4 Cumulative model for predicted areas which may be suitable for parasitoids
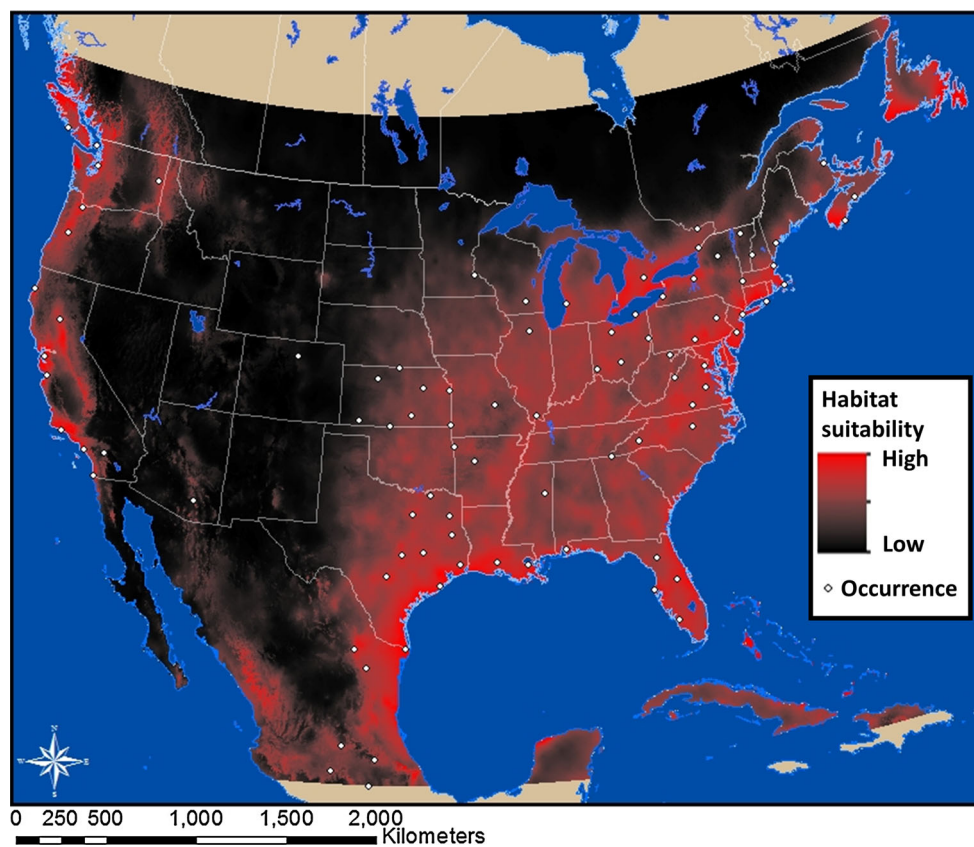

Fig. 5 Model of environmental suitability for the generalist predator *A. cristatus*, which attacks *D. plexippus* larvae. Occurrence data from GBIF (2015a)
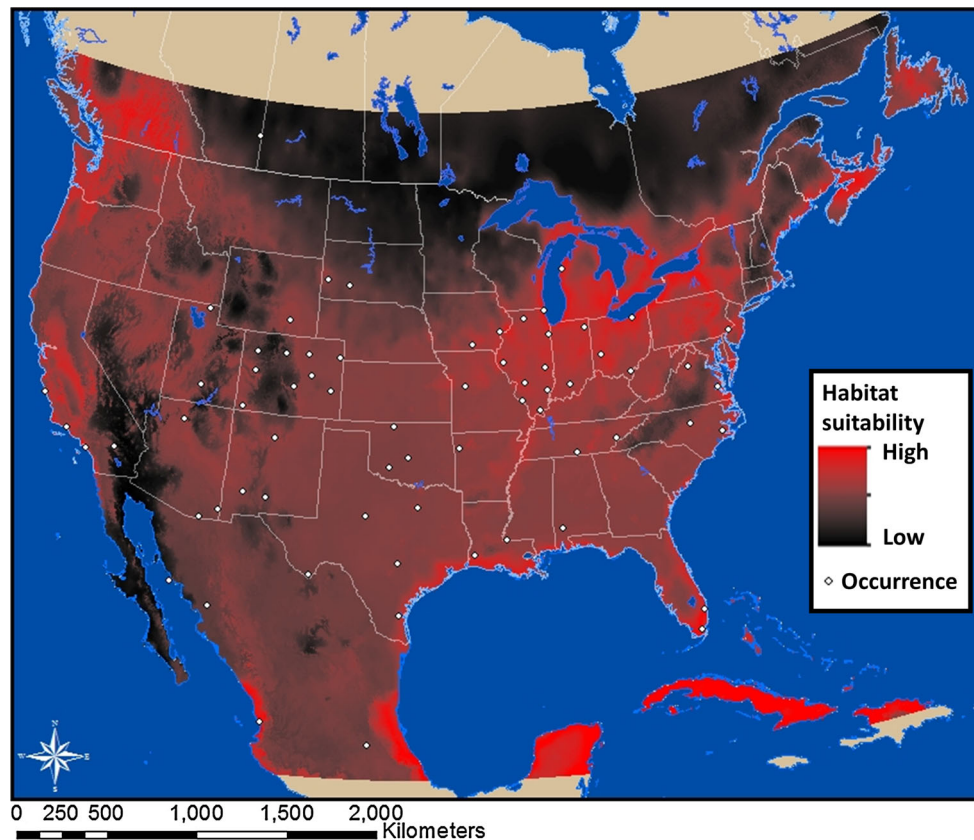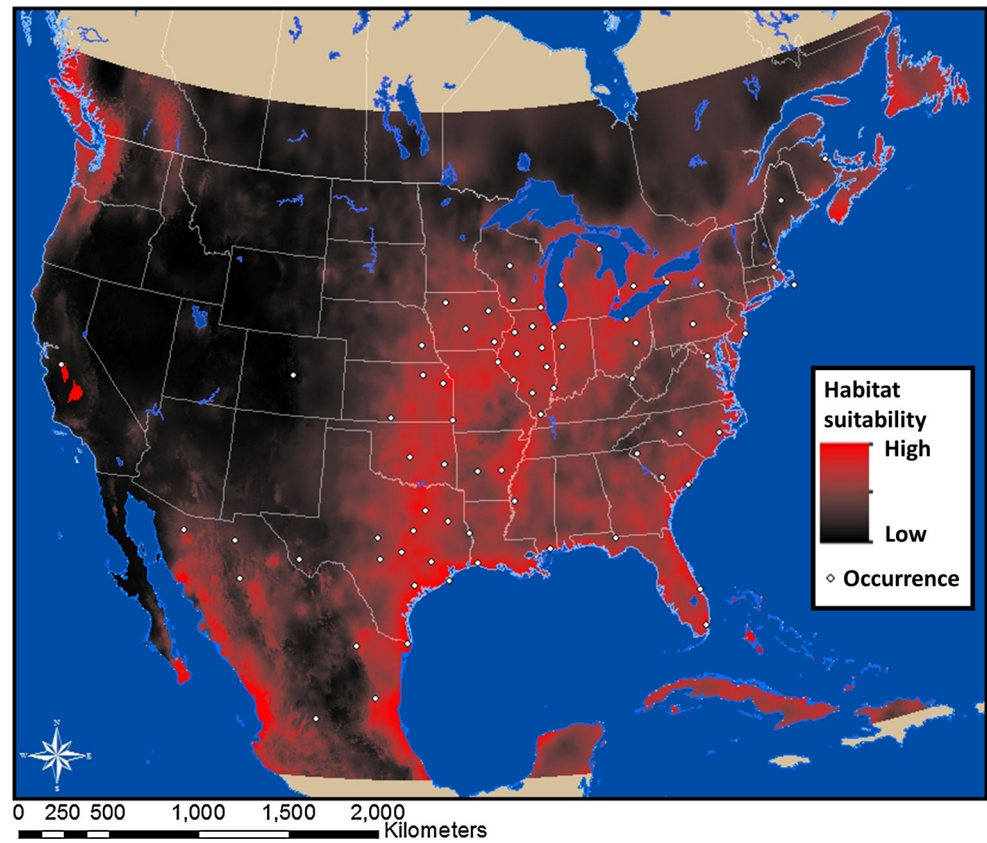
Fig. 6 Model of environmental suitability for the invasive generalist predator *H. axyridis,* which attacks *D. plexippus* larvae. Occurrence data from GBIF (2015b)
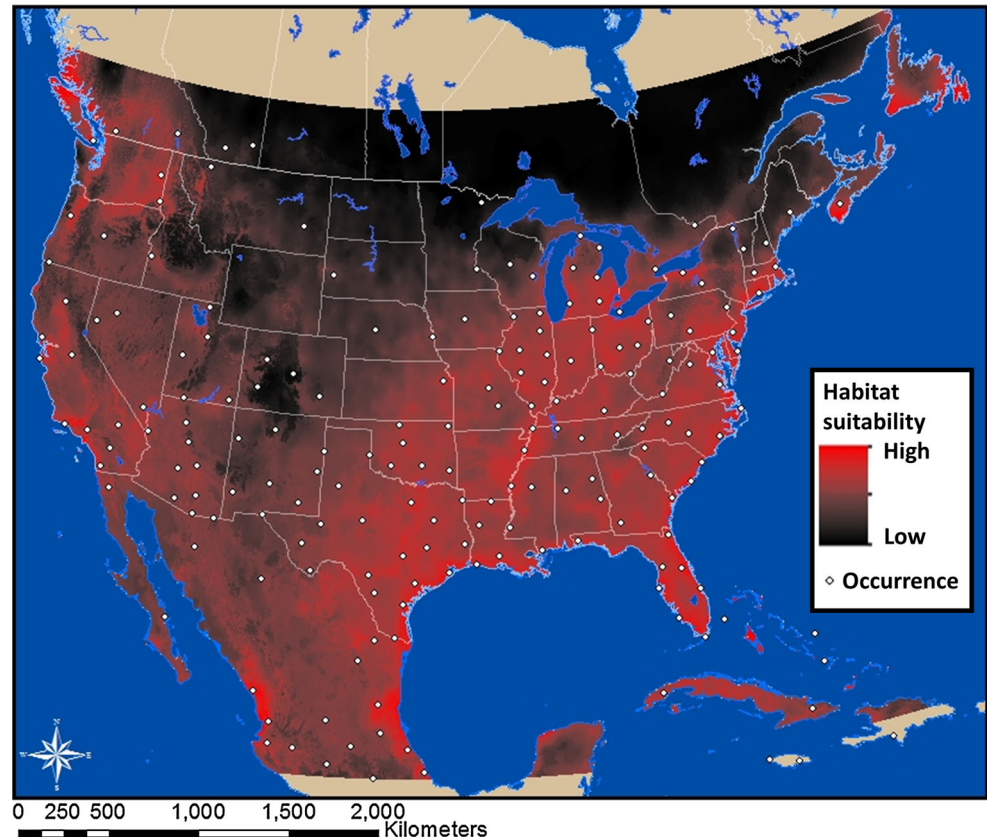

Fig. 7 Model of environmental suitability for the generalist predator *M. minimum*, which attacks *D. plexippus* pupae. Occurrence data from GBIF (2015c)

Fig. 8 Model of environmental suitability for the generalist predator *P. maculiventris*, which attacks *D. plexippus* larvae. Occurrence data from GBIF (2015d)
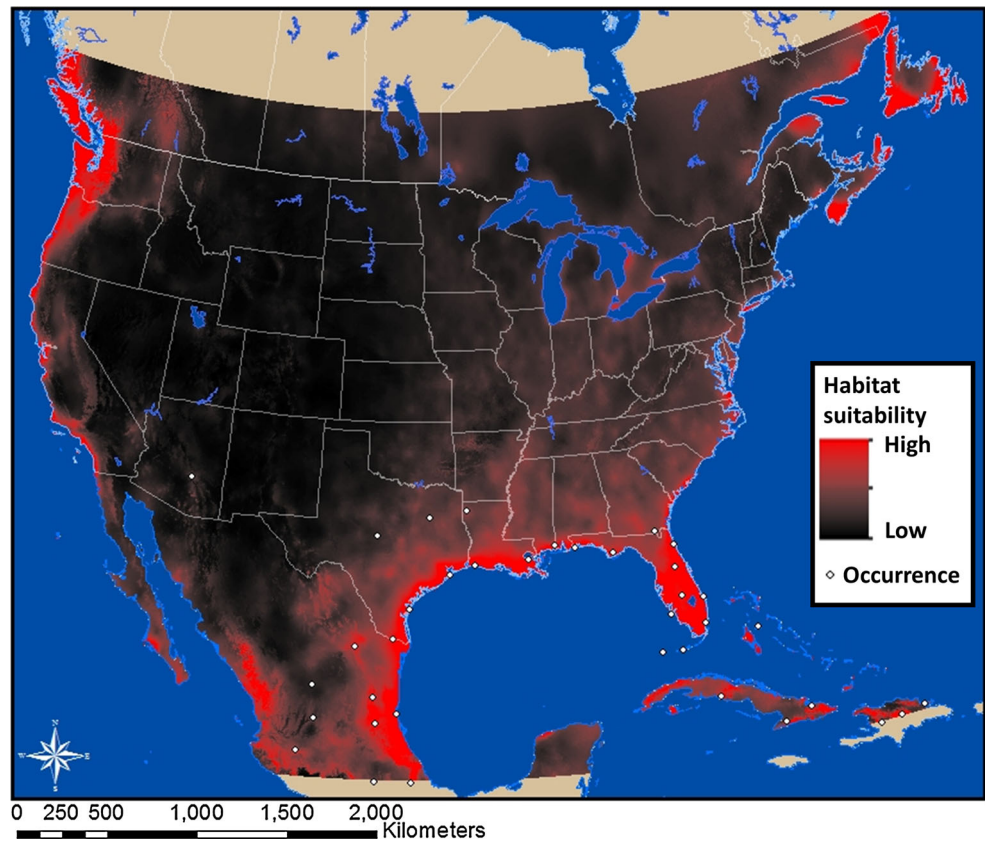

Fig. 9 Model of environmental suitability for the generalist predator *Polistes* spp., which attack *D. plexippus* larvae and chrysalids. Occurrence data from GBIF (2015e)
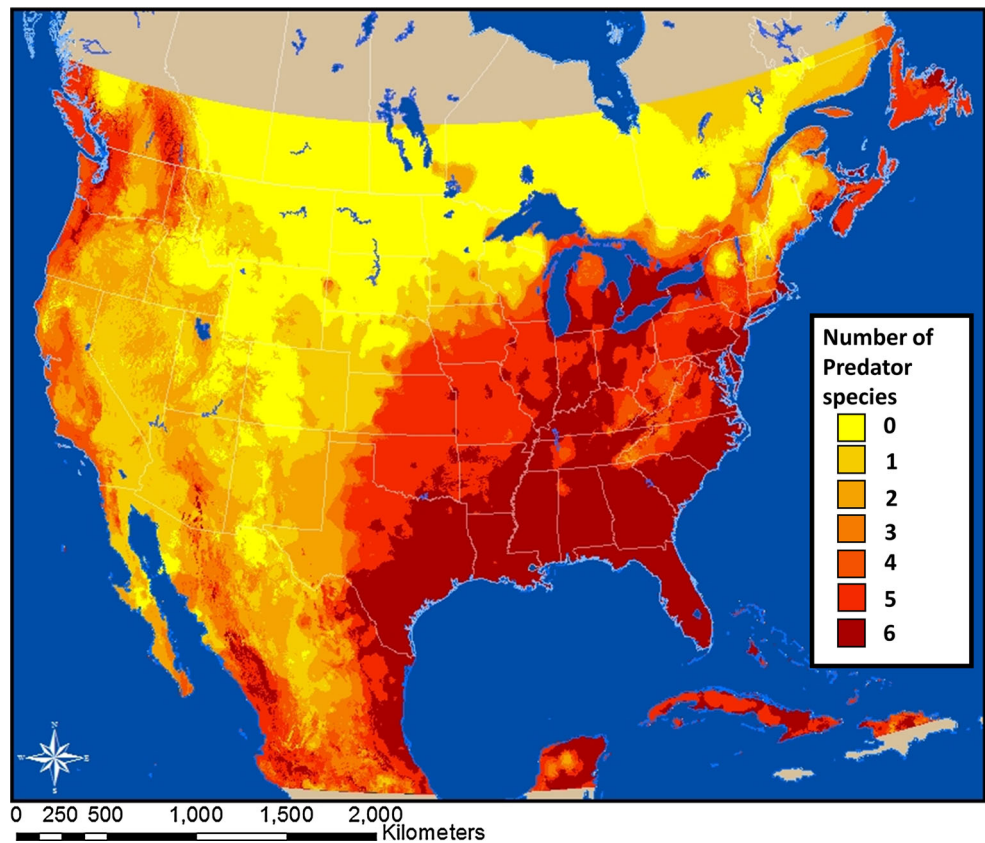
Fig. 10 Model of environmental suitability for the generalist predator *S. geminata*, which attacks *D. plexippus* larvae. Occurrence data from GBIF (2015g)

Fig. 11 Cumulative occurrence prediction for the potential number of predator species

previous local extinction had occurred (Van Nouhuys and Hanski 1999). Human perturbations could affect spatial and temporal overlap between monarchs and their natural enemies. Reduction of milkweed in agricultural settings since the 1980s and 1990s (Hartzler and Buhler 2000; Hartzler 2010; Pleasants and Oberhauser 2013) has resulted in a more patchy distribution of monarch host plants, and agricultural practices have probably reduced the nectar resources available to both natural enemies and adult monarchs. Efforts to subsidize host plant loss include the creation of gardens and other small habitats (Cutting and Tallamy 2015), but the degree to which these areas affect exposure to natural enemy populations is unknown. Human perturbations may also have resulted in additional local disturbances including tilling, pesticide application, or resource changes that could affect the persistence of natural enemies. Reduction of areas in which host plants can grow could reduce the areas to which monarchs can escape or be isolated from their natural enemies, concentrate monarchs and their natural enemies in the same areas, or limit the distribution of natural enemies that are less mobile than monarchs.

Many studies elucidate ways in which parasitoid populations can be sustained to reduce costs of pest management in crops (Van Nouhuys and Hanski 1999; Kruess 2003; Haddad et al. 2009); these studies document the importance of landcover types. For example, phytophagous flies were parasitized more often in uncultivated areas and had persistent food from year to year in fallow fields (Kruess 2003). Natural lands, or uncultivated areas like fallow fields, are often positively correlated with parasitoid presence and are therefore suggested in management plans (Barbosa 1998; Landis et al. 2000; Kruess 2003). Our models do not take into account landcover or natural enemy introductions and the ability of these natural enemies to persist once introduced. For example, *P. puparum*, a parasitoid that can cause monarch mortality (even though monarchs are a dead end host; Ramsay 1964, CMS personal observations), and *L. archippivora* were used for biocontrol in croplands in the past (Stapel et al. 1997; Barron et al. 2004), although neither has been introduced in several decades. Therefore, areas where landcover may provide suitable habitats and areas where introductions have persisted could potentially affect monarch mortality rates, and may not be identified by our models.

Our results provide outputs which align with known ranges for *A. cristatus* (Mead 1974), *P. cassotis* (Noyes 2015), and *P. maculiventris* (McPherson 1982; GBIF 2015) and suggest areas where these species may be present. We assumed fly data collected from MLMP were *L. archippivora*, but these data may include other fly species as no published data document the North American range of *L. archippivora*. Similarly, *P. cassotis* is reported from a number of states (Noyes 2015; Stenoien et al. 2015), but there are few exact location data from collections. Data from GBIF are likely more accurate in their identification, but accuracy of location data is not published with these reports. We encourage further reporting of monitoring data to citizen science programs or other databases, or via specimen deposits, to increase our knowledge of where these predators and parasitoids occur to help inform future conservation decisions.

Our models suggest areas for additional monitoring for monarch predators and parasitoids, and are not meant to represent absolute ranges of these organisms. Each model required extrapolation from occurrence points and therefore may not include some suitable habitat; conversely, we did not include information on monarch host plant availability, and thus may have included habitat that is not biologically suitable for monarchs. We utilized environmental data that we considered to be biologically relevant to create our models, but because we removed highly correlated data from our analyses we cannot assign biological significance to the data layers contributing to our models. The models do not indicate if the environmental data alone or factors correlated with them affect species distribution. Future modelling should consider incorporating alternative data (e.g., water availability, plant community composition and structure, habitat fragmentation, growing degree days [which will affect the number of monarch generations produced in an area and thus possibly predator pressure], land cover type, and biocontrol introductions) which could further our understanding of the factors influencing the distributions of these species. Our models are also limited by the availability of occurrence data, which do not necessarily include all areas these species may occur nor the areas where they may have been released and captured (e.g., the multicolored Asian lady beetle, *H. axyridis*) (Koch et al. 2003, 2006). Finally, further research is needed to determine if and how predation risk to monarchs varies with land use or management practices. For example, our models did not incorporate human population density, which could affect the distribution of some of the natural enemies.

Predators and parasitoids likely play an important role in habitat suitability for monarchs throughout much of their range, and should be considered when developing management plans to support monarchs. For example, if a managed area has high parasitoid populations year after year, leading to high monarch mortality, new management approaches may have to be taken to reduce the natural enemy population. Additional research should evaluate spatial and temporal distributions of monarch predators and parasitoids as well as frequency of their interactions, whether monarch mortality rates differ with land use or habitat characteristics, and how each species affects

monarch larvae and pupae, including species for which models have not yet been developed.

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