





2022 Monarch RESEARCH REVIEW



Prepared by

MONARCH JOINT VENTURE

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The Monarch Joint Venture's Mission

is to protect monarchs and their migration by collaborating with partners to deliver habitat conservation, education, and science across the United States.

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EXECUTIVE SUMMARY

Research papers in this review were published from January to December of 2022, and include a wide range of topics. Among them are collaborative conservation, monarch population dynamics, impacts of threats and stressors, existing monarch habitat, and habitat establishment and management. These studies highlight the importance of partnership in driving forward effective conservation action and explore multiple ways in which collaboration can occur (e.g., botanical gardens, Association of Zoos and Aquariums). Individuals often showed a strong willingness to support large scale, multinational conservation efforts, and researchers provide recommendations for international conservation programs and policies.

Several papers advanced our understanding of the threats that impact monarch habitat and population dynamics. One study found that fall migration timing and weather conditions have been consistent during the last 25 years in Canada, while another documented positive effects of increased temperature on monarch adult abundance in historically cooler locations, but negative effects on those in hotter areas. Researchers also found that monarch larvae have become lighter in color during the last five years with increasing summer temperatures, and others predict that temperature and precipitation changes in the Upper Midwestern US over the next 80 years will drive monarch numbers lower. Other studies discuss the potential negative consequences of non-native tropical milkweed (*Asclepias curassavica*) on migratory monarch populations, highlight the connection between nighttime light pollution and disrupted circadian rhythms of migratory monarchs, and predict significant avocado expansion in Mexico by 2050, potentially impacting forest ecosystems and further threatening pollinator species.

Multiple studies improved our understanding of milkweed distribution and phenology, as well as monarch use of habitat. *Asclepias viridis, A. syriaca, A. verticillata*, and *A. speciosa* were the dominant species observed across US non-federal rangelands in 17 states, with highest densities occurring at latitude N35-40 and longitude W95-100 (parts of eastern and central Oklahoma and Kansas). Monarch reproduction was documented throughout the Mexican states of Sonora, Chihuahua, and Sinaloa during winter months on *A. curassavica*. New data on monarch larval abundance in northeast Texas suggests that the southern US makes a significant contribution to the fall monarch migratory population. *Asclepias asperula ssp. capricornu, A. viridis, A. oenotheroides,* and *A. latifolia* were identified as particularly important to breeding monarch butterfly populations in the south-central US. Lastly, 29 different flowering plant species were identified as being important nectar resources for overwintering monarchs in Mexico.

This year, the western monarch population grew to more than 330,000 individuals (from 250,000 in 2021 and fewer than 2,000 in 2020, though these population counts fall well behind historic highs). At the time of publication (February 2023), we await the eastern monarch overwintering numbers as well as a <u>final Endangered Species Act ruling</u> from the U.S. Fish & Wildlife Service. In the meantime, we continue to collaborate with our network to refine strategies, advance conservation action, and consider how to best apply the newest research findings to our existing plans and management activities. For monarch (and other insect) populations to thrive, we need to establish diverse habitat on a large scale,



and multiple studies have improved our understanding of where habitat may be most effective. Researchers suggest that establishing habitat near crop fields in the north-central US will have an overall positive impact on monarch populations and others recommend planting a minimum density of 15 milkweed stems per hectare to avoid monarch search-time limitation.

METHODS & PURPOSE

The Monarch Joint Venture (MJV) has organized this annual research review to keep its partner organizations, network, and monarch enthusiasts abreast of the latest monarch conservation research. MJV staff, partners, and other contributors summarized 69 individual papers, and MJV staff compiled and condensed key takeaways. The set of papers summarized in this review includes peer-reviewed research papers and two commentary pieces. We selected articles published between January-December 2022 that were searchable by the terms "Danaus plexippus," "Asclepias," "monarch butterfly," "milkweed," and "pollinators." The MJV does not necessarily endorse these findings, nor does this review analyze the integrity of the science conducted in these studies.

NAVIGATING THE REVIEW

The review is organized into five general sections with additional topics within each: I) General Takeaways, Goals, & Participation, II) Monarch Ecology, III) Threats & Stressors, and IV) Habitat. Within each section is a high level overview of the research findings followed by a short summary of each paper. Full paper citations and links are provided at the end of the review.

REVIEWERS

Reviewers include the following MJV stakeholders, staff, and board members: Ann Earley, Cindy Neu, Craig Hensley, Dana Boyle, Elena Tyler, Elise Willcox, Gail Morris, Jennifer Thieme, Karen Oberhauser, Kelly Mercier, Kim Pegram, Kristin Szabo, Laura Lukens, Laurie Scott, Liz Goehring, Mercy Manzanares, Natalie Melkonoff, Sarah Gomes, Shiran Hershcovich, and Stacy Simanonok. Thank you to the many volunteers who helped make this possible!



RESEARCH REVIEW

I. General Takeaways, Goals, & Participation

a. Policy & Collaboration

Botanical gardens can fill key roles in the broader landscape of conservation. They can be sites for conducting ecological research, nurseries for propagating native plants, and classrooms for educating the public. Individuals are often willing to pay for conservation initiatives in other countries, demonstrating the importance of multinational conservation programs. Collaboration and partnerships are necessary for improving conservation impact.

- Raschke et al. (2022) reviewed collaborative conservation efforts involving Arizona's Desert Botanical Gardens and summarized key takeaways for successful collaboration. Four case studies were presented, including one specific to monarchs, the Great Milkweed Grow Out. This case study highlights the importance of using native plants in conservation and states that botanical gardens (experts in native plants, plant propagation, and ecological research) can spearhead conservation throughout a region. Botanical gardens can also play other vital roles, such as visitor education and outreach.
- Thogmartin et al. (2022) examined the willingness of residents in Canada, the United States, and México to pay for transborder migratory species conservation. The researchers found that when adjusting for income, individuals were willing to pay for conservation initiatives in other countries. These results may encourage lawmakers and other stakeholders to support new and existing multinational conservation policies and programs, specifically those that direct resources to locations where critical habitat is located, rather than places where funding is generated.
- Maynard et al. (2022) evaluated the AZA SAFE (Association of Zoos and Aquariums Saving Animals from Extinction) North American Monarch Program (involving zoos, aquariums, and conservation groups), based on conservation psychology principles. The authors state that collaboration and partnerships are necessary to increase conservation impact. Collaboration produced goals and activities for 109 partner groups, focusing on threats of habitat loss, pesticides, and climate change.



b. Research Methods & Technology

Belt transect sampling was more effective than plot sampling in predicting milkweed density and species richness in Nebraska. A GIS-based remote sensing tool may improve forest cover change monitoring within the Monarch Butterfly Biosphere Reserve. Methods used to understand the orientation of fall migratory monarchs may also be useful for studying other generations and lepidopteran species.

- In order to evaluate habitat for monarchs in Nebraska, two sampling methods were compared for their accuracy in predicting milkweed abundance and richness: belt-transect sampling (milkweed plants are counted along the length of a transect line) and plot sampling (milkweed plants are counted within quadrats placed in increments along the length of a transect). More milkweed species and stems were detected with belt transects compared to plot sampling. Authors suggest that the belt-transect method is more effective than the plot method for predicting milkweed stems per hectare as well as milkweed species richness while expending similar effort in the field (Manzanares et al., 2022).
- Mishkin & Navarette-Pacheco (2022) describe a rapid appraisal and monitoring tool that may be useful for monitoring forest cover change in the Monarch Butterfly Biosphere Reserve (MBBR). Regular monitoring of forests is important for understanding threats and impacts to monarchs, though on-the-ground monitoring may not always be possible in areas with complicated land management policies. The tool may help determine patterns of monarch use and impacts of interventions and may complement on-the-ground conservation efforts. Results of the properties assessed to date suggest that the MBBR conservation rules are being followed and the tool is a reliable non-invasive method of assessing forest canopy cover via imagery and geographic information systems (GIS).
- Parlin et al. (2022b) present methods for assessing the flight and orientation behavior of
 migratory monarch butterflies and provide recommendations for conducting and optimizing
 indoor flight simulator trials. While the protocols have been used in past studies to understand
 fall migratory behavior specifically, they suggest that they can be more broadly used to
 understand the orientation of monarchs from other generations, such as spring migrants and
 summer breeding individuals, as well as other lepidopteran species.



II. Monarch Ecology

a. Monarch Physiology

Monarch larvae developing in warmer climates are lighter in color; larvae have become lighter in color during the last five years, correlating with increasing summer temperatures. Eastern and western monarchs do not significantly differ in melanism (development of the dark-colored pigment). Monarchs fed tropical milkweed (*Asclepias curassavica*) were larger and exhibited higher muscle development than those fed native milkweed, which authors suggest may be detrimental to migrating monarchs who need to conserve energy. A study found no evidence that monarch caterpillars rely on their sense of smell to find milkweed.

- Tseng et al. (2022) used iNaturalist, an online community science platform, to review photos of monarchs from Ontario and the northeastern US. They investigated the relationship between temperature and pigmentation in larval monarchs and found that caterpillars developing in warmer climates (lower latitudes) were lighter in color, displaying thinner black stripes than those in cooler climates. The authors also note that larvae have become less black over the last five years as summer temperatures increased in the region.
- Davis et al. (2022b) analyzed community science photos to compare the melanism level (or the amount of black coloration) of monarch larvae in the eastern vs. western US. Lower average temperatures were associated with darker larvae, and larvae tended to be lighter in color earlier in the season. The authors concluded that temperature plays a role but is not predictive of the latitude of the larvae's location. The seasonal change is likely based on decreasing temperatures as the season advances; however, other factors may also contribute to darker larvae. The authors found no significant difference in larvae melanism between the eastern and western US.
- Pocius et al. (2022) found that monarch flight varies with the milkweed species consumed as a larva and was correlated with the concentration of milkweed toxins. Monarchs reared on non-native tropical milkweed (Asclepias curassavica, highly toxic) were larger and exhibited higher flight muscle investment compared to those fed native, less-toxic species (common, Asclepias syriaca; prairie, A. sullivantii; and whorled, A. verticillata). Increased size and muscle development requires high energy investment; when resources are limited and/or saving energy is necessary (e.g., during migration and overwintering), tropical milkweed may be detrimental for migrating monarchs.
- Monarch caterpillars often need to find another host milkweed plant as they grow, but their mechanism for doing this is unknown, as their eyesight is quite poor. Medina (2022) found no evidence that monarch caterpillars rely on sense of smell to find their next milkweed meal, and it was hypothesized that they might rely on chance and/or taste. The author recommended milkweed be planted in groups to increase the chances of caterpillars finding a new milkweed plant without expending excess energy.



b. Monarch Population Dynamics

Increased temperature had a positive effect on monarch adult abundance in historically cooler locations but a negative effect in hotter areas. Projected temperature and precipitation changes in the Upper Midwestern US over the next 80 years are predicted to drive monarch numbers lower. An analysis of monarch counts suggests there has been an overall increase in monarch abundance over time, but when broken apart regionally, some important monarch production regions showed negative trends. Monarch reproduction was documented throughout the Mexican states of Sonora, Chihuahua, and Sinaloa during winter months on tropical milkweed. Monarch abundance peaked 3-4 weeks before the main migration passage of monarchs in northeast Texas, suggesting that the southern US makes a significant contribution to the fall monarch migration. In a captive environment, migratory monarchs did not avoid inbreeding through mate selection (they were equally likely to choose siblings as non-siblings). Two commentaries discuss a 2021 publication on western monarch winter breeding populations and the claim that non-native milkweed in California may be helpful to the migrating western monarch population.

- Zylstra et al. (2022) examined potential associations between eastern monarch counts and local climate conditions, as well as between the counts and winter area occupied by monarchs in Mexico (utilizing North American Butterfly Association and state Butterfly Monitoring Network data). The effects of temperature on monarch counts depended on location; temperature increases resulted in a positive effect on monarch counts in cooler locations while in hotter locations, increased temperature had a negative effect on monarch counts. The area occupied in Mexico was positively associated with peak population size during the summer. Projected temperature and precipitation changes in the Upper Midwestern US over the next 80 years are predicted to drive monarch numbers lower. The authors suggest that it may be most prudent to focus habitat restoration in areas most likely to be suitable for monarchs in the future. Model projections predict, for example, that northern Ohio could see stable or even increasing monarch numbers.
- A recent analysis of North American Butterfly Association data compiled monarch numbers from 403 sites from June 1 August 31 throughout the monarch breeding range. Modeled trends for all of the sites were averaged, showing a slightly positive overall trend and suggesting an increase in monarch abundance over time at those sites. When broken apart regionally, trends were the most negative in the northern parts of the eastern breeding range (including in the most important breeding areas in the midwestern US) and in northern California, while the most positive trends were observed in the southeastern and northwestern US. While trends averaged across all sites were slightly positive, it is important to consider regional differences in overall monarch production. Including the times that monarchs are most abundant in the southern US is also an opportunity to expand this study. Additional research is needed to support these conclusions (Crossley et al., 2022).
- Van Devender & Reina-Guerrero (2022) describe the current knowledge of monarch occurrence in the Mexican states of Sonora, Chihuahua, and Sinaloa, those of which are not generally



considered to be part of the migratory population. Monarchs were found in Sonora through most of the year, except during May and June (during the hot pre-monsoon period). Breeding occurred throughout the winter on non-native tropical milkweed (*Asclepias curassavica*). These data help draw connections between monarch migration roots and winter habitats outside key overwintering sites.

- Inbreeding is typically detrimental to offspring and may be avoided in some species via
 dispersal or mate selection. A laboratory experiment showed that migratory monarchs do not
 avoid inbreeding through mate selection by males or females. They are just as likely to choose
 siblings as non- siblings in a captive environment. This may have negative implications for
 monarchs, especially amongst on the declining population (Villa et al., 2022).
- Davis (2022a) comments on a recent paper by James et al. (2021), contending that the data do
 not support the paper's conclusions that non-native milkweed in California is helpful to the
 migrating western monarch population. In reviewing James' data, Davis points to smaller
 wingspan and lack of significant distance traveled by tracked winter-breeding monarchs as
 evidence that those which over-wintered by feeding on non-native milkweed are unlikely to
 have produced migratory offspring.
 - o James et al. (2022) responds to Davis (2022a), disagreeing with the claim that shorter forewing length of winter-reared monarchs precludes those offspring from contributing to the northward and eastward spring migration. James et al. (2022) contends, based on their prior research (James et. al., 2021), that large wings are not necessarily required for monarch migration and that some part of these winter-reared monarchs likely contributed to the western population rebound. James highlights the need for further research to understand the conservation of urban sites with tropical milkweed and disentangle the impacts of non-native plants and pathogens on the monarch population.

c. Migration & Movement

Monarchs were triggered into directional flight at night when exposed to light, demonstrating potential consequences of nighttime light pollution. Monarchs do not appear to use inherited geomagnetic map cues to locate overwintering sites. A study documents how monarchs' neurons change when monarchs are flying versus inactive, describing the function and process of their internal compass. Monarch butterflies primarily use the angle of the sun to navigate during their migration with polarized-light sensitivity utilized during overcast conditions.

 Parlin et al. (2022a) highlights the negative consequences of nighttime light pollution on diurnal animals, including migratory monarch butterflies. Monarchs were triggered into directional flight when exposed to a full-spectrum light source at night (similar to lights used outdoors at night by the public). Authors suggest that conservation practitioners consider the proximity to artificial light and avoid creating habitat in areas experiencing nighttime light pollution.



- Guerra et al. (2022) studied whether migratory monarchs use inherited geomagnetic map cues to locate overwintering sites in Mexico. They examined overwintering locations from 2004-2018 to understand whether overwintering locations shifted with the natural alterations of Earth's magnetic field. Monarchs selected the same overwintering sites during that time period, despite shifts in the magnetic field, suggesting that monarchs do not use a fine-scale magnetic map to locate the sites. Previous research has shown that monarchs use a magnetic compass to help navigate during migration, however this research concludes that there may be other mechanisms that help them consistently find specific overwintering locations.
- Beetz et al. (2022) studied how migrating animals like the monarch butterfly navigate via internal compasses and whether there are differences in brain properties when inactive versus flying. They determined that neurons can change their tuning as the monarchs' behavior changes (e.g., begins flying), helping them adapt to external stimuli. For instance, when inactive, neurons utilized directions in front of the butterfly's head; when flying, the neurons utilized directions covering 360 degrees around the individual.
- Freas & Spetch (2022) conducted a review of past research studies regarding the navigational strategies of different types of insects. This review illustrates that monarch butterflies primarily use the angle of the sun to navigate when migrating. In addition, polarized-light sensitivity is used as a backup mechanism, allowing them to continue navigating in overcast conditions. In the final stretch of their migration, it is proposed that olfactory senses (smells) are used to pinpoint individual overwintering sites, though this concept is largely understudied.

d. Habitat Selection & Use

A study documents seasonal changes in western milkweed—monarch interactions, illustrating how female monarchs juggle trade-offs between plant quality and quantity when determining where to lay eggs. Monarchs regularly moved among milkweed in a greenhouse study, abandoning their natal stem before biomass was depleted. In a review of potential monarch host plant species, 34 were identified as high performing, 42 as low performing, and 33 as non-hosts. Urbanization was not found to negatively impact interactions between milkweeds and herbivores in Ontario.

• Yang et al. (2022) examined milkweed-monarch interactions in the western United States to identify how seasonal timing influences monarch developmental success. They identified distinct early and late season windows of opportunity for monarch developmental success in the Central Valley of California and suggest that these windows are constrained by different factors. In the early season, monarchs are limited by host plant quantity while in the late season, they are limited by host plant quality (plants become better defended with age). They also highlight the effects of climate on these dynamics. They observed direct thermal stress resulting from heat waves as well as early milkweed senescence in dry years. This study highlights the importance of seasonal research which takes the many external factors that influence milkweed-butterfly interactions into consideration.



- In a greenhouse study, monarch larvae regularly moved among common milkweed (*Asclepias syriaca*) plants, regardless of whether or not other monarch larvae were present, demonstrating a lack of intraspecific competition. Larvae abandoned their natal stem (i.e., the plant where they were born) before biomass was depleted, both when reared together and alone. Authors recommend planting milkweed in small patches (e.g., 2-4 plants) to support monarch larval movement (Fisher & Bradbury, 2022).
- Greenstein et al. (2022) conducted a review of 127 species reported to be monarch host plants (including milkweeds and a variety of other species) and tested monarchs' performance (palatability and survival) on them. They examined whether performance could be explained by cardenolide content or trichome density, and conducted lab trials to identify causes of low performance. In the end, they identified 34 high-performing species, 42 low-performing species, 33 non-hosts, and 18 species with unsubstantiated claims. Cardenolide concentration was a significant predictor of host status, with higher cardenolides in high-performing hosts (other cardenolide properties and trichome density were not significant predictors of host status). 62% of larvae attempted to eat low-performance hosts; only 3.5% of them survived to the adult stage, compared to 85% of those that consumed high-performance hosts.
- Miles et al. (2022) measured nine specialist milkweed herbivores (including monarchs) on common milkweed (Asclepias syriaca) in urban and rural sites in Ontario to identify potential impacts of urbanization. Herbivore abundance was higher in urban settings than rural, but the percentage of leaf area consumed by herbivores was higher in rural areas than urban. Some insect species (including monarchs) were more common in urban sites while other species were more common in rural areas. The authors suggest that the higher abundance in urban areas could be due to urban saturation (fewer plants resulting in a higher abundance of specialists). Overall, their results suggest that species interactions remain intact in urban environments, and that urbanization might not be as influential among milkweed specialist species.

e. Growth & Survival

Monarch survival was relatively high on *Asclepias viridis* in the fall in southeast Texas, demonstrating the importance of the southern region in contributing monarchs to the eastern fall migration. Monarch survival was positively impacted when feeding on drought-stressed aridadapted milkweed species but negatively affected when feeding on drought-stressed mesic milkweeds.

• Scott et al. (2022) examined *Asclepias viridis* (common names include green milkweed, green antelopehorn, and spider milkweed) for queen and monarch eggs and larvae in a 28-acre field in northeast Texas in 2017 and 2018. They tracked individual larvae through the third instar to estimate survival, and also recorded other arthropods on the milkweed as well as fire anthill abundance. Egg hatch rate, daily survival, and survival to third instar of both monarchs and queens (grouped) was lower in 2017 than 2018 (note that precipitation was lower than normal in 2017 and higher than normal in 2018). Authors attribute lower survival inpart



due to drought conditions in 2017, which negatively impacted milkweed phenology. Fire ants, jumping spiders, and oleander aphids were negatively correlated with monarch survival. They suggest that the southern US makes an important contribution of monarchs to the fall migration, and that habitat should be maintained to promote native milkweed growth in the fall.

Carvajal Acosta et al. (2022) investigated how drought stress indirectly affects monarch caterpillars by examining the plant traits associated with drought adaptation in 13 milkweed (Asclepias) species from arid and mesic environments. They found that arid-adapted Asclepias species shifted resources away from herbivory resistance to maintain plant function under water-limiting conditions, which then had a positive effect on monarch larvae. Conversely, caterpillars displayed a negative response on drought-stressed mesic plants because mesic plants are not well-adapted to drought conditions and will experience reduced physiological function when water is limited.

III. Threats & Stressors

a. Pesticides & Toxins

A large number of pesticides were found on milkweed plants from nurseries across the U.S., containing levels known to be harmful to monarchs. In a greenhouse study, glyphosate soil residues did not impact showy milkweed (*Asclepias speciosa*) plant growth or its production of cardenolides.

- Halsch et al. (2022) examined pesticides found in U.S. nursery milkweeds, documenting an alarmingly high number of insecticides, fungicides, and herbicides in milkweeds from both large and small retailers across 15 states. They detected multiple pesticides in each milkweed sampled (including those labeled as wildlife friendly), and over one-third of milkweeds contained concentration levels known to be harmful to monarchs. Authors recommend purchasing plants from nurseries that implement robust approaches to minimizing their pesticide use and suggest that the U.S. Environmental Protection Agency further restricts and reduces permissible nursery application rates.
- Klassen et al. (2022) studied the effects of soil pollutants on showy milkweed (*Asclepias speciosa*) growth and toxin production in a greenhouse setting. Authors applied various soil treatments of Ready-To-Use Roundup (also known as glyphosate, a non-selective herbicide) and arbuscular mycorrhizal fungi (AMF) in order to understand whether the introduction of either or both would impact the growth of the plants and/or its production of cardenolides. Cardenolide concentrations were not influenced by residual Roundup in the soil but may interact with AMF to influence growth. Overall, the authors suggest that residual Roundup will not adversely impact milkweed restoration efforts.



b. Climate Change

An analysis of fall monarch migration phenology in Canada found migration timing and weather variables to be consistent during the last 25 years. Projected temperature and precipitation changes in the Upper Midwestern US over the next 80 years are predicted to drive monarch numbers lower. Eastern monarch larvae may not be negatively affected if larval growth fails to align with peak milkweed quality due to phenological shifts associated with climate change. When modeling drivers of population dynamics (e.g., climate change), it may be best to use a smaller subset of validated global models in order to exclude excessive uncertainty.

- Ethier & Mitchell (2022) investigated the potential impacts of climate change on fall migratory monarchs. In contrast to a recent study by Culbertson et al., (2021) which showed a 16-19 day delay in Cape May fall migration (in Cape May, NJ) as well as temperature increases during their study period, the authors detected no change in migration timing or weather covariates during the last 25 years. The authors caution against extrapolating climate change results across regions and stress the need for long-term monitoring to investigate regional drivers of variability in migration timing.
- Zylstra et al. (2022) utilized North American Butterfly Association and state Butterfly Monitoring Network data to examine potential associations between eastern monarch counts and local climate conditions. The effects of temperature on monarch counts depended on location; temperature increases resulted in a positive effect on monarch counts in cooler locations, while in hotter locations, increased temperature had a negative effect on monarch counts. Projected temperature and precipitation changes in the Upper Midwestern US over the next 80 years are predicted to drive monarch numbers lower.
- Climate change may impact the timing of species' life history events, such as when monarchs reach their summer breeding grounds. Gilmour & Kharouba (2022) studied the potential effects of phenological asynchrony with milkweed (Asclepias spp.) on the eastern monarch population. Plant quality typically declines over the season, and if climate change delays the timing of monarch larval stages relative to the availability of younger plants, their performance could be negatively affected. They conducted field surveys in Ottawa, Canada to identify the seasonal availability of common milkweed (A. syriaca), monarch egg-laying preference, and the effects of milkweed size on larval performance (development time and final size). They found that plants of good condition and early stage of development were consistently available throughout the summer, and that declines in leaf quality did not result in decreased larval performance. Thus, they suggest that eastern monarch larvae may not be negatively affected if asynchrony with peak milkweed occurs.
- Neupane et al. (2022) investigated how to best predict species' responses to future climate scenarios via the selection of climate models in a process called ensemble building. They incorporated estimates of migratory monarch population drivers to understand how multiple sources of uncertainty impact population projections. Global climate models based on best-



performing metrics resulted in more information and excluded excessive uncertainty (compared to those that included all metrics). Authors recommend using a smaller subset of validated global climate models when trying to identify drivers of population dynamics.

c. Predators & Parasites

Harvest mice were found to forage on monarch body parts with a higher calorie content and lower cardenolide levels when monarch abundance in overwintering colonies was high. High monarch larval density negatively impacted development time, adult lifespan, and wing morphology when food resources were limited, but did not impact transmission of the parasite, *Ophryocystis elektroscirrha* (OE). Another study of monarch OE rates found that on average, infection prevalence has been four times higher in western subpopulations than eastern, and that rates have been increasing since 2002 for eastern monarchs and since 2015 for western. Monarchs that were experimentally infected with OE had lower mating success, suggesting that high OE infection rates may reduce mating activity in wild populations.

- Weinstein & Dearing (2022) studied the feeding behavior of harvest mice (*Reithrodontomys megalotis*) on monarchs from a central California overwintering site. Observations of harvest mice foraging on monarchs suggest the mice have cardenolide tolerance similar to known rodent predators in monarch overwintering sites in Mexico. Mice preferentially fed on body parts with higher calorie and lower cardenolide levels if the number of available monarchs was high, suggesting that foraging preferences balance nutritional value with detoxificationcosts.
- Alaidrous et al. (2022) found no evidence that the crowding of monarch larvae in a captive, greenhouse setting impacts the transmission of the protozoan parasite, *Ophryocystis elektroscirrha* (OE). However, high larval density negatively impacted development time, adult lifespan, and wing morphology when food resources were limited.
- Majewska et al. (2022) investigated trends in monarch Ophryocystis elektroscirrha (OE) infection rates through time as well as potential factors affecting them, such as monarch abundance, temperature, breeding season length, and resource availability. Average infection prevalence was four times higher in western subpopulations than eastern, and for eastern monarchs, rates increased threefold since the mid-2000s. OE rates in the western population decreased during 2000-2015 and increased after. Eastern monarch infection rate was highest for migrating adults and lower for overwintering and summer breeding adults. Western monarch infection probability was higher during summer breeding but did not differ between overwintering and migrating monarchs. Authors estimate that OE may be responsible for reducing the eastern overwintering population by tens of millions of monarchs per year, and emphasize the need for future research examining how human practices (e.g., captive rearing, tropical milkweed) have contributed to increases in infection among eastern monarchs since 2002.
- Babaloa et al. (2022) experimentally infected monarch larvae with Ophryocystis elektroscirrha
 (OE) spores and conducted mating trials of the surviving adult monarchs in three groups: all



uninfected, mixed infection, and all infected. Researchers used measurements of copulation attempts and success between groups to determine the influence(s) of OE on monarch mating systems. Data demonstrated that OE-infected male monarchs had significantly lower copulation success and that uninfected males achieved significantly more copulations in their lifetimes, regardless of females' infection status. Authors discussed that high levels of OE within a wild population may reduce mating activity, and that monarch mating systems may be more complex than previously thought.

IV. Habitat

a. Breeding & Migration Habitat

Researchers suggest that a minimum density of 15 milkweed stems per hectare is needed to avoid monarch search-time limitation, in which individuals spend too much time looking for resources and are unable to meet their reproductive capacity. Establishing habitat near crop fields in the north-central US is predicted to have an overall positive impact on monarch populations. Asclepias viridis (green milkweed), A. syriaca (common milkweed), A. verticillata (whorled milkweed), and A. speciosa (showy milkweed) were the dominant species observed across non-federal US rangelands, with highest densities occurring at latitude N35-40 and longitude W95-100. A study identified Asclepias asperula ssp. Capricornu (antelopehorns milkweed), A. viridis, A. oenotheroides (zizotes milkweed), and A. latifolia (broadleaf milkweed) as being particularly important to monarch butterfly populations in the south-central US. Suitable A. tuberosa (butterflyweed) habitat in Mississippi typically occurs in silty loam soils, open developed areas, and in acidic to slightly acidic soils. A. brachystephana (bract milkweed) was documented throughout the Chihuahuan Desert and surrounding regions, including in roadsides, expanding knowledge of the species' distribution and ecology. Herbivory timing influenced A. fascicularis (narrowleaf milkweed) plant size and seed production in California; early-season herbivory impacted plant size while late-season herbivory impacted seed production. Cardenolide concentration of A. syriaca seeds was found to be highest in the center of the plant's range compared to other latitudes studied. A Pacific Northwest study found that milkweed is capable of growing in more diverse conditions than previously expected, including areas with moderate shading. Flies, honey bees, and bumble bees were identified as important pollinators of A. syriaca in Virginia. Researchers documented impacts of milkweed plant defensive traits on monarchs and suggest that some may be more effective when expressed together versus individually. A study identified flowering plant species that are both cost-effective, likely to establish, and preferred by bees in the Upper Midwest.

• Two types of host plant limitations can exist for insect herbivores: density-dependent food competition and density-independent search-time limitation. While density-dependent competition assumes that the amount of available food creates a carrying capacity for a population, density-independent search-time limitation can occur even when plants are uneaten, if host plant densities are below certain thresholds. If individuals spend too much time looking for food resources, they are unable to meet their reproductive capacity, effectively reducing population size, while density-dependent resource limitation impacts the



population growth rate. Calculations suggest that approximately 15 milkweed stems per hectare are necessary to avoid monarch search time limitation and the authors estimate that many North American locations have milkweed densities below this threshold (Crone & Schultz, 2022).

- Spaeth Jr et al. (2022) analyzed USDA-NRCS National Resource Inventory data (2009-2018) and characterized the distribution and density of 22 milkweed species across rangelands in 17 US states. Green milkweed (Asclepias viridis), common (A. syriaca), whorled (A. verticillata), and showy (A. speciosa) were the dominant species observed on non-federal rangelands. Showy milkweed was highest in density while green milkweed (A. viridis) occurred most frequently. 89% of the total milkweed area was located in the following states: KS, TX, NE, SD, ND, OK, and MT. Density was highest at latitude N35-40 and longitude W95-100. Milkweed dominance was correlated with mollisol soil, non-saline sites, neutral pH, well-drained soils, loam and sandy loam soil textures, and soil organic matter at 1.5-3 percent.
- Tracy et al. (2022) identified four south-central US milkweed species as being particularly important to monarch butterflies: antelopehorns (*Asclepias asperula ssp. capricornu*), green (*A. viridis*), zizotes (*A. oenotheroides*), and broadleaf milkweed (*A. latifolia*). Broadleaf was an important late-season host for monarchs, with the other three utilized most frequently during the early season. Butterfly milkweed (*A. tuberosa*) and green comet (*A. viridiflora*) were selected less than other species, despite being available in the region. Honeyvine (*Cynanchum laeve*) was among the top five utilized species but was lower in availability. 70% of monarch larval activity occurred during mid-March to mid-July, with 30% occurring during mid-August to late November. The study mapped the distribution of 26 milkweed species, located two migratory funnels, and identified a potential gap in habitat connectivity within South Texas. The authors suggest that conservation of grassland, herbaceous, and developed land coverage (including roadsides and urban areas) may benefit migrating monarchs by improving milkweed and nectar plant resources. They also emphasize the importance of future studies that incorporate random sampling, as they had to correct for biases in community science data clustered around population centers (Tracy et al., 2022).
- Grant et al. (2022) modeled the impacts of habitat improvement on monarch populations in the
 north-central US. Results indicate that establishing monarch habitat near crop fields (even with
 herbicide and insecticide use) would have a positive impact on monarch populations. A scenario
 where monarch habitat was only established outside a 38m radius around fields (insecticide
 drift zone buffer) would likely be detrimental to monarch populations due to a vast reduction in
 available habitat establishment area.
- Neigel et al. (2022) mapped and quantified suitable butterfly milkweed (Asclepias tuberosa L.)
 habitat in Mississippi based on soil pH, soil texture, and land cover type. Mapping results
 suggest that the species occurs most often in silty loam soils (followed by sandy loam) and that
 it prefers open developed areas as well as acidic to slightly acidic soils. Areas bordering the
 Mississippi Delta, northern state line, and outer edges of the Golden Triangle region of



- northeast Mississippi were predicted to be most suitable for butterfly milkweed, suggesting that they may be best suited for future monitoring and/or habitat plantings.
- McCoshum et al. (2022) explored the ecology of bract milkweed (Asclepias brachystephana), via species distribution modeling using MaxEnt population surveys, plant phenology, presence of insect herbivores, pollinators and beneficial insects, and cardenolide analyses. They documented bract milkweed within the Chihuahuan Desert and surrounding ecoregions and observed plants occurring in roadside habitats. They also found that the species has high cardenolide levels, with wild populations generally having higher and more variable concentrations than plants grown in the greenhouse. They conclude that bract milkweed should be considered for a variety of planting projects.
- Rasmussen & Yang (2022) studied how narrowleaf milkweed (Asclepias fascicularis)
 performance is influenced by shifts in timing of monarch larval herbivory. Early-season herbivory
 most strongly influenced plant size while late season herbivory had greatest effects on viable
 seed production. As phenological shifts continue to occur, further research is necessary to
 understand the effects of insect herbivory on milkweed growth and reproduction.
- Milkweed cardenolide toxins are known growth inhibitors of milkweed herbivores. Agrawal et al. (2022) quantified cardenolide content of common milkweed (Asclepias syriaca) seeds across a latitudinal gradient and investigated how various herbivores sequester and metabolize the compounds. Cardenolide concentrations were found to be highest in the center of the plant's range, where herbivores are the most prevalent. One toxin, labriformin, has evolved to higher concentrations in higher latitudes. Monarchs do not sequester labriformin and instead break it down into less toxic secondary products.
- Research on milkweeds of the Pacific Northwest (Asclepias fascicularis and A. speciosa) demonstrates the importance of both plant biodiversity and moderate levels of shade in facilitating successful milkweed growth. Optimizing the factors that contribute to effective milkweed growth will help western monarch populations prosper, as the increasing scarcity of milkweed in their traditional migratory paths and breeding grounds may have reduced their numbers. The study also found that milkweed is capable of growing under more diverse conditions than originally known, allowing for a greater possibility of establishing successful milkweed populations (Silva et al., 2022).
- Gustafson et al. (2022) experimentally added long-horned milkweed beetles to common
 milkweed stems at a study site in Virginia. The plants with higher herbivory severity had fewer
 flowers per inflorescence and ultimately fewer pods produced. They also watched or videorecorded pollinators visiting a subset of ramets and collected a subsample of flower visitors to
 evaluate their pollination efficacy. Flies, small bees, bumble bees, honey bees, and soldier
 beetles all removed or inserted a similar amount of pollinaria (a mass of pollen grains);
 Japanese beetles and longhorned milkweed beetles never had pollinaria attached to their
 bodies. They determined thatflies,



followed by honeybees and bumblebees, were most important pollinators due to the amount of pollinaria removals and insertions.

- Edwards et al. (2022) investigated how milkweed plant defensive traits affect the performance
 of monarchs and other herbivores, and whether they are more effective when co-expressed
 ("defense synergies") versus when expressed alone. Effects on herbivores varied among plant
 defensive traits but authors suggest increased trait expression could be beneficial to monarchs
 in some cases.
- Simanonok et al. (2022) identified flowering plant species that were most often observed blooming at study sites, those with low seed cost, and those that were highly preferred by honey and wild bees in North Dakota and Minnesota. Species that met all three of these criteria include: wild bee preferred Echinacea purpurea (eastern purple coneflower), Gaillardia aristata (great blanket flower), Helianthus maximiliani (maximillian sunflower), Heliopsis helianthoides (false sunflower), Monarda fistulosa (wild bergamot), Ratibida columnifera (upright prairie coneflower), and Ratibida pinnata (gray headed coneflower). While they didn't measure monarch butterfly preference specifically, these forb species may be valuable inclusions within pollinator seed mixes due to their low seed cost and high preference from bees.

b. Overwintering Habitat

Overwintering monarchs in Mexico foraged on nectar plants within and outside of the forest on sunny days, utilizing 29 different plant species. Avocado exports are continuing to increase, impacting pine-oak forest, mesophilic montane forests, as well as oyamel fir forests that support overwintering monarchs. Avocado expansion is predicted to impact ten threatened pollinator species within the Trans-Mexican Volcanic Belt, demonstrating the importance of creating new protected areas to conserve habitat for these at-risk species. Within the Monarch Butterfly Biosphere Reserve, disturbance was greater than recovery during 1994-2017 (forest recovery predominated outside of the MBBR). Similarly, a study of forest recovery programs implemented during 2007-2018 in Zitácuaro, Mexico found that although deforestation was the dominant change during the period, forest densification also occurred in areas of similar size. Another study found no evidence that locations where western monarchs cluster have distinct microclimates relative to other locations in overwintering groves.

- Observations of monarchs overwintering in Mexico show that they forage for nectar both inside and outside of the forests on sunny days. Sánchez-Tlacuahuac et al. (2022) identified the primary species visited by monarchs in the Monarch Butterfly Biosphere Reserve.
 Monarchs fed on 29 plant species from 10 families, many of which contained white, yellow or blue flowers. Salvia mexicana and S. plurispicata were the most visited species, and also the most abundant. Other frequently visited species include Prunus serotina, Crataegus mexicana, Buddleja sessiliflora, Verbesina oncophora, and Roldana albonervia.
- Avocado exports from Michoacán, Mexico have increased due to demand, and are predicted to



continue to increase 1.5% annually. Using data from the past 25 years of avocado expansion alongside climate projections, Arima et al. (2022) predict 1,000 km² of expansion by 2050. The model predicts loss of rare, biodiverse, and delicate ecosystems including pine-oak forest and mesophilic montane forests as well as encroachment into the oyamel fir forests that support overwintering monarchs.

- Sáenz-Ceja et al. (2022) used satellite imagery and occurrence records of threatened pollinator species in the Trans-Mexican Volcanic Belt to examine potential habitat loss due to avocado expansion. Of the ten species identified (4 insects, 4 bats, and 2 birds), species distribution models showed overlap between current pollinator ranges and expanded avocado farming. The most affected pollinators were two bumble bee species, Bombus brachycephalus and B. diligens, monarch butterflies (Danaus plexippus), and the sparkling-tailed woodstar (Tilmatura dupontii), but there was overlap with all 10 species. The study suggests that new protected areas should be created to prevent future expansion of avocado plantations into areas with atrisk pollinators.
- López-García et al. (2022) provides an overview of forest cover trends from 1994 to 2017 in areas within and outside of the Monarch Butterfly Biosphere Reserve (MBBR) in central Mexico. Their results suggest a trend of forest recovery, including a 1% increase in total forest area, a slight increase in deforested land, and a 3% decrease in non-forest surface due to afforestation (forest establishment). Disturbance was greater than recovery within the MBBR (4,009 ha lost in 23 years), but forest recovery predominated outside of the MBBR. The authors state that establishment of protected areas such as the MBBR requires broad support from all relevant communities prior to its establishment in order to achieve effective conservation and minimize (or avoid) hostility, protests, and further forest disturbance.
- Spiric et al. (2022) studied forest recovery programs implemented during 2007-2018 in Zitácuaro, Mexico. They found that although deforestation was the dominant change during the period, forest densification also occurred in areas of similar size. They state that forest recovery programs may not be the primary cause of forest densification; forest regrowth also resulted from agricultural abandonment and postfire regeneration.
- Villablanca et al. (2022) quantified microclimate conditions at western monarch overwintering sites and examined how wind, temperature, relative humidity, and solar radiation are related to sites selected by monarchs. They found no evidence that locations where monarchs cluster have distinct microclimates relative to other locations in overwintering groves. Authors suggest management actions should not only be adopted within aggregation sites but within the entire grove. Managing grove interiors for light exposure from the southeast is favorable, while tree coverage in the northeast quadrant should be managed so as to blunt winds while maintaining favored light exposure. Planting live ground cover may help maintain relative humidity within the grove.



c. <u>Establishment & Management</u>

Asclepias incarnata (swamp milkweed) performance varied with seed source location, suggesting the need for reductions in seeding zones and species-specific seed sourcing guidelines for milkweeds. Researchers suggest that fall prescribed burns may be optimal for conserving plant and insect communities in Kansas compared to spring or summer burns. In Texas, researchers recommend mowing and burning during July instead of September-October (when monarch eggs and larvae are present) to promote high-quality milkweed for fall monarch reproduction. A review of U.S. public land management activities recommends various strategies for conserving pollinators, including prescribed burning to reduce invasive species, reduced grazing pressure and logging intensities, and further research studying pollinator plant preference. Grazing and prescribed burning elicited different effects on bee and butterfly communities in Minnesota, demonstrating the importance of integrating a variety of management practices to support overall pollinator diversity. Reintroduction of native arbuscular mycorrhizae may aid conservation efforts by improving the establishment success of certain milkweed species (Asclepias tuberosa, A. meadii, and A. speciosa). Effects of arbuscular mycorrhizal fungi inoculation on milkweed cardenolide content varied among species. Forb establishment is low in former cropland of the Great Plains, highlighting the need for improving establishment success via reduced grass seeding rates, increased forb rates, and/or reduced weed competition. Planting during the dormant season and first-year mowing improved native plant establishment success in the midwestern U.S.

- Finch et al. (2022) compared seed germination, emergence, establishment, and above-ground biomass in two milkweed species, swamp (*Asclepias incarnata*, a habitat specialist) and common (*A. syriaca*, a habitat generalist), collected across a latitudinal gradient including three regions in the Midwest U.S. The impact of seed source on species performance differed; early life stages of swamp milkweed varied by collection location (while common did not), and regeneration studies suggest that the swamp is more sensitive to seed source, requiring smaller seed zones. The authors recommend species-specific seed sourcing guidelines for *Asclepias* species in order to capture species-level variation within the genus.
- Prescribed burn season (spring, summer, fall) was not found to affect flowering plant density in Kansas, but flowering plant diversity was higher following summer and fall burns. Milkweed species also did not differ in the sucrose concentrations of their nectar following different seasonal burns, indicating that burn timing does not affect milkweed's investment in pollinator recruitment. The authors suggest that fall burns may be optimal in providing a balance between plant and insect community conservation, where plant diversity is increased over that of spring burns, with decreased insect mortality compared to summer burns (Roberton & Rebar, 2022).
- Scott et al. (2022) examined queen and monarch butterfly abundance on *Asclepias viridis* (green milkweed) in Texas, concluding that the southern US is an important contributor of monarchs to the fall migration. They stress the importance of maintaining habitat to promote native milkweed growth in the fall and recommend the use of mowing and burn schedules that



promote high quality milkweed host plants for monarch reproduction. In Texas specifically, mowing and burning should be done in July rather than September or October, since monarch eggs and larvae are often present in fall months.

- Glenny et al. (2022) reviewed 63 studies to determine the effects of common U.S. public land management actions on pollinators and to identify knowledge gaps in which future pollinator research should address. They found that prescribed burns had predominantly positive or neutral effects on bee and butterfly richness, abundance, and diversity, with occasional negative effects on butterflies. Logging had positive or neutral effects, grazing had neutral or negative effects, invasive plant species removal had positive or neutral effects, and revegetation with wildflower mixes had clear positive effects. A number of pollinator management recommendations are provided:
 - Less intensive logging strategies should be implemented to avoid soil compaction, introduction of invasive species, and edge effects.
 - O Grazing pressure from ungulates should be reduced by use of fences, while grazers should be excluded from areas where flowers are in bloom.
 - Prescribed burning is recommended to remove invasive plant species.
 - O Pollinator visitation surveys should be conducted to determine which plant species may be most attractive to pollinators, and to design of seed mixes.
 - Plants with antimicrobial properties should be prioritized in seed mixes to increase the abundance of foraging resources which protect wild bees from commercial bee pathogens.
- Leone et al. (2022) examined impacts of grazing and prescribed burning on bee and butterfly communities in Minnesota tallgrass prairie. Management effects differed by pollinator group; butterfly abundance was higher in burned prairies than grazed. Grass-feeding butterflies were more abundant at sites with higher plant species richness. Bee abundance did not differ by management type but was higher at sites with sandier soils. Bee species richness was positively associated with forb frequency. Because of these differing results, the authors stress the importance of mosaic of management practices across grassland habitats to support pollinator diversity, and recommend that management plans be tailored to wide groups of pollinators instead of using one species as a proxy for others.
- Native arbuscular mycorrhizae inoculation was found to increase growth and latex production of seven milkweed species, but the magnitude of benefits was dependent on both milkweed and fungal species. For instance, commercial inoculants decreased milkweed growth relative to non-inoculated plants. Butterfly weed (Asclepias tuberosa) in-field survival was strongly dependent on inoculation by native mycorrhizae, while swamp milkweed (A. incarnata) was not. Species with high conservation value, such as butterfly weed and Mead's milkweed (A. meadii), were often most dependent on specific native mycorrhizae and would likely benefit from inoculation during restoration plantings (Koziol et al., 2022).
- Rinella et al. (2022) studied forb establishment in former cropland of the Great Plains (Colorado and Montana). Seeded forb cover was lower than 10% in most sites, with no seeded forbs found



in 23% of sites (28/120 sites). The study provides recommendations for improving establishment success such as reducing grass seeding rates, increasing forb seeding rates, suppressing weed competition, and recommends further research on the impacts of herbicides on forbs pre- and post-establishment.

- Glidden et al. (2022) evaluated the effects of seed mix design and management on ecosystem services (erosion control, weed resistance, pollinator resources) in the midwestern US. First-year mowing accelerated native plant establishment in all seed mixes and planting in the dormant season improved establishment success of spring and fall forbs. The authors recommend planting a diverse, grass-to-forb balanced seed mix in the dormant season, and mowing in the first year to improve multifunctionality of restoration projects.
- Mattson et al. (2022) investigated the impacts of arbuscular mycorrhizal fungus (AMF) on two native milkweed species, showy (A. speciosa) and narrowleaf (A. fascicularis), examining whether low, moderate or high levels of AMF affect the above- and below-ground biomass of the plants. Inoculation had significant effects on most growth parameters for showy milkweed, but only one parameter was affected in narrowleaf. Further research on the relationship between milkweed species and various AMF species may improve western habitat restoration efforts.

d. Urban Gardens & Landscapes

Urban spaces can provide important habitat for pollinators when designed appropriately. Insects were more abundant on native perennials than non-native perennials or non-native annuals. Residential landowners surveyed in Ohio had more knowledge on where to purchase wildflowers than how to plant and care for them.

- When designed appropriately, urban spaces can provide important habitat for pollinators.
 Braman & Griffin (2022) reviewed a wide range of research on pollinator conservation in urban settings, and the roles communication, education, and community science play in garnering public support. Five case studies highlighting Integrated Pest and Pollinator Management (IPPM) concepts are described, including one on milkweeds and monarchs, where selection of milkweed species and garden design result in a significant effect on habitat suitability for monarchs.
- Palmersheim et al. (2022) surveyed insects visiting native and ornamental plants in Virginia in order to aid gardeners in making landscaping decisions that best support insect populations. Insects were more abundant on native perennials than non-native perennials or non-native annuals. Black-eyed Susan (*Rudbeckia fulgida*) was the most visited species, with 42 times more insects than the least visited plant, petunia (*Petunia* sp.). Purple coneflower (*Echinacea purpurea*) and Helen's flower (*Helenium sp.*) had high insect diversities and moderately high insect abundances. Joe-Pye weed (*Eupatorium dubium*, most common), purple coneflower, black-eyed Susan, bluebeard (*Caryopteris x clandonensis*), and dahlia (*Dahlia x hybrida*) were the only species that *Nymphalidae* (monarch family) visited.



• Davis & Stoyko (2022) surveyed private residential landowners in Ohio to identify barriers to native plantings. Most landowners did not have a strong intent to plant native species, even when provided with support in terms of cost, labor, and online resources. Landowners had more knowledge on where to purchase wildflowers than how to plant and care for them and were more knowledgeable about tree care than pollinator-beneficial plants. These findings can inform educational and outreach efforts designed to expand residential pollinator habitat.

REFERENCES

- Agrawal, A.A., Espinosa del Alba, L., López-Goldar, X., Duplais, C. 2022. Functional evidence supports adaptive plant chemical defense along a geographical cline. PNAS. Volume 119. doi.org/10.1073/pnas.2205073119
- Alaidrous, W., Villa, S.M., Jacobus, C.dR., Majewska, A.A. Crowding does not affect monarch butterflies' resistance to a protozoan parasite. Ecology and Evolution 2022;12:e8791. doi.org/10.1002/ece3.8791
- Arima, E.Y., Denvir, A., Young, K.R., González-Rodríguez, A., García-Oliva, F. 2022. Modelling avocado- driven deforestation in Michoacán, Mexico. Environ. Res. Lett. 17: 0 doi.org/10.1088/1748-9326/ac5419
- Babalola TS, de Roode JC, Villa SM. 2022. Experimental infection with a naturally occurring protozoan parasite reduces monarch butterfly (Danaus plexippus) mating success. Journal of Parasitology. 108(3), 289–300. doi.org/10.1645/21-121
- Beetz, M.J., Kraus, C., Franzke, M., Warrant, E.J., Merlin, C. et al. 2022. Flight-induced compass representation in the monarch butterfly heading network. Current Biology, 32 (2): 338-349. doi.org/10.1016/j.cub.2021.11.009
- Braman, S.K., Griffin, B. 2022. Opportunities for and Impediments to Pollinator Conservation in Urban Settings: A Review. Volume 13, Issue 1. doi.org/10.1093/jipm/pmac004
- Carvajal Acosta, A. N., Agrawal, A. A., Mooney, K. 2022. Plant water-use strategies as mediators of herbivore drought response: Ecophysiology, host plant quality, and functional traits. Journal of Ecology, 00: 1–14. doi.org/10.1111/1365-2745.14059
- Crone, E., Schultz, C.B. 2022. Host Plant Limitation of Butterflies in Highly Fragmented Landscapes. Theoretical Ecology. doi.org/10.21203/rs.3.rs-855105/v1
- Crossley, M.S., Meehan, T.D., Moran, M.D., Glassberg, J., Snyder, W.E., Davis, A.K. 2022. Opposing global change drivers counterbalance trends in breeding North American monarch butterflies. Global Change Biology, 28, 4726–4735. doi.org/10.1111/gcb.16282
- Davis, A.K. 2022a. Monarchs Reared in Winter in California Are Not Large Enough to Be Migrants. Comment on James et al. First Population Study on Winter Breeding Monarch Butterflies, Danaus plexippus (Lepidoptera: Nymphalidae) In the Urban South Bay of San Francisco, California. Insects 2021, 12, 946. Insects, 13,63. doi.org/10.3390/insects13010063
- Davis, A.K., Nibbelink, N., Deneka, C.J. 2022b. Revisiting geographic variation in melanism of monarch butterfly larvae in North America using iNaturalist photos. Journal of Thermal Biology 110. doi.org/10.3390/land12010114



- Davis, A., Stoyko, K. 2022. Barriers to Native Plantings in Private Residential Yards. Land 12, no. 1: 114. doi.org/10.1016/j.jtherbio.2022.103374
- Edwards, C.B., Ellner, S.P., Agrawal, A.A. 2022. Plant Defense Synergies and Antagonisms Affect Performance of Specialist Herbivores of Common Milkweed. Ecology e3915. doi.org/10.1002/ecy.3915
- Ethier, D.M., Mitchell, G.W. 2023. Effects of climate on fall migration phenology of monarch butterflies departing the northeastern breeding grounds in Canada. Global Change Biology, 00, 1–10. doi.org/10.1111/gcb.16579
- Finch, J., Segalis, A.E., Kramer, A.T., Havens K. 2022. Recruitment varies among milkweed seed sources for habitat specialist but not generalist. Restoration Ecology. doi.org/10.1111/rec.13725
- Fisher, K.E., Bradbury, S.P. 2022. Plant abandonment behavior and fitness of monarch larvae (Danaus plexippus) is not influenced by an intraspecific competitor. Journal of Insect Conservation. doi.org/10.1007/s10841-022-00408-0
- Freas, C. A., Spetch, M. L. 2022. Varieties of visual navigation in insects. Animal cognition, 1-24. doi.org/10.1007/s10071-022-01720-7
- Gilmour, S. M., Kharouba, H. M. 2022. Eastern monarch larval performance may not be affected by shifts in phenological synchrony with milkweed. Ecology and Evolution, 12, e9131. doi.org/10.1002/ece3.9131
- Glenny, W., Runyon, J.B., Burkle, L.A. 2022. A review of management actions on insect pollinators on public lands in the United States. Biodiversity and Conservation. doi:org/10.1007/s10531-022-02399-5
- Glidden, A.J., Sherrard, M.E., Meissen, J.C., Myers, M.C., Elgersma, K.J., Jackson, L.L. 2023. Planting time, first-year mowing, and seed mix design influence ecological outcomes in agroecosystem revegetation projects. Restor Ecol e13818. doi.org/10.1111/rec.13818
- Grant, T.J., Fisher, K.E., Krishnan, N., Mullins, A.N., Hellmich, R.L., Sappington, T.W., Adelman, J.S., Coats, J.R., Hartzler, R.G., Pleasants, J.M., Bradbury, S.P. 2022. Monarch butterfly ecology, behavior, and vulnerabilities in north central United States agricultural landscapes. BioScience. doi.org/10.1093/biosci/biac094
- Greenstein, L., Steele, C., Taylor, C.M. 2022. Host plant specificity of the monarch butterfly Danaus plexippus: A systematic review and meta-analysis. PLoS ONE 17(6): e0269701. doi.org/10.1371/journal.pone.0269701
- Guerra, P., Gegear, R., Reppert, S. 2014. A magnetic compass aids monarch butterfly migration. Nature Communications 5, 4164. doi.org/10.1038/ncomms5164
- Gustafson, NW., Couture JJ., Dalgleish, HJ. 2023. Herbivory, plant traits and nectar chemistry interact to affect the community of insect visitors and pollination in common milkweed, Asclepias syriaca. Oecologia 201, 91-105. doi.org/10.1007/s00442-022-05290-w
- Halsch, C.A., Hoyle, S.M., Code, A., Fordyce, J.A., Forister, M.L. 2022. Milkweed plants bought at nurseries may expose monarch caterpillars to harmful pesticide residues. Volume 273. doi:org/10.1016/j.biocon.2022.109699



- James, D.G., Schaefer, M.C., Krimmer Easton, K., Carl, A. 2022. "Reply to Davis, A.K. Monarchs Reared in Winter in California Are Not Large Enough to Be Migrants. Comment on "James et al. First Population Study on Winter Breeding Monarch Butterflies, Danaus plexippus (Lepidoptera: Nymphalidae) in the Urban South Bay of San Francisco, California. Insects 2021, 12, 946. Insects 13, no. 1: 64. doi.org/10.3390/insects13010064
- Klassen, K.G.; Dizney, L.; Mattson, R.; and Silva, E. 2022. The Effect of Residual Roundup on Showy Milkweed Growth and Cardenolide Production. RURALS: Review of Undergraduate Research in Agricultural and Life Sciences: Vol. 15: Iss. 1, Article 5.
- Koziol, L., Schultz, P.A., Parsons, S., Bever, J.D. 2022. Native mycorrhizal fungi improve milkweed growth, latex, and establishment while some commercial fungi may inhibit them. Ecosphere. Volume 13. doi.org/10.1002/ecs2.4052
- Leone, J.B., Pennarola, N.P., Larson, J.L., Oberhauser, K., Larson, D.L. 2022. Divergent responses of butterflies and bees to burning and grazing management in tallgrass prairies. Ecology and Evolution, 12, e9532. doi.org/10.1002/ece3.9532
- López-García, J., Navarro-Cerrillo, R.M., Manzo-Delgado, L.L. 2022. Forest land-cover trends in the Monarch Butterfly Biosphere Reserve in Mexico, 1994–2017. Environmental Conservation page 1 of 11. doi.org/10.1017/S0376892922000327
- Majewska, A.A., Davis, A.K., Altizer, S., de Roode, J.C. 2021. Parasite dynamics in North American monarchs predicted by host density and seasonal migratory culling. Journal of Animal Ecology. 91(4):780-93. doi:org/10.1111/1365-2656.13678
- Manzanares, M.L., Panella, M.J., Wonkka, C.L., Steinauer, G.A., Stoner, K.J. 2022. Comparison of Two Milkweed (Asclepias) Sampling Techniques on Eastern Nebraska Grasslands. Prairie Naturalist, Special Issue 1 (2022): 54–64.
- Mattson, R.; Silva, E.; Klassen, K.; and Dizney, L. 2022. The Effect of Arbuscular Mycorrhizae on Milkweed Growth and its Implications for Western Monarchs. RURALS: Review of Undergraduate Research in Agricultural and Life Sciences: Vol. 15: Iss. 1, Article 4.
- Maynard, L., Howorth, P., Daniels, J., Bunney, K.-L., Snyder, R., Jenike, D., Barnhart, T., Spevak, E., Fitzgerald, P., & Gezon, Z. (2022). Conservation psychology strategies for collaborative planning and impact evaluation. Zoo Biology, 1–14. doi.org/10.1002/zoo.21692
- McCoshum, S.M., Agrawal, A.A. 2021. Ecology of Asclepias brachystephana: a plant for roadside and right-of-way management. Native Plants Journal. doi.org/10.3368/npj.22.3.256
- Medina, R. 2022. Monarch butterfly larvae and airborne chemicals in relation to identifying milkweed. Centaurus. Volume 30 p. 14-16.
- Miles, L.S. Murray-Stoker, D., Nhan, V.J., Johnson, M.J.T. 2022. Effects of urbanization on specialist insect communities of milkweed are mediated by special and temporal variation. Ecosphere. doi.org/10.1002/ecs2.4222
- Mishkin, M., Navarette-Pacheco, J.A. 2022. Rapid assessment remote sensing of forest cover change to inform forest management: Case of the Monarch reserve. Ecological Indicators 137: 108729. doi.org/10.1016/j.ecolind.2022.108729



- Neigel, E.R., Harkess, R.L., Fox, A.A.A. 2022. Mapping potential butterfly milkweed (Asclepias tuberosa) habitat in Mississippi using Species Distribution Modeling (SDM) and Geographic Information Systems (GIS). Native Plants Journal 23(1):84–96.
- Neupane, N., Zipkin, E.F., Saunders, S.P, and Ries, L. 2022. Grappling with uncertainty in ecological projections: a case study using the migratory monarch butterfly. Ecosphere 13(1):e03874. doi.org/10.1002/ecs2.3874
- Palmersheim, M.C., Schurch, R., O'Rourke, M.E., Slezak, J., Couvillon, M.J. 2022. If you grow it, they will come: ornamental plants impact the abundance and diversity of pollinators and other flower-visiting insects in gardens. Horticulturae. Volume 8. doi.org/10.3390/horticulturae8111068
- Parlin, A.F., Stratton, S.M., Guerra, P.A. 2022a. Oriented migratory flight at night: consequences of nighttime light pollution for monarch butterflies. iScience 25 (5): 104310. doi.org/10.1016/j.isci.2022.104310
- Parlin, A.F., Stratton, S.M., Guerra, P.A. 2022b. A behavioral assay to test sensory-cue-guided oriented flight in monarch butterflies under controlled conditions. STAR Protocols, 3(4): 101920. doi.org/10.1016/j.xpro.2022.101920
- Pocius VM, Cibotti S, Ray S, Ankoma-Darko O, McCartney NB, Schilder RJ, Ali JG. 2022. Impacts of larval host plant species on dispersal traits and free-flight energetics of adult butterflies. Communications Biology. (2022)5:469. doi.org/10.1038/s42003-022-03396-8
- Raschke AB, Pegram KV, Melkonoff NA, Davis J, Blackwell SA. 2022. Collaborative Conservation by Botanical Gardens: Unique Opportunities for Local to Global Impacts. Volume 3. doi.org/10.3390/jzbg3030035
- Rasmussen NL, Yang LH, 2022. Timing of a plant-herbivore interaction alters plant growth and reproduction. Ecology: Ecological Society of America. doi.org/10.1002/ecy.3854
- Rinella, M.J., Porensky, L.M., Bellows, S.E., Knox, J.M., Metier, E.P. 2023. Establishing forbs for pollinators in agricultural landscapes of the Great Plains, U.S.A. Restor Ecol e13846. doi.org/10.1111/rec.13846
- Roberton B, Rebar D. 2022. Timing of prescribed burns impacts plant diversity but not investment in pollinator recruitment in a tallgrass prairie. Ecosphere. Volume 13. doi.org/10.1002/ecs2.3914
- Sáenz-Ceja, Jesús E., J. Trinidad Sáenz-Reyes, and David Castillo-Quiroz. 2022. Pollinator Species at Risk from the Expansion of Avocado Monoculture in Central Mexico. Conservation 2: 457-472. doi.org/10.3390/conservation2030031
- Sánchez-Tlacuahuac, N., Pimentel-Equihua, J.L., Espinosa-Hernández, V. et al. 2022. What do monarchs feed on in winter? Nectar sources at hibernation sites. J Insect Conserv. doi:org/10.1007/s10841-022-00433-z
- Scott, A., Contreras, K., Stevenson, M., Hudman, KL, Kopachena, JG. 2022. Survival of eggs to third instar of late-summer and fall-breeding monarch butterflies (Danaus plexippus) and queen butterflies (Danaus gilippus) in north Texas. Journal of Insect Conservation, doi.org/10.1007/s10841-022-00446-8



- Silva, Estrella V.; Mattson, Rylee; Klassen, Katherine; and Dizney, Laurie. 2022. The Effect of Species Diversity and Shade on Milkweed Growth and Cardenolide Concentration. RURALS: Review of Undergraduate Research in Agricultural and Life Sciences: Vol. 15: Iss. 1, Article 3. digitalcommons.unl.edu/rurals/vol15/iss1/3
- Simanonok SC, Otto,CRV, Iovanna R. 2022. Forbs included in conservation seed mixes exhibit variable blooming detection rates and cost-effectiveness: implications for pollinator habitat design.

 Restoration Ecology. e13657. doi.org/10.1111/rec.13657
- Spaeth KE Jr, Barbour PJ, Moranz R, Dinsmore SJ, Williams CJ. 2022. Asclepias dynamics on US rangelands: implications for conservation of monarch butterflies and other insects. Ecosphere, Volume 13(1). doi.org/10.1002/ecs2.3816
- Špirić, J., Salinas-Melgoza, M.A., Merlo-Reyes, A., Ramírez, M.I. 2023. Estimating the causal effect of forestry programs on forest recovery in a REDD+ priority area in Michoacán, Mexico. Forest Policy and Economics (146) 102879. doi.org/10.1016/j.forpol.2022.102879
- Thogmartin WE, Haefele MA, Diffendorfer JE, Semmens DJ, Derbridge JJ, Lien A, Huang T. 2022. Multi-species, multi-country analysis reveals North Americans are willing to pay for transborder migratory species conservation. People and Nature. Volume 4, Number 2. doi.org/10.1002/pan3.10307
- Tracy JL, Kantola T, Baum KA, Coulson RN. 2022 Distribution and phenology of monarch butterfly larvae and their milkweed hosts in the South Central US. Volume 31. doi.org/10.1007/s10531-022-02432-7
- Tseng M, Bevanda C, Singh Bhatti S, Black EN, Chang E, et al. 2022. Effects of temperature of monarch caterpillar pigment variation in nature. Insect Conservation and Diversity. doi.org/10.1111/icad.12608
- Van Devender TR, Reina-Guerrero AL. 2022. Monarch butterflies in Sonora and Adjacent Northwestern Mexico. Dugesiana. 29: 181-193.
- Villa, S.M., Kelly, K.P., Hollimon, M.G., Protil, III K.J., de Roode, J.C. 2022. Lack of inbreeding avoidance during mate selection in migratory monarch butterflies. Behavioural Processes. Volume 198. doi.org/10.1016/j.beproc.2022.10463
- Villablanca, F.X., Saniee, K. 2022. Hierarchy and Scale Influence Western Monarch Butterfly Overwintering Microclimate. Frontiers in Conservation Science. Volume 3. doi.org/10.3389/fcosc.2022.844299
- Weinstein SB, Dearing MD. 2022. Harvest mice (Reithrodontomys megalotis) consume monarch butterflies (Danaus plexippus). Ecology 103(3): e3607. doi.org/10.1002/ecy.3607
- Yang, L. H., Swan, K., Bastin, E., Aguilar, J., Cenzer, M., Codd, A., et al. 2022. Different factors limit early- and late-season windows of opportunity for monarch development. Ecology and Evolution, 12(7), e9039. doi.org/10.1002/ece3.9039
- Zylstra ER, Neupane N, Zipkin EF. 2022. Multi-season climate projections forecast declines in migratory monarch butterflies. Global Change Biology, 00, 1–17. doi.org/10.1111/gcb.16349

Additional Papers Referenced within Summary

Culbertson, K. A., Garland, M. S., Walton, R. K., Zemaitis, L., & Pocius, V. M. (2022). Long-term monitoring indicates shifting fall migration timing in monarch butterflies (Danaus plexippus). Global Change Biology,



28, 727- 738. doi.org/10.1111/gcb.15957

James, D.G., Schaefer, M.C., Krimmer Easton, K., Carl, A. 2021. First Population Study on Winter Breeding Monarch Butterflies, *Danaus plexippus* (Lepidoptera: Nymphalidae) in the Urban South Bay of San Francisco, California. Insects 12(10): 946. doi:org/10.3390/insects12100946



How You Can Help Protect Monarchs

Create habitat. Plant native milkweed and flowering plants. Visit www.plantmilkweed.org for recommendations on how to create a pollinator-friendly garden.

Report observations. Participate in community science projects, such as tagging monarchs and butterfly counts.

Educate others. The Monarch Joint Venture offers monthly webinars and a variety of free, educational resources for teachers and others. Help spread the word!

Make Connections. Consider the circles of people and groups in your life and invite them to connect with the MJV and our growing partner network.

Share our work. Share the work of the MJV with your friends and family. You can share a video that provides an overview of our work, a post on Facebook, a photo on Instagram, or news from Twitter.

Contribute financially. Invest today and help ensure that resources are available to help the Monarch Joint Venture and other conservation-focused organizations implement the science-based recommendations in the annually updated Monarch Conservation Implementation Plan.

Walk, run, hike, or paddle. As an individual, or with a team, participate in Miles for Monarchs to help raise funds and awareness for monarch conservation.



