PATTERNS AND CONSEQUENCES OF MONARCH WINTERING BEHAVIOR IN THE SOUTHEASTERN US

by

CHARLOTTE P. HOVLAND

(Under the Direction of Sonia Altizer)

ABSTRACT

Eastern North American monarchs (*Danaus plexippus*) employ a diversity of overwintering behaviors, including long distance migration to central Mexico, but also winter-breeding and non-breeding overwintering in the southeastern United States. Winter-breeding alters infectious disease dynamics, increasing the prevalence of the monarch parasite *Ophryocystis elektroscirrha* (O.E.) in winter-breeding populations. I modeled interactions between returning spring migrants and resident winter-breeding monarchs in a simulated habitat patch and found that fewer new migrants were recruited from the patch into the migration when residents were present, and that migrants eclosing in habitat patches shared with residents were more likely to be parasitized than in habitat used only by migrants. Additionally, I fit logistic regression models to associate the breeding status of winter monarchs in the Southeast with habitat characteristics. My results concur with the idea that winter-breeding monarchs use human-modified habitat and suggest non-breeding monarchs may winter in wetlands in warm regions.

INDEX WORDS: Partial Migration, *Danaus plexippus*, Infectious disease

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BS, University of Chicago, 2018

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2025

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December 2025

ACKNOWLEDGEMENTS

I would like to thank the members of my committee for their guidance and feedback on various drafts of this thesis. I would also like to thank the members of the MOVERS Working Group (Anna Yellin, Nancy Sheehan, Susan Myers, Amaad Blades, and Reagan Montalvo) for their collaboration. Thanks to the Monarch Butterfly Fund for funding my field explorations. I owe thanks to Pej Rohani and Scott Carver for their feedback on early versions of the compartmental modelling chapter and to Jeff Hepinstall-Cymerman and Seth Wenger for their patience with my questions about habitat modeling. Thank you to the Altizer and Hall labs for their support, and especially to the Altizer lab's research professionals: Julia Berliner and Emilee Story. I was hugely fortunate to supervise two brilliant undergraduate researchers: Cindy Lor and Lindsey Curtis, both of whom I'm sure will do amazing things. Finally, thank you to the volunteer contributors to Journey North and iNaturalist, whose observations made my work possible!

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

In many animal species, migration is a key behavioral adaptation that can allow animals to track favorable conditions, exploit resources across wide spatial ranges, find mates, and evade scarcity (Kubelka et al., 2022; Shaw, 2016; Teitelbaum et al., 2018). ‘Partial migration’ is common and occurs when some individuals in a population migrate while others remain resident (Chapman et al., 2011; Toledo et al., 2020). It’s been theorized that this flexibility in migratory strategy reflects the competitive fitness trade-offs that individuals make between migration and residency (Chapman et al., 2011; Fudickar et al., 2013; Menz et al., 2019). By Chapman et al.’s definition (2011), the term ‘partial migration’ can be applied to “any population with 1-99% migrants.” Following this expansive application, almost every migration on Earth can be said to be a partial migration. In this sense, ‘partial migration’ can be considered as just one expression of variation in migratory behavior over time or between individuals, the significance of which is often overlooked when considering generalized trends over larger scales.

While partial migration is naturally common, migratory propensity within populations is being altered by human impacts such as climate change (Clairbaux et al., 2019; Howard et al., 2020; Menz et al., 2019; Steele et al., 2023) and habitat fragmentation (Mumme et al., 2023), as well as changes in land use (Howard et al., 2020) and resource provisioning (reviewed in Satterfield et al., 2018). One impact of these changes has been the development of novel resident populations and sub-populations in which members of otherwise migratory species have been observed persisting as residents in times and places counter to historical precedent (Smith et al., 2022; Steele et al., 2023; Tortosa et al., 2002). Novel instances of residency have been reported across a broad range of taxa, including in winter-breeding resident monarch butterfly populations in the United States (Steele et al., 2023) and in white storks overwintering in Spanish refuse dumps (Tortosa et al., 2002). These resident populations are made possible by milder winter weather caused by climate change and by anthropogenic resource provisioning that continues to supply food through otherwise lean periods, when an area's natural resources alone would not suffice to sustain residents (Griswold et al., 2011; Satterfield, Marra, et al., 2018; Tortosa et al., 2002). Given these drivers, and the changes that have been observed so far, it appears likely that populations across many taxa will continue to experience weakening tendencies towards migration.

One area in which changing migration behavior may be highly impactful is infectious disease and host-parasite interactions. Host-parasite dynamics are shaped by migration through mechanisms including migratory culling, migratory escape, and migratory recovery (Altizer et al., 2011; Shaw & Binning, 2016). In the case of migratory culling, infected individuals experience elevated mortality relative to healthy individuals due to the combined effects of sublethal parasitism and the physical demands of migration. As a result, infected individuals are differentially removed from the population during migration (Altizer et al., 2011). Migratory escape allows healthy migrants to leave habitats where parasites or infectious propagules have built up in the environment, and to return when the risk of infection has declined (Altizer et al., 2011). In contrast, migratory recovery gives infected individuals the opportunity to resolve their infections, often by temporarily moving to a habitat that is less conducive to continued infection and where the parasite is not well adapted (Shaw & Binning, 2016). While these migration-related processes can reduce the prevalence of disease, migrants can also play important roles in the introduction of pathogens to resident populations and sub-populations, picking up infections on their journeys and passing them on to other migrants, to resident conspecifics, or to members of other susceptible species (Donaldson et al., 2024; Teitelbaum et al., 2018). In addition to migration's effects on host-pathogen dynamics, disease can also impact migration, affecting diseased individuals' ability and proclivity to migrate (Narayanan et al., 2020; van Gils et al., 2007). These processes result in complex feedback interactions between a population's migratory behavior, including partial migration, and its disease ecology.

Both the eastern and western North American migratory monarchs (*Danaus plexippus*) have established growing resident populations in the past several decades (Crone & Schultz, 2021; Erickson et al., 2025; Satterfield et al., 2015; Steele et al., 2023). Rather than entering reproductive diapause and migrating to Central Mexico or California, these monarchs continue to breed in place throughout the fall and winter in addition to the spring and summer breeding period. These winter-breeding residents are thought to be responding to anthropogenic pressures and opportunities, including increased temperatures during the traditional migration season (Rich et al., 2025) and the introduction of tropical milkweed (*Asclepias curassavica*) and other exotic host plants that maintain their foliage throughout the year in warm climates (Batalden & Oberhauser, 2015; Majewska & Altizer, 2019). Winter-breeding monarchs are widely distributed in the southeastern United States, particularly along the Gulf Coast from Florida to eastern Texas (Fyson et al., 2025).

Several recent studies have focused on the effect of residency on the dynamics of *Ophryocystis elektroschirrha* (hereafter referred to as O.E.) infection in monarchs. O.E. is a specialist protozoan parasite that spreads through environmental contamination as well as vertical transmission from infected adults and spore transfer during mating. Majewska et al. (2022) gathered evidence that migratory culling acts on migratory monarchs infected with O.E., with higher infection rates observed in fall populations correlating to fewer monarchs arriving at overwintering sites. Consistent with the expected effects of the loss of migratory culling, several studies have now confirmed that winter-breeding resident monarchs have significantly higher rates of O.E. infection relative to migratory monarchs (Satterfield et al., 2015, 2016, 2018b).

While recent research in the western North America suggests that Northern California residents and migrants have unlinked population dynamics (Erickson et al., 2025), questions remain about how residents and migrants may interact in the eastern North American population, and what these interactions may mean for the health of the eastern North American monarch migration. Worryingly, Satterfield et al. (2018) found that not only do resident monarchs have higher rates of infection than migrants, but migrants captured at winter-breeding locations in Texas were 13 times more likely to be infected with O.E. than were migrants captured at stopover sites without resident populations. Adding to the complexity of the story, the southeastern United States is also home to little-understood local overwintering monarchs, which appear to remain throughout the winter in the southeast in a non-reproductive state (Brower, 1995; Kendrick & McCord, 2023). These non-breeding overwintering monarchs have so far only been reported from a few locations in Florida and South Carolina, but may represent an important alternative overwintering strategy for eastern North American monarchs (Bostian, 2023; Kendrick & McCord, 2023; Satterfield et al., 2015).

The overarching goals of my research are 1) to better understand varied monarch wintering behaviors in the southeastern United States, including both winter-breeding and non-breeding overwintering, and 2) to extend knowledge about wintering monarchs in the Southeast to its implications for the eastern North American monarch migration. In Chapter 2, I model the potential effects of interactions between winter-breeding resident and migrant monarchs in a common habitat on migrant health and abundance, as mediated by a shared parasite. In Chapter 3, I attempt to identify distinguishing features of winter-breeding and non-breeding overwintering monarch habitat in the

Southeast from participatory science observations and publicly available landcover and climate data. This work will expand our knowledge of eastern North American monarch behavior outside of the comparatively well-studied central flyway.

CHAPTER 2

HABITAT SHARING BETWEEN RESIDENT AND MIGRANT MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS*) LEADS TO INCREASED INFECTION PREVALENCE AND REDUCED RECRUITMENT IN MIGRANTS[1]

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[1] Charlotte Hovland, Sonia Altizer, Richard Hall. To be submitted to a peer reviewed journal.

Abstract:

Anthropogenic changes, including climate change and supplemental resource provisioning, are contributing to decreasing migratory propensity across taxa. In partially migrant populations, lowered migratory propensity can lead to more individuals becoming resident, even as other members of the population continue to deploy a migratory strategy. Shifts towards residency that allow year-round parasite transmission are expected to increase prevalence of parasitic infection in residents, as in the case of recently-formed resident populations of monarch butterflies (*Danaus plexippus*) in the southeastern United States, where the protozoan parasite *Ophryocystis elektroscirrha* reaches high (70 – 100%) prevalence in residents. Where residents and migrants overlap and share habitat, interactions between residents, migrants, and their parasites may lead to detrimental effects on migrants due to exposure to highly infected resident populations. In this study, we model the interaction of residents, migrants, and their shared parasites, using monarch butterflies and their protozoan parasites as a model system to understand infectious disease dynamics in coupled resident-migrant systems. Evaluating effects of residents' presence in a habitat patch used by migrants, our study finds that sharing habitat with residents leads to elevated parasite prevalence in migrants and lowered recruitment into the next migrant generation. In the presence of residents, modeled migrant recruitment was reduced by 38% as a result of both resource competition and effects of infection on fecundity and mortality. These findings emphasize the importance of movement behavior to infectious disease dynamics and support the idea that resident populations present a conservation concern for the eastern North American monarch, especially as the range of winter-breeding monarchs is projected to expand under climate warming.

Keywords: Partial migration, Host-parasite dynamics, Compartmental disease modeling

Introduction:

The study of partial migration can provide important insight into the consequences of anthropogenic changes for migratory behavior. Partial migration, in which some individuals in a population deploy a migratory strategy at least some of the time, while others remain resident, is common across a range of migratory taxa (Chapman et al., 2011; Menz et al., 2019). In these taxa, interactions between migrants and residents can drive complex coupled dynamics, affecting transmission of infectious diseases (Donaldson et al., 2024; Fecchio et al., 2021; Lisovski et al., 2018), food webs (Kelson et al., 2020; Peller et al., 2023; Toledo et al., 2020), and other ecological processes. Because migratory behavior and physiology in partially migratory taxa are often plastic, partial migrants are well positioned to respond to anthropogenic impacts (Menz et al., 2019). For instance, milder temperate winters under climate warming, and anthropogenic nutritional subsidies, such as ornamental plantings and discarded food waste, may favor the persistence of year-round resident populations (Brown & Hall, 2018; Griswold et al., 2011; Satterfield, Marra, et al., 2018). As a result, populations experience weakening tendencies towards migration, expressed either as decreased migration distance or as decreased migratory propensity, and corresponding increases in residency (Fox & Dennis, 2010; Stepanian & Wainwright, 2018; Tortosa et al., 2002; Xu et al., 2021).

Of particular concern, these changes in migratory behavior can trigger shifts in the spread of infectious disease. Migrants can harbor a higher diversity of parasites than residents, because migrants can sample diverse habitats and parasite communities and track environmental conditions favorable to infected host and pathogen survival (e.g. Teitelbaum et al., 2018). However, migration also acts to reduce the infection prevalence of some parasites in cases when infected migrants are less likely to survive during active migration, periodically vacate sites where transmission occurs, or if switching habitats promotes recovery from infection (Altizer et al., 2011; Shaw & Binning, 2016). Theoretical models suggest that shifts towards residency in partially migratory taxa will be accompanied by elevated infection prevalence in residents due to the loss or weakening of these processes (Balstad et al., 2021; Brown & Hall, 2018; Hall et al., 2014, 2016; but see Turjeman et al., 2020). While spatially separated, residents and migrants experience different infectious disease landscapes. When reunited, the interaction between residents and migrants can dramatically shift parasite dynamics. For example, waves of epidemiologically naïve migrants entering a wintering site shared by migrant and resident mallard ducks have been shown to explain seasonal spikes in avian influenza prevalence (Lisovski et al., 2018), while connectivity between resident flying fox (*Pteropus* spp.) camps influences the frequency and intensity of Hendra virus outbreaks and spillover events (Plowright et al., 2011). Mechanistic modeling is an important tool for us to predict and understand the complex effects of anthropogenically driven changes in migration behavior on infectious disease dynamics in these coupled resident-migrant systems because it allows us to directly compare simulated populations in which different migratory processes are represented.

North American monarch butterflies (*Danaus plexippus*) are an excellent system in which to study infectious disease dynamics in coupled resident-migrant populations. In eastern North America, where historically monarchs recolonized their breeding range from sites in Central Mexico (Urquhart & Urquhart, 1976), monarchs appear to be undergoing a shift towards partial migration. While the seasonal dynamics of their larval host plants historically compelled seasonal migration, the introduction of non-native milkweeds (especially *Asclepias curassavica*) has expanded the monarch's potential breeding season where winters are mild (Batalden & Oberhauser, 2015). Recently, monarchs have been observed breeding throughout the year as residents in the US Southeast (Fyson et al., 2025; Satterfield et al., 2015; Satterfield, Maerz, et al., 2018; Steele et al., 2023), and residents and migrants are known to co-occur at sites in the Southeast during the Fall and Spring migrations (Kendzel et al., 2023; Satterfield, Maerz, et al., 2018) (Figure 2.1). Relative to migrants, resident populations are infected at high prevalence with the specialist protozoan parasite *Ophryocystis elektroscirrha* (O.E.) (Majewska et al., 2022; Satterfield et al., 2015). Continued occupancy of and breeding in contaminated environments, along with the loss of migratory culling, result in O.E. prevalence in residents far higher than that in migrants (Majewska et al., 2022). O.E. is only able to infect monarchs during their larval stage, but it does so by multiple modes of transmission: 1) vertical transmission from an infected female to her eggs, 2) environmental transmission via consumption of contaminated milkweed, and 3) horizontal transfer, in which a healthy adult female is contaminated through mating with an infected adult and then transmits infectious spores to her offspring (Majewska, Sims, et al., 2019; McLaughlin & Myers, 1970). Thus, this system offers both strongly contrasting disease dynamics between migrants and residents, and numerous mechanisms by which residents, migrants, and their pathogens might interact in a shared environment.

Understanding how residency and pathogen sharing impact migratory monarchs is critical because monarch butterflies are a species of conservation concern (United States Fish and Wildlife Service, 2024). Since 2002, O.E. infection in eastern North American monarchs has increased by ~200% (Majewska et al., 2022), while overwintering monarch abundances in recent years have been both highly variable and well below historical highs (Rendón-Salinas et al., 2024). O.E. infection imposes costs on both survival and reproduction in monarchs (Altizer & Oberhauser, 1999; Crone & Schultz, 2021; De Roode et al., 2007, 2008), leading to fears that increased infection prevalence resulting from changing migration behavior may contribute to population declines, or even that resident-occupied sites may represent hazardous demographic sinks for North American monarchs (Crone & Schultz, 2021, but see Erickson et al., 2025). In order to address these concerns, more research is needed into infectious disease dynamics in paired migrant-resident systems in general, and in monarchs in particular.

In this study, we develop a compartmental model to simulate parasite transmission between residents and migrants, parameterized for the monarch-O.E. system, in a single habitat patch. We use this model to explore the effect of resident monarchs' presence in migrant breeding habitat on infection prevalence in the migrant population, as well as on the number of new migrants recruited from the habitat patch. Through this study, we address the questions: How does the co-occurrence of residents and migrants in shared habitat in the US Southeast influence O.E. prevalence in eastern North American migratory monarchs during the spring return migration? And: how does overlap between migrants and residents in the southern breeding range of returning migratory monarchs affect the recruitment of the next generation of spring migrants to recolonize eastern North America?

Methods:

a) Model Description

Resident population dynamics: This model builds on an existing stage-structured differential equation model of monarch-OE interaction during the establishment of a single resident patch with limited milkweed host plants (Majewska, Sims, et al., 2019). As in the prior model, individuals are assigned to compartments based on life stage (larval or adult) and infection status (susceptible or infected for larvae, susceptible, infected, or contaminated for adults; see Figure 2.2a).

Healthy adults produce eggs at rate b_s, while infected adults produce eggs at a reduced rate, b_i ($b_i < b_s$). Eggs hatch into the larval compartment after a developmental time delay of t_e days. Larvae experience density dependent (μ_d) and density independent (μ_0) mortality, where density independent mortality is a constant per-capita rate, while density dependent mortality is relative to the ratio of total larvae to available milkweed (M), scaled by the constant μ_d. Surviving larvae develop to pupae at rate g (equivalent to 1 / average duration of larval stage) and remain pupae for a developmental time delay t_p. Pupae survive to emergence at some rate, ρ. Infected pupae (pupae originating as infected larvae) undergo additional mortality due to infection and survive to emergence at the rate (ρ *q). After t_p days, adults emerge and are assumed to mate shortly after eclosion. Uninfected adults die at per capita rate μ_S. Infected adults experience increased mortality and die at rate μ_I, where $\mu_I > \mu_S$.

Milkweed (*M*) is measured as the number of leaves in the patch. Milkweed is assumed to grow logistically with a carrying capacity of *K* and a maximum growth rate, *r*. The value of *r* depends on the season, with little growth in the winter (r_{win}) relative to the spring growth rate (r_{spr}). Milkweed leaves are lost to consumption relative to the number of larvae in the patch, scaled by a constant, c.

Parasite transmission within patch: In the model, as in life, monarchs can only become infected with the O.E. parasite during their larval life stage. However, larvae are vulnerable to multiple routes of transmission, each of which contributes to population level infection dynamics (Majewska et al., 2019).

Vertical transmission occurs when an infected adult lays eggs that are contaminated with parasite spores. Hatchlings are then at risk of being infected when they consume their egg casings during and after hatching. In the model, a fraction p_V of eggs laid by infected adults become infected themselves through vertical transmission.

Environmental parasite transmission occurs when larvae feed on milkweed that has been contaminated with spores. The amount of contaminated milkweed in the patch (M_C) increases with the total population of infected adults, who spread spores across the leaves with a per capita milkweed visitation rate λ. Larvae must ingest infectious spores from the environment in order to become infected, and thus the rate of larval infection via environmental transmission depends on the larvae's per capita milkweed consumption rate (c), weighted by the proportion of available milkweed that is contaminated (M_C / M). Spores decay over time at rate s_{dW}, reducing the number of contaminated milkweed leaves over time, in the absence of new contamination.

Finally, infection via horizontal spore transfer occurs in two steps. First, susceptible females mate with infected males, becoming contaminated with spores in the process. Then, without ever becoming infected themselves, these females lay eggs that are contaminated with spores, putting their offspring at risk for infection with a probability p_h that an egg laid by a contaminated adult will be infected. In the model, the adult contamination rate increases with the infection prevalence in potential mates (infected adults / total adults), scaled by a mating probability δ. Contamination resolves as spores are lost at rate s_d and contaminated adults return to the susceptible class over time.

At each timepoint, the model tracks the number of resident larvae infected by vertical transmission, environmental transmission, and horizontal transmission (I_v, I_E, and I_H, respectively), as well as the susceptible resident larvae (S_L), susceptible resident adults (S_A), infected resident adults (I_A), and contaminated resident adults (C_A).

Migration: After a winter burn-in period (t_{win}), in which residents are either present or absent in the milkweed patch, we introduce a transient pulse of spring migrants (Figure 2.2b). Migrants arrive following a quadratic distribution centered on a peak arrival rate, a_{max}, which occurs halfway through the migratory season ($t_{mi} / 2$) (Eq. 1). Migrants are assumed to depart the patch at a constant rate, γ, corresponding to 1 / average migrant residence time in the patch. After departing the patch, the migrants are moved into a 'departed' compartment in order to track the cumulative export of migrants from the patch, and not only the in-patch dynamics over time. Migration into the patch continues for t_{mi} days, after which the in-migration rate falls to zero and the model continues to run for t_{dev} days in order to allow eggs laid during the final days of the migratory period to develop to adulthood and depart the patch, where $t_{dev} = t_e + t_p + \frac{1}{\gamma}$.

Eq. 1: $$\alpha = \max\left\{0, \frac{-a_{max}}{\frac{\tau_{mi}^2}{2}}\left(t - \frac{\tau_{mi}}{2}\right)^2 + a_{max}\right\}$$

Parasite transmission operates by the same mechanisms for the migrant population within the patch as it does within a patch of residents, and the model tracks the susceptible, contaminated, and infected migrant adults (S_{AM}, C_{AM}, I_{AM}) and susceptible and infected migrant larvae (S_{LM}, I_{VM}, I_{EM}, I_{HM}) within the modeled patch. However, as surviving adult migrants depart the patch, they are assigned to one of three additional compartments, departed-susceptible (D_{SM}), departed-contaminated (D_{CM}), and departed-infected (D_{IM}). This departed class tracks the cumulative export of individuals and infections from the patch in the direction of the summer breeding grounds. Migrant and resident status are treated as maternal effects, with female migrants producing migrant offspring and residents producing resident offspring.

Interactions between residents and migrants: When present in the same patch, resident and migrant monarchs utilize a single, shared pool of milkweed leaves. As a result, density-dependent larval mortality is based on the total number of larvae present at any timepoint, regardless of migrant or resident status. Milkweed contamination is also driven by the total number of infected adults within the patch.

The sex ratio among adult monarchs is assumed to be 50:50 and, where both residents and migrants are present, mating within the patch is assumed to be non-assortative both between residents and migrants and between infected and susceptible individuals. The risk of horizontal parasite contamination during mating is thus dependent on the overall proportion of infected adults present in the patch.

Experimental Scenarios: Our analyses include comparisons among three migration scenarios, and between these scenarios and a control in which migrants are immune to infection:

Scenario 1: Residents only – residents are present throughout the winter burn-in period and during the spring migration period. A single pair of residents, one of which is infected, are initialized at the start of the burn-in period and are allowed to breed through the end of the 'migration period' with no arrival of migrants.

Scenario 2: Migrant only – no residents are present during the winter burn-in period or during the spring migration period. Migrants begin to arrive after τ_{win} days of milkweed growth. Migrants arrive with a low initial prevalence of O.E. infection based on values reported in the literature for prevalence in Mexico overwintering populations (reviewed in Majewska et al., 2022).

Scenario 3: Shared patch – both residents and migrants use the patch. Residents are present throughout the winter burn-in period and during the spring migration. Migrants begin to arrive after τ_{win} days of resident-only dynamics. Migrants arrive with a low initial prevalence of O.E. infection based on values reported in the literature for prevalence in Mexico overwintering populations (reviewed in Majewska et al., 2022). Residents are initialized at the start of the burn-in period with two individuals and 50% O.E. prevalence and are allowed to breed. At time of migrant arrival, infection rates in residents are comparable to literature values for winter-breeding residents (Satterfield et al., 2015).

Scenarios 4a and 4b: Migrant Immune – We developed two additional scenarios in which residents are competent hosts while migrants are immune to infection and free of disease. This does not reflect any real-world conditions, but allows the effects of infection on migrant populations to be more clearly distinguished from the effects of competition with residents. Without infection in migrants, we can determine the effects of competition on migrants separately from the effects of disease, and without releasing the resident population from the disease that limits its population density, thus dramatically altering the conditions of competition between the populations. Migrant Immune versions of the model were run for both Migrant-Only (4a) and Shared-Patch (4b) scenarios.

While the behavior of the resident population when migrants are immune to infection is not precisely identical to that of the resident population in Scenario 3, we compared the resident population between Scenario 3 and Scenario 4b and found their behavior to be sufficiently similar to allow for comparison, with qualitatively similar patterns in their population dynamics and only a 1.7% decrease in the resident larval population and 0.4% decrease in the resident adult population in the migrant-immune scenario when compared to Scenario 3 and averaged over the spring breeding period.

Parameterization: When possible, parameter values (Table 2) were retained from Majewska et al. (2019). When extending the model to include spring migrants, we assumed that migrant adults produce eggs at the same rate as residents and that migrant adults and larvae experience density-dependent, density-independent, and infection-related mortality identically to residents.

The stopover duration of migrants, $\frac{1}{\gamma}$, was based on Knight and Brower's observations from a spring remigrating population in northern Florida (1999). The maximum number of migrants arriving per day was set to be consistent with long-term observations from the same site (Brower et al., 2018). Parameters describing the costs of infection were held constant between residents and migrants. This choice reduced the number of parameters in the model, but costs of infection in migrants may, in reality, be higher than in residents (Majewska et al., 2022). t_{mi} of 40 days represents March through mid-April (Knight et al., 1999).

Milkweed growth rates were parameterized based on reported literature values for tropical milkweed. The spring growth rate was retained from Majewska et al. (2019), and the winter growth rate was based on a greenhouse study in which plants were raised at 10 °C under 9 hours of artificial light per day (Zimmer, 1972).

Initialization:

<u>Milkweed</u>: All scenarios were initialized at the start of winter with the same number of milkweed leaves. We retained the patch layout described by Majewska et al. (2019) with 90 tropical milkweeds distributed over ~3 hectares. To estimate an appropriate number of leaves per plant for a tropical milkweed in a garden plot in the US Southeast in early winter, we counted the number of leaves visible on tropical milkweed plants in photographs submitted to iNaturalist and Journey North in December, January, and February of 2019 – 2025 in Florida, Texas, Louisiana, Georgia, South Carolina, and Alabama. Leaves were only counted if the majority of at least one plant was visible in the image. All image analysis was conducted using FIJI/ImageJ2 (Rueden et al., 2017; Schindelin et al., 2012). No milkweed was contaminated at the onset of winter.

<u>Monarchs</u>: For scenarios in which resident monarchs were present through the winter, the model was initialized on the first day of the winter season with a single mating pair of resident adults, one of which was infected. We chose this initial condition because it is conservative and agnostic to the issue of multi-year resident persistence and stability. These two initial residents can be understood to colonize the patch either from a local resident population, or as drop-outs from the fall migration that break out of migratory diapause and adopt a resident strategy at the start of winter.

Model analysis: We wrote the model script in R (R Core Team, 2024) and solved the time-lagged differential equations numerically using the function dede from the package 'deSolve' (Hindmarsh, 1983; Soetaert et al., 2010).

At each timestep, we recorded the number of migrant and resident adults, as applicable, in each category. We calculated prevalence within each population of interest as the number of infected individuals / the total number of individuals. For some analyses, we simplified the infection status into a binary outcome of 'infected' or 'healthy.' In these cases, contaminated individuals are counted as 'healthy.'

Throughout the migration period, incoming migrants with low overwintering infection prevalence made up a large proportion of the healthy adults in the population and threatened to overwhelm any signal of changing infection dynamics within the new generation of monarchs hatching within the patch. In order to determine how many migrants passed through the patch vs. hatched from eggs laid in the patch, we integrated the migrant arrival function over the migration period to determine the total number of migrants that arrived over the season. We then assigned these in-migrants to healthy and infected classes based on the fixed prevalence in the incoming migrant population (p_{mi}) and multiplied these totals by the proportion remaining alive after accounting for in-patch mortality of healthy and infected migrants each day for the average duration of stopover ($\frac{1}{\gamma}$ days) (Eq. 2). The differences between these values and the final abundance of healthy and infected monarchs departing the patch category after the end of migration period represent the monarchs that hatched within the patch and survived to continue the migration.

Eq. 2a - Healthy Individuals:

$$Patch\ hatched = Cumulative\ departed\ abundance - \left(\int_0^{\tau_{mi}} Eq1 + 1 \right) (1 - p_{mi}) \left((1 - \mu_S)^{\frac{1}{\gamma}} \right)$$

Eq. 2b – Infected Individuals:

$$Patch\ hatched = Cumulative\ departed\ abundance - \left(\int_0^{\tau_{mi}} Eq1 + 1 \right) (p_{mi}) \left((1 - \mu_I)^{\frac{1}{\gamma}} \right)$$

Following Majewska et al. (2019), at each timepoint, we divided the number of larvae infected by vertical transmission, environmental transmission, and horizontal transfer, respectively, by the total number of infected larvae within the population of interest (residents or migrants) to assess the relative contribution of each transmission mode to the spread of infection in the population over time.

Sensitivity analysis: In their 2022 review, Majewska et al. compiled data on the proportion of infected individuals sampled from the Mexican overwintering population during assessments made between 1968 and 2019. They report a minimum observed proportion of 0 and a maximum of 0.145. Considering this range, we varied the initial infection prevalence in arriving migrants (formerly of the overwintering population) between 0 and 0.15. Reflecting dramatic interannual variation in overwintering monarch abundance (Fernández-Islas et al., 2024), we also varied the maximum migrant arrival rate between 1 and 20 incoming migrants per day. We looked at the effects of these factors on infection prevalence within the patch over time, the final infection prevalence in the departing migratory population, and the number of new healthy and infected migrants produced within the patch.

Results:

a) Model analysis of infection prevalence in single migration strategy and shared habitats

As in Majewska et al., O.E. quickly achieved high prevalence in resident populations (Majewska, Sims, et al., 2019). From an initial prevalence of 50% on the first day of winter, by the end of the spring migration period, the resident population in the resident-only patch showed an 87% infection prevalence in adults and 92% in larvae. These values correspond well with the 80% - 100% prevalence observed by Satterfield et al. (2018) in predominantly resident breeding populations in East Texas.

Migrant-only populations maintained their relatively low infection prevalence through the first weeks of migration. Because adult monarchs cannot become infected, infection prevalence was flat for the first 10 days as adult, overwintered migrants moved in and out of the patch prior to the emergence of any of their first-generation offspring. After this, prevalence in migrant populations increased gradually, with the largest increases coming late in the migration, when second-generation offspring began to emerge. We found that for a migrant population using a migrant-only habitat, an incoming, overwintering generation O.E. prevalence of 0.047 resulted in a prevalence of 0.102 among migrants that hatched within the patch before departing, a 117% increase (Figure 2.4). This is consistent with the observation that O.E. builds up throughout the breeding season (Majewska et al., 2022).

In patches utilized by both resident monarchs and spring migrants, contamination and infection of migrants were more common than in migrant-only environments. This effect was particularly marked in migrant offspring that hatched within shared patches before departing to join the migration. The cumulative prevalence among these adults was 0.46, approximately 4.5 times greater than in a migrant-only patch (Figure 2.4). This represented an 879% increase from the prevalence in the incoming, overwintered migrant population.

b) Effects of infection vs. competition on migrant and resident abundance

Sharing habitat with resident populations affected migrants both indirectly, through shared parasites, and directly through resource competition. Our model scenarios allowed us to disentangle the effects of infection and competition on monarch populations.

Relative to a migrant-only patch, export of patch-hatched migrants was 38% lower from a shared patch where migrants experienced both density-dependent mortality and increased prevalence of OE in the presence of residents (Figure 2.4). When the model was re-run in a ‘migrant immune’ scenario, in which migrants could not pick up or transmit infections, patch-hatched migrants declined by only 27% in shared patches relative to migrant-only habitat. This indicates that declines in export of new migrants from shared habitat patches are due to both resource competition with residents and to increased mortality and decreased fecundity associated with the increased infection prevalence experienced by migrants in these patches.

c) Transmission modes in migrant population infection dynamics

In the migrant-only patch, vertical transmission was initially the most important driver of new infections, with the few infected adults from the overwintered generation laying eggs that hatched into infected larvae (Figure 2.5). While this mode of transmission had the highest relative importance early in the migration, the actual disease prevalence in the population at this stage was low. Initially, no milkweed leaves were contaminated and there was no contribution from environmental transmission. Over time, contamination from infected adults built up on milkweed leaves in the environment and environmental transmission overtook vertical transmission.

In a shared patch, the opposite trend prevailed among migrants: initially, incoming migrants arrived in an environment that had already been heavily contaminated by infected residents and environmental transmission was high. Only at the end of the spring migratory period, when infected 1st generation migrant offspring began to produce 2nd generation larvae, did vertical transmission overtake environmental transmission in relative importance. Meanwhile, resident populations maintained high infection prevalence principally through vertical transmission, with some contributions from environmental transmission and the horizontal transfer of spores to healthy adults, as in Majewska et al. (2019).

In both the migrant-only and the shared patch, horizontal transfer caused about 25% of infections in migrants over time.

d) Sensitivity analysis

Initial infection prevalence in migrants: When we varied the initial infection prevalence in the incoming migrants from 0 to 0.15, the general pattern held true of gradually increasing infection prevalence within the patch throughout the spring migration period (Supplemental Figure 2.S1). In the migrant-only scenario, the final prevalence in-patch increased with increasing initial prevalence, however, in the shared patch, the final infection prevalence among migrants in the patch was high (~0.6) irrespective of the initial infection prevalence among incoming migrants.

Migrant arrival density: The density of incoming spring migrants arriving at a given patch of habitat is likely to depend, at least in part, on overwintering abundance, which has varied considerably over recent overwintering seasons (Fernández-Islas et al., 2024). In migrant-only environments, infection prevalence increases with increasing peak migrant arrival density (a_{max}), from 1 – 20 individuals arriving per day (Supplemental Figure 2.S2a). In contrast, increasing migrant arrival density decreased in-patch infection prevalence in adult migrants in patches where residents were also present (S2a), as healthy migrants made up a larger proportion of the population using the patch. Parasite transmission did continue in these higher density patches and the absolute number of infected migrants increased with the total number of migrants present (S2b). The relative contribution of each transmission mode in a shared plot with a higher density of incoming migrants (a_{max} = 10) followed a qualitatively similar pattern as in a lower density plot (default parameterization a_{max} = 3).

Discussion:

Overall, our model predicts that habitat patches shared by both resident and migrant monarchs will export fewer, sicker migrant monarchs into the next phase of the migration when compared with patches used by migrants alone. Within shared patches, both intraspecific resource competition and disease transmission contribute to reductions in the number of surviving migrant offspring in the presence of residents. In addition to being fewer in number, we found that migrant offspring that develop as larvae in patches used by residents have higher infection prevalence, primarily driven by environmental transmission through contamination of milkweed host plants in areas used by resident populations. Our findings highlight the importance of understanding infectious disease dynamics in coupled resident-migrant populations and support the establishment of winter-breeding resident monarchs in the US Southeast as a conservation concern for the monarch migration.

Across many animal species, seasonal movement behavior patterns are being disrupted by anthropogenic changes (Clairbaux et al., 2019; Howard et al., 2020; Plowright et al., 2011; Tortosa et al., 2002; Xu et al., 2021). As a result, members of some migratory, partially migratory, and nomadic taxa have been observed persisting as residents in times and places that have not historically supported year-round occupancy, including winter-breeding North American monarch butterflies in the US Southeast (Steele et al., 2023). These changes may have important effects on infectious disease transmission and population dynamics not only within resident populations, but also for migrants that encounter residents during the course of their migrations and life cycles. A prior model by Brown and Hall (2018) predicts increased infection prevalence of a vector-borne pathogen in both residents and migrants with increased resident survival in a partially migrant population. In empirically studied systems as well, it’s been shown that the presence of resident individuals in shared habitats with migrants can drastically alter the course of infection in populations. Krkošek et al (2005) found that passing by a fish farm where captive resident salmon are heavily burdened with sea lice (*Lepeophtheirus salmonis*) increased infection pressure on wild salmonids within 30 miles due to transmission of lice from residents to migrants. Like migrant monarch butterflies, which begin their return migration with low infection prevalence of O.E., the juvenile wild salmonids taking part in this seasonal migration initially arrive free of sea lice, which cannot survive in freshwater. After contracting sea lice from residents, infected fish harbor and carry the lice along their migratory route, fostering a second generation of parasites that further extend the influence of the salmon farms on infection dynamics across the seascape (Krkošek et al., 2005). Similarly, studying avian influenza in partially migratory mallard ducks (*Anas platyrhynchos*), Lisovski et al. found that the flow of immunologically naïve migrants over the course of the migration best explained the trajectories of influenza outbreaks observed at a wintering site used by both resident and migrant mallards (2018). As naïve birds arrived, they picked up and amplified the influenza virus present in the resident population (Lisovski et al., 2018). In a similar study, Hill et al. found that resident mallards maintained year-round circulation of endemic flu lineages in wintering grounds used seasonally by migrants (2012). Across both vertebrate and invertebrate taxa, the presence of residents at a site alters the infectious disease landscape in ways that present potential threats to migrant health.

In our monarch-specific model, the numbers of new migrants recruited from modeled habitat patches into the migrant population declined in the presence of residents because of both density-dependent competition and mortality and fecundity effects of disease. Density-dependent competition between monarch larvae is known to limit monarch population growth, although the effects of competition vary across the breeding range (Flockhart et al., 2012; Marini & Zalucki, 2017; Nail et al., 2015). Larval competition may be particularly fierce in the southern portions of the spring breeding range, the area approximated by our model, where larval and egg densities are highest (Flockhart et al., 2012; Marini & Zalucki, 2017). Accordingly, we included density-dependent mortality in our model, following Majewska et al. (2019). Focusing on migrant recruitment, competition with residents – absent any effect of infection— was responsible for a 27% decline in the export of new migrants from shared habitat patches to join the spring migration. Including the effects of disease, the presence of residents in habitat used by migrants reduced the export of fresh migrants to just 62% of recruitment from a habitat patch used only by migrants.

In addition to decreased recruitment due to infection-related mortality and lowered fecundity within a given habitat patch, sharing habitat with residents led to elevated infection prevalence in migrants leaving the patch to continue the migration. While adult members of the overwintering generation that entered the resident-occupied patch were not susceptible to new infections, those of their offspring that survived to join the migration carried a heavy burden of infection compared to offspring that completed development in a patch used by migrants only. The cumulative infection prevalence among adult migrants that originated in and departed from shared patches was 0.46, which is comparable to the prevalence observed among some winter-breeding resident populations in the southeast (Satterfield et al., 2015). Because O.E. infection lowers monarch fecundity and decreases mating success (Altizer & Oberhauser, 1999; Crone & Schultz, 2021; De Roode et al., 2008), high infection prevalence in early spring generations could inhibit migratory monarch population growth at a key stage in the recolonization of their northern range and may compromise their ability to bounce back after low overwintering abundance (Flockhart et al., 2013; Ries et al., 2015). Furthermore, as O.E. infection is sub-lethal in many cases, allowing infected individuals to fly, mate, and reproduce, spring-generation migrants hatched and infected in shared migrant-resident patches are likely to carry the pathogen with them as they disperse (Altizer & Oberhauser, 1999). Dispersal of early spring migrants from areas of the southern US that support residents could propagate increased infection into late spring and summer breeding grounds farther north where residents are not present. Our findings are consistent with the idea that the establishment of winter-breeding residents has likely contributed to the threefold increase in OE prevalence observed among eastern North American monarchs since 2002 (Majewska et al., 2022). However, given that winter-breeding residents currently overlap with only a relatively small area of spring breeding habitat in the Southeast (Fyson et al., 2025), other factors may be required to explain the full magnitude of increase.

Unlike in patches used by migrants only, we found that environmental transmission was the main driver of new infections in migrants in shared patches over time. Whereas migrant-only patches start the season free from contamination, residents in shared patches continue to spread infectious spores across the environment throughout the winter and quickly contaminate new milkweed growth in the spring. Infectious O.E. spores are known to persist in the environment for up to 35 weeks at moderate temperatures and up to 93 weeks at cool temperatures (Sánchez et al., 2021). As a result, environmental transmission could also play a role as a 'persistence mechanism' (Breban et al., 2009), with the potential to spark infections in migrants even if residents' and migrants' use of habitat does not overlap in time. Under the right conditions, a resident population could even suffer local extinction at the onset of winter and still leave spores that might remain viable through cool –but not freezing— winter temperatures, going on to infect early spring migrants.

The effects of habitat sharing with residents on migrant monarchs could be exacerbated (in terms of population declines) or mitigated (in terms of disease prevalence) by migratory drop-out, when individuals abandon the migration mid-way. Batalden and Oberhauser showed that exposure to the imported tropical milkweed *Asclepias curassavica*, which supports winter-breeding among residents, can trigger migrants to break reproductive diapause and drop out of the fall migration (2015), while Rich et al. demonstrated that elevated temperatures promote reproductive development in wild-caught female fall migrants (2025). While fall migratory diapause and its disruption are outside the temporal scope of our model, migratory drop-out during the fall is likely an important mechanism coupling resident and migrant populations. Additionally, the likelihood of drop-out may vary with infection status (Narayanan et al., 2020). Satterfield et al. found higher OE infection prevalence in eastern North American fall migratory monarchs (identified to natal origin by stable isotope analysis and cardenolide fingerprinting) at sites where they co-occurred with residents (2018). This trend could be indicative of differential drop-out by infected individuals, which join or establish resident populations rather than attempting to complete their migration. Interestingly, if resident patches also differentially capture infected migrants during the spring, the drop-out phenomenon may blunt or even reverse the expected increase in population-level prevalence in migrants due to transmission from residents, as infected migrants remove themselves from the migration (Becker et al., 2018). Models that integrate both the spring and fall migrations and include drop-out on the patch and the landscape scale could help elucidate the implications of drop-out for infectious disease dynamics, as would more empirical work on the incidence and causes of drop-out.

Looking to the future, the effects of patch sharing between residents and migrants may become more significant with anticipated shifts in North American monarch habitat in the context of global change. While climate models predict relatively little near-term change in monarch habitat in the important spring breeding area of eastern Texas, drastic climate-based reductions in summer breeding habitat are possible in the upper Midwest (Zylstra et al., 2022). If these predicted changes come to pass, monarchs will lose habitat in areas where there are no documented residents (and where residents are extremely unlikely to survive the harsh winters), and milkweed patches in the Southeast may correspondingly make up a higher proportion of the total breeding habitat. Concurrently, Momeni-Dehaghi et al.’s habitat suitability models project a significant northward expansion in the extent of winter-breeding by 2100 (2024). In addition, conversion of open grasslands and disused agricultural lands to residential development could increase the proportion of monarchs using human-provided habitats, including the urban and suburban gardens that support resident monarchs and their parasites (Majewska, Satterfield, et al., 2019). In time, a high proportion of eastern North American monarchs may originate in regions where habitat sharing occurs between residents and migrants. In a supplemental analysis, we completed ‘back of the envelope’ calculations to estimate the expected increase in O.E. prevalence that would occur on a regional scale across a single generation, given increased overlap between resident and migrant breeding habitat. In a scenario in which 1 in 5 spring migrants uses habitat shared with residents, we would expect to see about a 70% increase in infection prevalence in the first spring generation (see supplement).

Our work suggests that shared habitat patches can reduce migratory monarch recruitment and compromise migrant health, with effects that reverberate beyond the areas where migrants and residents overlap. These effects may be countered by investment in maintaining and expanding high quality migrant habitat, including seasonal, native milkweeds that do not support winter-breeding residents. Fortunately, there is broad public interest in and concern for monarchs and their migration, as evidenced by robust engagement in existing volunteer monitoring programs and habitat management initiatives (Lewandowski & Oberhauser, 2017). Our findings highlight the need for locally targeted education and communication for members of the public who are interested in providing habitat for monarchs. While monarch host plants are needed, non-native milkweeds that promote monarch residency can harm the migrating population. Even when gardeners and landowners are aware that native milkweeds are preferable, native milkweed seeds and plants can be difficult to find and acquire commercially (Midwest Association of Fish and Wildlife Agencies, 2018). Seed bank and distribution programs like the Native Seed Network and Monarch Watch Milkweed Market are doing crucial work to close the gap between the public desire to create quality monarch habitat and the availability of local plants with which to do so. Expanding partnerships with commercial retailers to provide native plants could be an important next step to bring native milkweeds to land managers who may be less aware of or less likely to seek out specialized resources. Finally, while recent publications have shown great progress in documenting the spatial distribution of winter-breeding (Fyson et al., 2025; Momeni-Dehaghi et al., 2024), more research is needed into the abundance and persistence of resident monarchs and especially into their interactions with migrants and their influence on the infectious disease landscape.

Table 2.1: Model equations	
Migrant dynamics:	
Adults:	Larvae:
$\frac{dS_{AM}}{dt} = \alpha(1 - p_{mi}) + gS_{LM}(t - \tau_p)\rho - \delta S_{AM}((I_A + I_{AM})/A_{tot}) - \mu_S S_{AM} + s_d C_{AM} - \gamma S_{AM}$ $\frac{dI_{AM}}{dt} = \alpha(p_{mi}) + \theta g\left(I_{EM}(t - \tau_p) + I_{VM}(t - tau_p) + I_{HM}(t - tau_p)\right)\rho - \mu_I I_{AM} - \gamma I_{AM}$ $\frac{dC_{AM}}{dt} = \delta\, S_{AM}((I_A + I_{AM})/A_{tot}) - \mu_S C_{AM} - s_d C_{AM} - \gamma\, C_{AM}$ Departed adults: $\frac{dD_{SM}}{dt} = \gamma S_{AM}$ $\frac{dD_{IM}}{dt} = \gamma I_{AM}$ $\frac{dD_{CM}}{dt} = \gamma C_{AM}$ Where $\alpha = max(0, \frac{a_{max}}{\left(\frac{\tau_{mi}}{2}\right)^2}\left(t - \frac{\tau_{mi}}{2}\right)^2 + a_{max}$	$\frac{dS_{LM}}{dt} = 0.5b_s S_{LM}(t - \tau_e) + 0.5b_i(1 - p_v)I_{AM}(t - \tau_e) + 0.5b_s(1 - p_h)C_{AM}(t - \tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)S_{LM} - c\left(\frac{M_c}{M}\right)S_{LM} - gS_{LM}$ $\frac{dI_{VM}}{dt} = 0.5b_i p_v I_{AM}(t - tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_{VM} - gI_{VM}$ $\frac{dI_{EM}}{dt} = c\left(\frac{M_C}{M}\right)S_{LM} - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_{EM} - gI_{EM}$ $\frac{dI_{HM}}{dt} = 0.5b_s p_h C_{AM}(t - tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_{HM} - gI_{HM}$
Resident dynamics:	
Adults:	Larvae:
$\frac{dS_A}{dt} = gS_L(t - \tau_p)\rho - \delta S_A((I_A + I_{AM})/A_{tot}) - \mu_S S_A + s_d C_A$ $\frac{dI_A}{dt} = \theta g\left(I_E(t - \tau_p) + I_V(t - tau_p) + I_H(t - tau_p)\right)\rho - \mu_I I_A$ $\frac{dC_A}{dt} = \delta\, S_A((I_A + I_A)/A_{tot}) - \mu_S C_A - s_d C_A$	$\frac{dS_L}{dt} = 0.5b_s S_L(t - \tau_e) + 0.5b_i(1 - p_v)I_A(t - \tau_e) + 0.5b_s(1 - p_h)C_A(t - \tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)S_L - c\left(\frac{M_c}{M}\right)S_L - gS_L$ $\frac{dI_V}{dt} = 0.5b_i p_v I_A(t - tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_V - gI_V$

	$\frac{dI_E}{dt} = c\left(\frac{M_C}{M}\right)S_L - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_E - gI_E$ $\frac{dI_H}{dt} = 0.5b_s p_h C_A(t - tau_e) - \left(\mu_0 + \mu_d\left(\frac{L_{tot}}{M}\right)\right)I_H - gI_H$
Milkweed dynamics:	
$\frac{dM}{dt} = (r_1 + r_2)M\left(1 - \frac{M}{K}\right) - cL_{tot}$ $\frac{dMC}{dt} = \lambda\left(1 - \frac{M_C}{M}\right)(I_A + I_{AM}) - s_{dW}M_C - cL_{tot}$	

Table 2.2: Parameters

Symbol	**Definition**	**Value/Range**	**Unit**	**Reference**
β_s	Susceptible host fecundity rate * probability of egg surviving	9.208333*0.5	eggs/adult/day	[1-3, 6]
B_i	Infected host fecundity rate * probability of egg surviving	6.5195*0.5	eggs/adult/day	[3, 6]
τ_e	Time in egg stage	3	days	[4, 6]
τ_p	Time in pupal stage	7	days	[4, 6]
g	Larval development rate	1/9	1/day	[4, 6]
ρ	Probability of pupa survival to time of eclosion	0.76		[5, 6]
μ_S	Mortality of uninfected adult	1/24	1/day	[2, 6]
μ_I	Mortality rate of infected adult	1/20	1/day	[2, 6]
μ_0	Density-independent per capita larval mortality rate	-log(0.06)/9	1/day	[6]
μ_d	Density-dependent per capita larval mortality rate	1370	1/day	[6]
ϑ	Probability of infected adult successfully eclosing and mating	0.72		[6-7]
p_v	Probability of vertical transmission given infected mother	0.9		[6, 8]
p_h	Probability of contaminated adult infecting their offspring	0.614		[6, 8]
δ	Daily adult mating probability	1/2	1/day	[6, 9]
s_d	Spore decay rate on butterfly, rate of spore loss for contaminated adults	1/14	1/day	[6, 10]
r_{spr}	Tropical milkweed growth rate (spring)	0.032	leaves/day	[6]
r_{win}	Tropical milkweed growth rate (winter = 9 daylight hours and 10°C)	0.004	leaves/day	[11]
K	End of season number of milkweed leaves	18,000	leaves	[6]*
c	Larval consumption rate of milkweed	3.889	leaves / day	[10]

λ	Milkweed leaf visitation rate by infected adults (number of visits resulting in deposition of an infectious spore dose)	50	leaves / day	[6]
a_max	Peak migrant arrival rate	3	Butterflies / day	[12, 13]
γ	1/ residence time	1 / 4	1 / day	[13]*
p_{mi}	Initial infection prevalence in migrants	0.047 range: 0 = 0.2		[14]
τ_{win}	Duration of winter (non-migratory period)	90	days	
τ_{mi}	Duration of spring (migratory period)	40	days	[12, 13]

*Model patch is assumed to be a suburban area of approximately 3 hectare, including 90 milkweed plants across the landscape (as in Majewska, 2019). Plants are assumed to have an average of 36 leaves each, based on the average number observed when counting leaves on images of tropical milkweed plants submitted to Journey North or iNaturalist with monarchs present in the Southeast during the winter and an end-of-season maximum of 200 leaves each

* (rounded to nearest whole #)

Table 2.3: Initial Conditions:

S_0	1
I_0	1
C_0	0
M_0	36 leaves per plant / 90 plants
M_{C0}	0

No larvae or migrants present at model initiation.

Parameter References:

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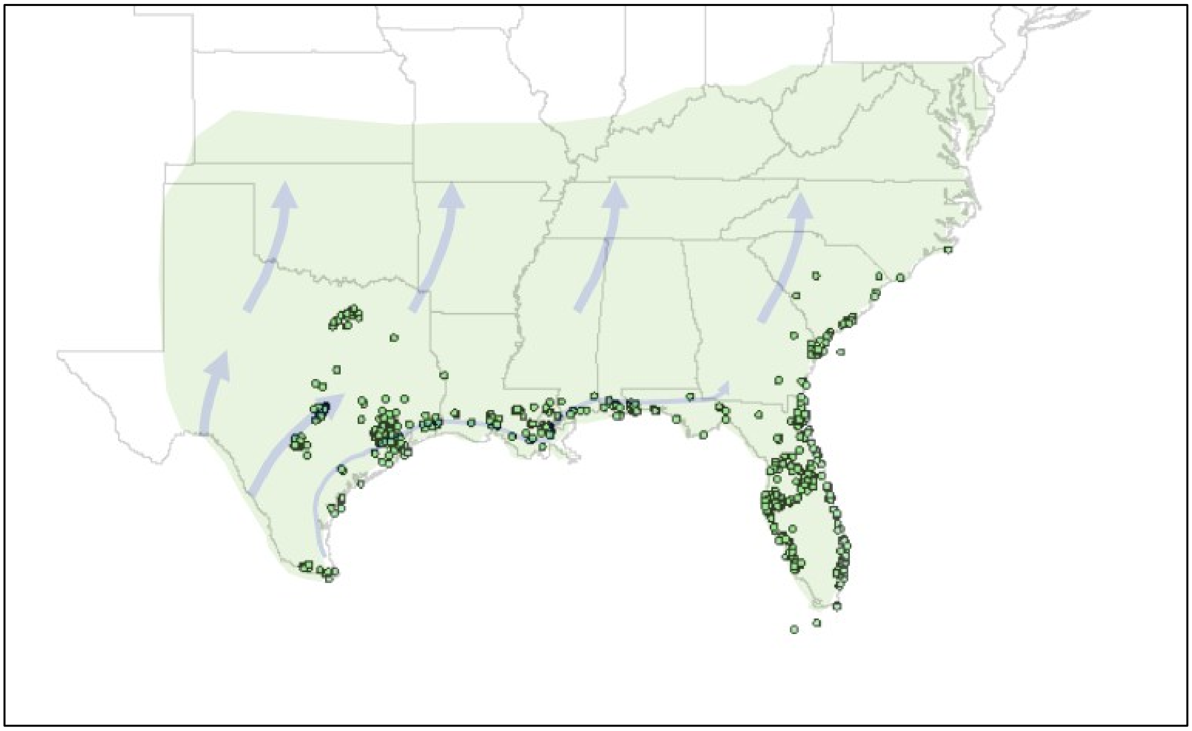
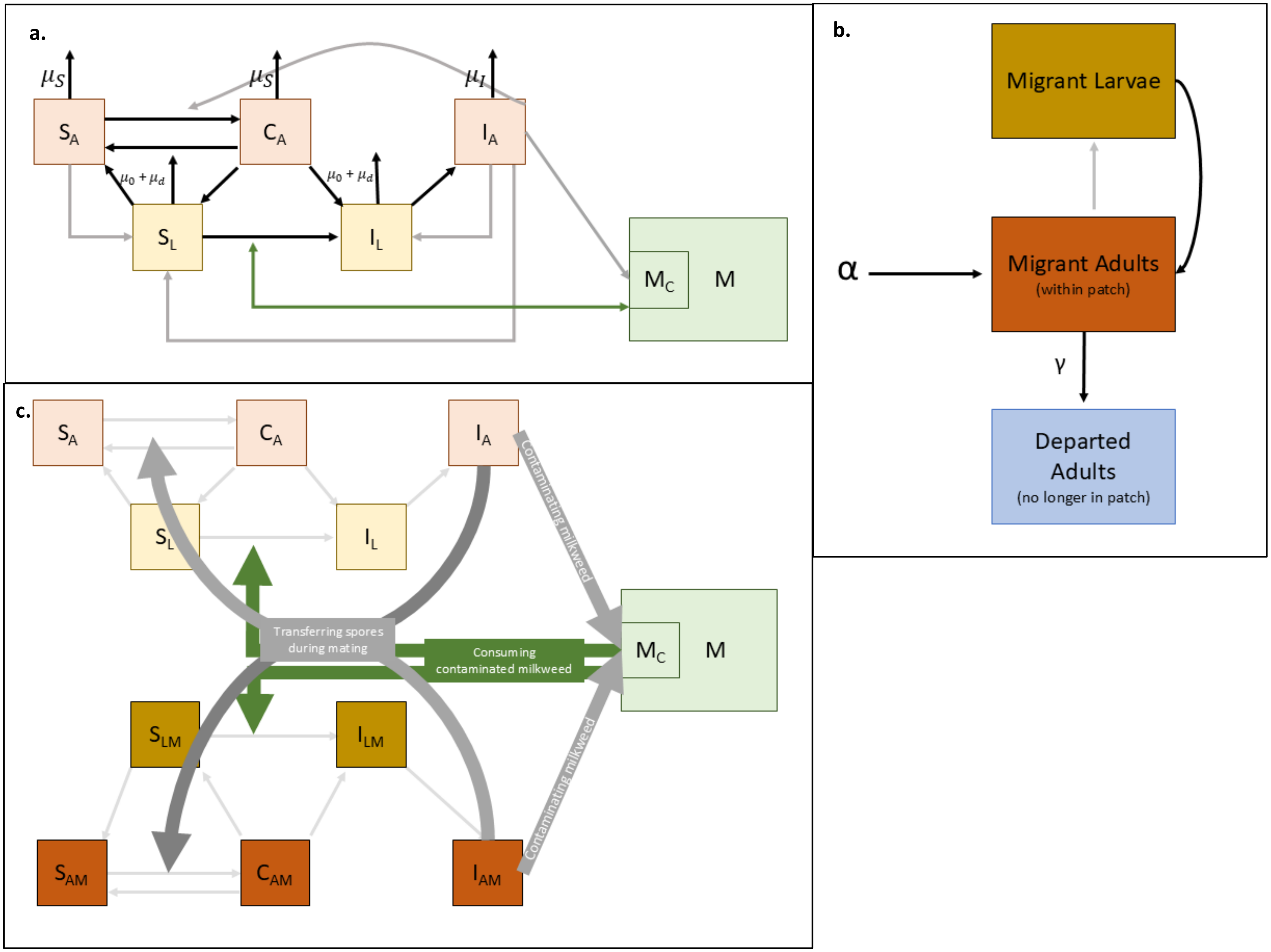


Figure 2.1: Map of the eastern North American monarch spring breeding range (green area). Blue arrows indicate migration routes and direction of recolonization. Points represent locations where winter breeding (as indicated by the presence of monarch larvae during December, January, or February), was reported in southeastern states between 2020 and 2023.

Figure 2.2: Schematics illustrating model structure. **a)** birth, death, and infection dynamics within a resident patch. Black lines show possible transitions between compartments, while grey lines show dependence of processes (reproduction, infection, contamination) on state variables. Green lines indicate consumption of contaminated milkweed by larvae. **b)** Flow of migrants through the patch and into the departed class. **c)** Infection dynamics within the shared patch, with an emphasis on connections and interactions between resident and migrant dynamics.


a.
μ_S
μ_S
μ_I
S_A
C_A
I_A
$\mu_0 + \mu_d$
$\mu_0 + \mu_d$
S_L
I_L
M_C
M
b.
Migrant Larvae
α
Migrant Adults
(within patch)
γ
Departed Adults
(no longer in patch)
c.
S_A
C_A
I_A
S_L
I_L
Contaminating milkweed
Transferring spores during mating
Consuming contaminated milkweed
M_C
M
S_{LM}
I_{LM}
Contaminating milkweed
S_{AM}
C_{AM}
I_{AM}

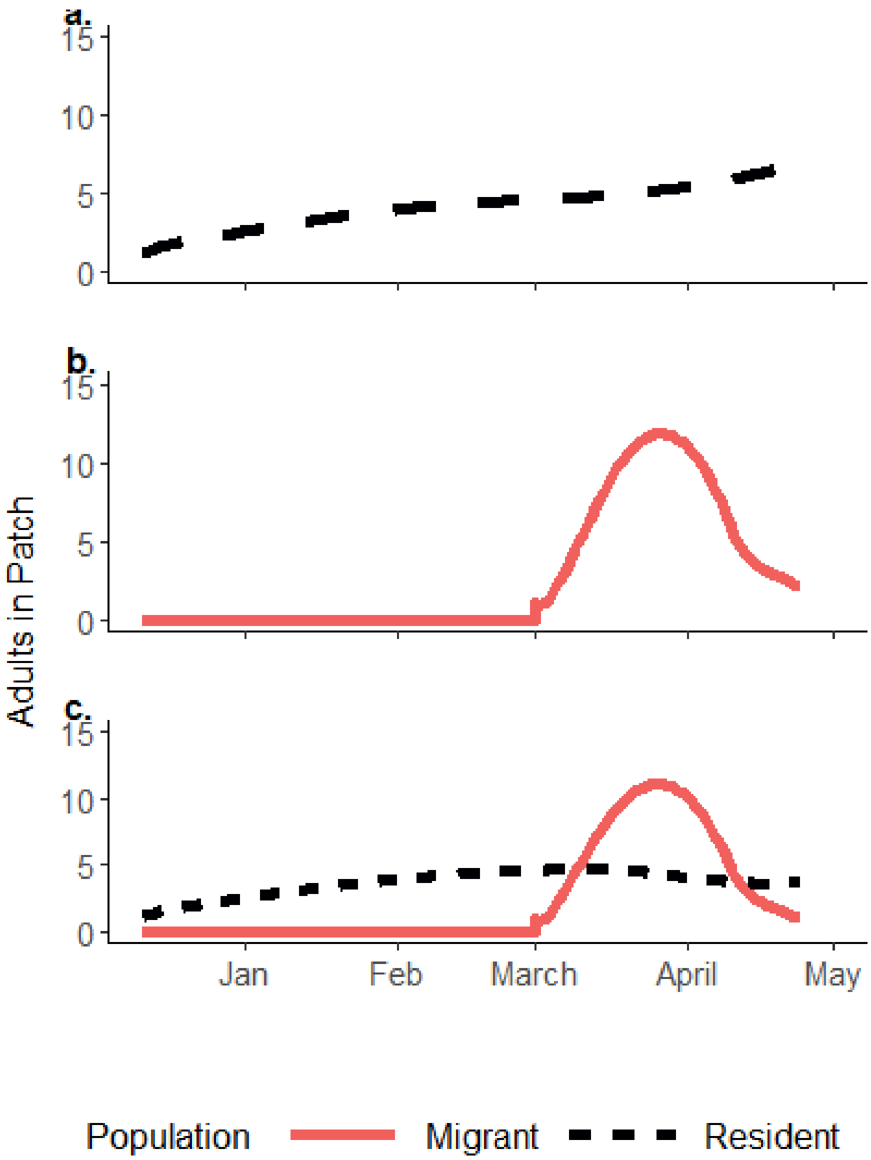


Figure 2.3: Modeled adult monarch abundance in a milkweed patch through the winter and spring seasons for three patch use scenarios: a) Scenario 1 - only residents use the patch, b) Scenario 2 - only migrants use the patch, and c) Scenario 3 – migrants and residents use the patch.

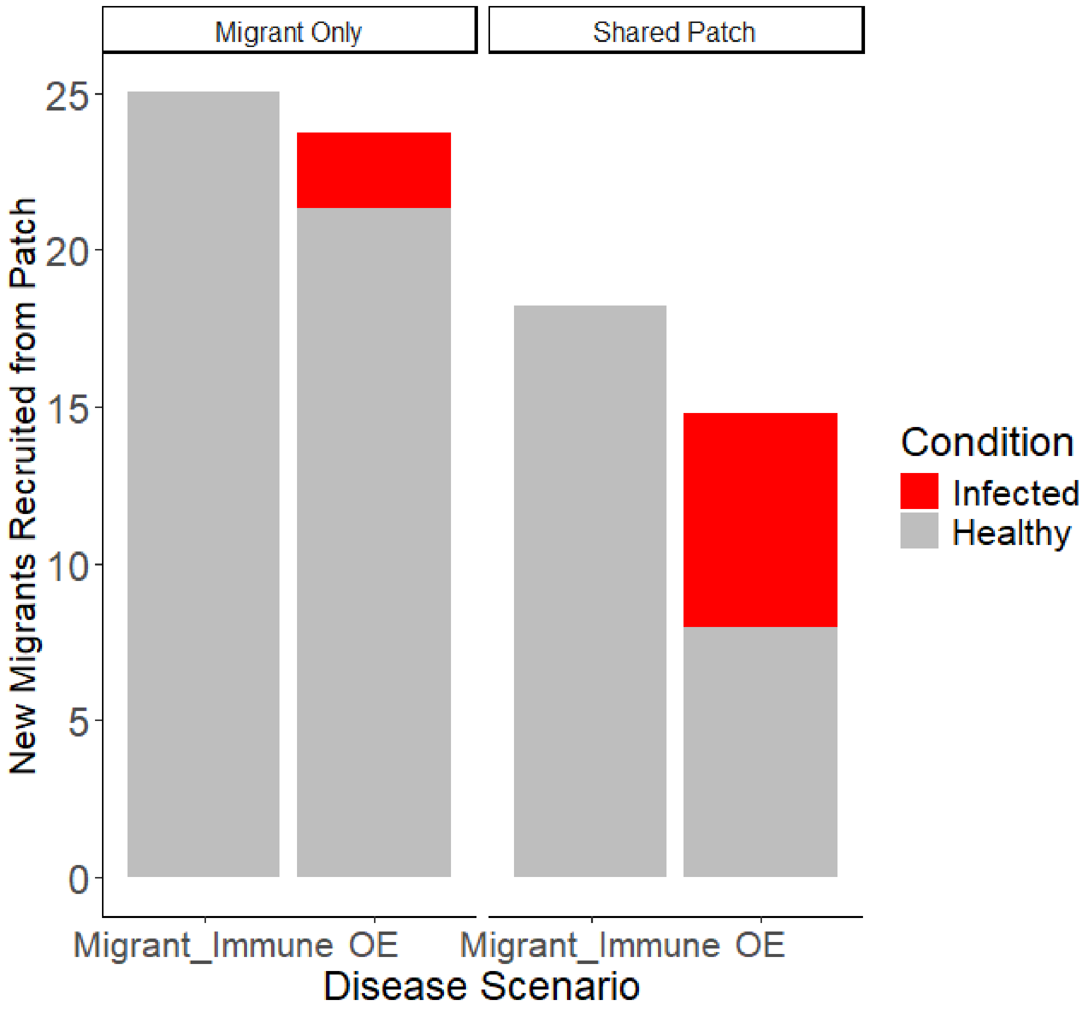


Figure 2.4: Recruitment of new migrants (all migrant individuals hatched in the patch that survived to enter the Departed class) from patches used by migrants only (left) and co-occupied by residents (right). Migrants that share habitat with residents show lower recruitment and higher infection prevalence. When disease is not a factor in migrant population dynamics (Migrant_Immune), patches used only by migrants still produce more recruits due to resource limitation.

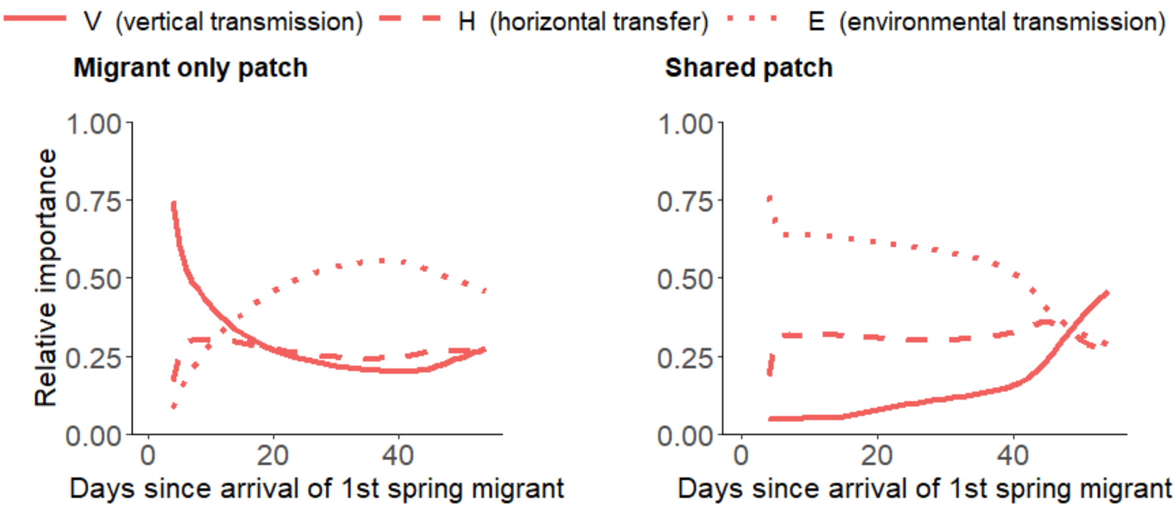


Figure 2.5: Changes in the relative contribution of each transmission route over the course of the migration season. Lines track the proportion of new cases (infected larvae) infected via each route over time. In the migrant-only scenario (left), vertical transmission (solid line) dominates early in the migration, after which its relative importance sharply declines. Environmental transmission (dotted line) is initially low and increases over time as the environment becomes more heavily contaminated. In the shared patch scenario (right), environmental transmission dominates in the migrant population until late in the migration. The contribution of horizontal transfer (dashed line), is intermediate across both scenarios.

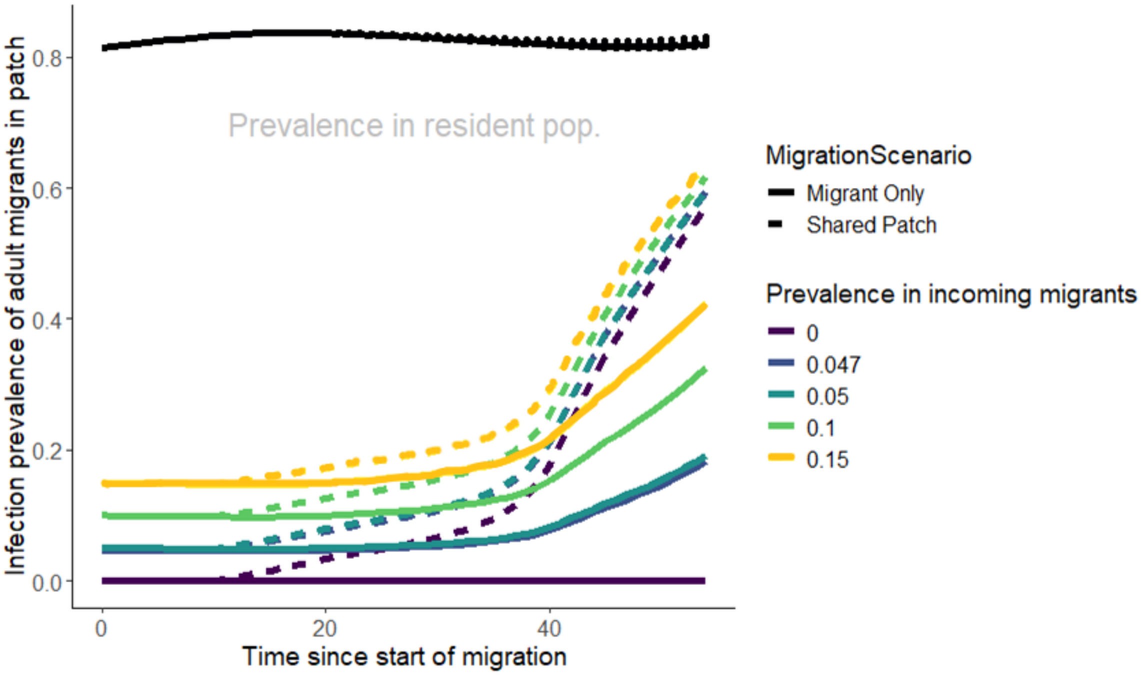


Figure 2.S1: Infection prevalence in adults within the patch changes with initial prevalence in incoming migrants. Infection prevalence in the shared patch (dotted line) increases more rapidly and is less sensitive to changes in prevalence in the incoming migrants than prevalence in the migrant only patch (solid line).

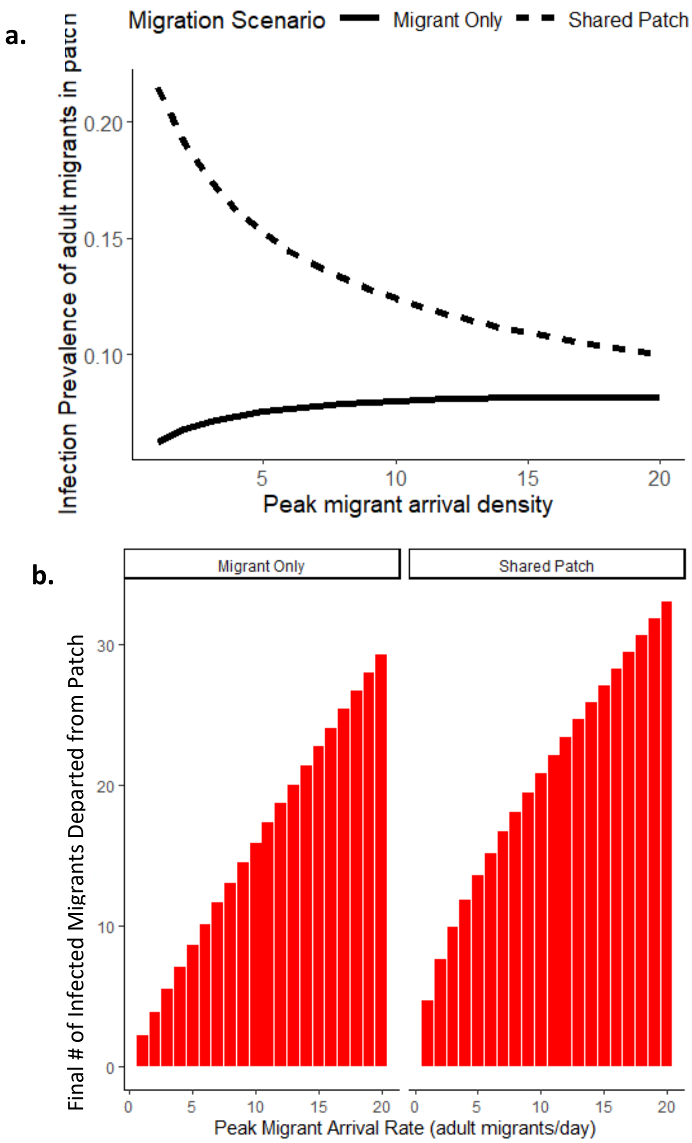


Figure 2.S2: In a migrant only patch, the average prevalence in the adult population over the migration season (**a.**) increases with increasing peak arrival density, while in a shared patch, prevalence declines as migrant arrival density increases. However, in both populations the absolute number of infected migrants departing the patch (**b.**) increases with increasing migrant arrival density and increasing total migrants.

CHAPTER 3:

DIFFERENTIAL HABITAT USE BY WINTER-BREEDING AND NON-BREEDING OVERWINTERING MONARCHS (DANAUS PLEXIPPUS) IN THE SOUTHEASTERN UNITED STATES[2]

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[2] Charlotte Hovland, Sonia Altizer. To be submitted to *Insects*.

Abstract:

While most eastern North American monarchs migrate to overwintering sites in central Mexico, monarch sightings are persistently reported in the southeastern United States throughout the winter. Some of these monarch sightings are associated with eggs and larvae, indicating continuous breeding over the winter; others are not associated with juvenile life stages and may belong to non-breeding overwintering populations in the Southeast. In this study, we used participatory science data to model the habitat conditions associated with both purported overwintering and winter-breeding monarchs in the southeastern US. We found that winter-breeding is positively associated with higher humidity, higher proportions of developed landcover, and higher human population density, while overwintering is specifically associated with wetland habitat in regions with warm climates. Through this work, we identify a need for more on-the-ground sampling in the Southeast during the winter, and particularly in wetland habitats.

Keywords: wintering, participatory science, habitat modeling

Introduction:

Overwintering behavior has allowed the North American monarch to survive from year to year, remaining reproductively dormant throughout the winter and then successfully recolonizing its breeding grounds each spring and summer. Since the eastern North American monarch's central Mexican overwintering grounds were first reported to the scientific community in 1976 (Urquhart & Urquhart), international efforts have formed to protect and monitor the overwintering monarchs and their habitat, alongside continued research, and an ecotourism industry dependent on the visually striking monarch aggregations (Brenner & López-Medellín, 2025; Lemelin & Jaramillo-López, 2020). The annual assessment of overwintering colony occupancy has become a valuable metric for estimating the size of the eastern North American monarch population, prompting widespread concern when, as in recent years, overwintering numbers are low (Fernández-Islas et al., 2024). However, a growing body of evidence suggests that eastern North American monarchs employ a diversity of overwintering strategies, including disaggregated overwintering in coastal environments in the southeastern United States, and, recently, winter-breeding where host plants are available (Bostian, 2023; Kendrick & McCord, 2018, 2023; Steele et al., 2023). If migratory monarchs are able to successfully overwinter in alternative, coastal overwintering sites, observations of the Mexican overwintering population may not be sufficient to characterize the overall health and stability of the eastern North American monarch migration. At the same time, the establishment of winter-breeding monarch populations throughout the southeast has the potential to alter infectious disease dynamics across the landscape (see Chapter 2) as well as changing monarch phenology in eastern North America. As land conversion and climate change alter monarch habitat, it's important to understand how monarchs are using winter habitats in the Southeast, to be aware of the unique threats that monarchs using these habitats may face, and to appreciate the impacts of southeastern overwintering and winter-breeding monarchs on the overall condition of the eastern North American monarch population. In this chapter, we attempt to leverage volunteer-reported monarch sightings in the winter (Dec – Feb) in the southeastern United States in order to characterize the habitat used by monarchs for winter-breeding and for local overwintering.

Winter-breeding occurs when late fall monarchs do not enter reproductive diapause and instead continue to reproduce between December and February (Satterfield et al., 2015). Winter-breeding was first reported in North American monarchs east of the Rockies by Lincoln Brower in 1961, describing what is now known as the South Florida resident population. However, winter-breeding has increased in recent decades to become common across the US Southeast (Fyson et al., 2025; Momeni-Dehaghi et al., 2024; Satterfield et al., 2015; Satterfield, Maerz, et al., 2018; Steele et al., 2023). Prior research indicates that winter-breeding in eastern North America is associated with anthropogenic influence (Steele et al.,

2023) and especially with the provisioning of non-native tropical milkweed (*Asclepias curassavica*) (Batalden & Oberhauser, 2015). *A. curassavica* does not reliably undergo seasonal senescence in the winter so long as temperatures remain warm, and exposure to *A. curassavica* has been linked to increased reproductive development in experiments on larvae reared under simulated fall-like conditions and on wild female migrants (Majewska & Altizer, 2019). Laboratory experiments have also found increased reproductive development in wild-caught female migrants held under warm conditions, even in the absence of milkweed (Rich et al., 2025). The emergence of winter-breeding has been met with concern for several reasons. Winter-breeding monarch populations have been found to sustain very high prevalence of the specialist protist parasite, *Ophryocystis elektroscirrha* (O.E.) compared to summer-breeding monarchs, fall migrants, and migrants at the Mexican overwintering sites (Majewska et al., 2022; Satterfield et al., 2015). Additionally, it’s been suggested that the adoption of a winter-breeding strategy may be favored not only by available milkweed resources, but also by stressors that decrease migration success and select against attempting a full migration and overwintering prior to investing in reproduction (Steele et al., 2023).

In contrast to winter-breeding, eastern coastal overwintering has been attested since at least 1873, when R. Thaxter reported large numbers of monarchs roosting through January in a pine forest in Apalachicola, Florida, before mating in the area in February (reviewed in Brower, 1995). After 150 years, eastern coastal overwintering (as opposed to coastal overwintering in southern California by western North American monarchs), has still only been described from a few sites -- indeed, in his 1995 review of the monarch migration, Lincoln Brower describes the search for overwintering populations in Florida as ‘frustrating.’ In recent seasons, overwintering monarchs have been observed in northeastern Florida, not far from Apalachicola (Bostian, 2023; Satterfield et al., 2015), as well as in maritime habitat on barrier islands in South Carolina (Kendrick & McCord, 2018, 2023). Tagging studies in maritime South

Carolina by Kendrick and McCord (2023) found that winter monarchs on the barrier islands had a low prevalence of mating compared to monarchs tagged during fall and spring in the same locations and had a long residence time with a 48% recapture rate. Additionally, Satterfield et al. found that infection with *Ophryocystis elektroscirrha* was rare in monarchs sampled at purported overwintering sites in Florida and South Carolina and the infection prevalence was comparable to that in Mexican overwintering populations, rather than winter-breeding populations nearby in the Southeast (2015).

Much of what is known about monarch overwintering physiology and behavior comes from studies carried out at the Mexican overwintering sites. While overwintering, monarchs are squeezed by a thermal tolerance that is limited on both ends: cold kills, but excess heat increases monarchs' metabolism, compromising the lipid reserves that they need to sustain themselves through the winter (Anderson & Brower, 1996; Brower et al., 2008; Masters et al., 1988). They roost in oyamel fir, pine, and cedar trees, whose cover protects them from temperature extremes and bird predation (Alonso-Mejla et al., 1998; Anderson & Brower, 1996; Calvert & Brower, 1981). Aggregating densely, they form clusters that maintain internal microclimates, buffering the butterflies from temperature extremes and protecting them from desiccation (Brower et al., 2008). Although some mating occurs during the overwintering period, most migrants at the Mexican overwintering sites remain in reproductive diapause until a mass-mating event that occurs as the colonies break down in February (Hook, 1996). Monarchs that overwinter at alternative, coastal overwintering sites in the Southeast experience similar environmental challenges to those in the Mexican overwintering sites. Overwintering monarchs in Mexico can survive at body temperatures down to a limit of about -8°C, but suffer mortality at warmer temperatures if they are wet (Anderson & Brower, 1996; Brower et al., 2008; Larsen & Lee, 1994). Similarly, Ray Moranz found that overwintering monarchs in Florida can survive to about -8.9°C before exhibiting high mortality (Bostian, 2023). However, Kendrick and McCord did not observe monarchs clustering at the South Carolina overwintering sites that they studied, and it’s not clear that aggregation is a common feature of overwintering outside of Mexico and the western coastal overwintering sites in California (Kendrick & McCord, 2023). More research is needed to better understand how monarchs withstand winter conditions at eastern coastal overwintering sites.

Participatory science (also known as citizen science or community science) volunteer observers have contributed greatly to our understanding of monarchs across North America (Ries & Oberhauser, 2015), through platforms and projects including: iNaturalist, JourneyNorth, Monarch Larvae Monitoring Project (MLMP), North American Butterfly Association (NABA) counts, Monarch Watch tagging, Project Monarch Health, and others. However, participatory science datasets often have known biases, from a tendency of users to report more sightings on the weekends (Courter et al., 2013), to uneven sampling effort across areas with different human population densities, accessibility, or appeal for volunteer observers (Phillips et al., 2009; Tracy et al., 2022). Additionally, several community monarch science platforms are designed to collect opportunistic sighting data that is generally presence-only (Tang et al., 2021). Despite these challenges, participatory science data has been a valuable resource for monitoring winter monarch behavior. For example, two recent papers, Momeni-Dehagi et al., using data from Journey North and Monarch Larva Monitoring Project (2024), and Fyson et al., using data from iNaturalist, Journey North, and Mission Monarch (2025), utilized volunteer observations to map the extent of winter-breeding in the U.S. Southeast.

The purpose of our study is to leverage participatory science data to better understand monarch winter behavior, including both winter-breeding and coastal overwintering, in the southeastern US. We categorized all adult monarch observations from Journey North and iNaturalist reported in Florida, Georgia, Texas, Alabama, Mississippi, Louisiana, North and South Carolina, and Tennessee between December and February of in the winters of 2019 – 2025 (Sheehan & Weber-Grullon, 2021; Dec 2021 and later by personal communication from Nancy Sheehan and Jacob Swason) by winter behavior (purported winter-breeding vs. purported overwintering) and used publicly available landcover and climate data to link habitat conditions with breeding status. We then fit models to determine which habitat characteristics distinguished breeding from overwintering monarchs in the volunteer-collected dataset. These models help us understand how winter-breeding and coastal overwintering monarch habitat use differs in the US Southeast and can inform where to look in search of overwintering monarchs.

We predicted that coastal overwintering sites would be cool and humid, with comparable climate conditions to those at Mexican overwintering sites (Kendrick & McCord, 2023). We also predicted that coastal overwintering sites would be found within short distances of the coastline and in forested areas, as canopy cover is important for protection and temperature regulation in Mexican overwintering monarchs (Alonso-Mejla et al., 1998; Anderson & Brower, 1996; Calvert & Brower, 1981). Finally, we predicted that winter-breeding would be associated with warmer temperatures (Rich et al., 2025) and with medium and low intensity developed landcover, where urban gardens could provide access to imported tropical milkweeds (Majewska & Altizer, 2019).

Methods:

a) Monarch observations and breeding status assignment:

Monarch sightings were submitted to Journey North (n = 3616) by volunteer observers and uploaded to iNaturalist (n = 2490) as part of ongoing participatory science initiatives. Sightings are opportunistic and observers report presence only. Observations were restricted to nine states in the US Southeast: Texas, Florida, Louisiana, Georgia, North and South Carolina, Tennessee, Mississippi, and Alabama, during Northern Hemisphere meteorological winter (December 1 to February 28/9) (Figure 3.1; Figure 3.S1).

We used sighting data from the years 2019-2024 to train models. Winter 2024 - 2025 data was set aside as a testing dataset (n = 846 for full dataset). We limited our dataset to recent years to avoid effects of change over time in climate, in reporting methods, and in the monarch population over the full span of Journey North's and iNaturalists' records, which date back to 1994 and 2011, respectively. Additionally, the Monarchs OVERwintering in the Southeast (MOVERS) Working Group, a collaboration between Journey North, Monarchs Across Georgia, the University of Georgia, and the Georgia Department of Natural Resources, began a public awareness campaign to solicit winter observations of monarchs in the Southeast in December 2020, initially directing the public to report to Journey North (2020-2024), and later to either Journey North or iNaturalist (2024-2025) (GA Department of Natural Resources, 2020, 2024). As a result of these efforts, winter sampling effort of monarchs by volunteer observers is likely to have increased in recent years.

We classified each sighting based on whether or not the sighting showed evidence of winter breeding, following the decision tree schematic in Figure 3.2. For observations that included photographs or written comments, we manually reviewed each picture and written description for signs of winter reproductive activity, including mating, oviposition, and pupation/eclosion of fresh adult monarchs. Observations in which reproductive activity was evident in the attached photograph or clearly described in comments were automatically classified as year-round breeding with high confidence (n = 1125). Using ArcGIS Pro (ESRI Version 3.5.0) we also assessed year-round breeding using sighted adult monarchs' proximity to juvenile life stages (eggs, larvae, and pupae) reported during the same winter. The presence of juveniles was taken as indirect evidence for winter-breeding within sites. Adult monarchs reported within 1 km of juveniles were also classified as winter breeding, albeit with only moderate confidence (n = 1235). Finally, because reproductive monarchs are thought to travel on the order of 12 km during the breeding season (Zalucki et al., 2016), we classified adult monarchs reported between 1 km and 2.5 km from winter-hatched juveniles as winter breeders with low confidence, as it was possible, though not evident, that they could be the parents of the juveniles in question (n = 495). We also assigned confidence levels to 'non-breeding' observations. We assigned high confidence to observations from sites where coastal overwintering was attested in the literature or by trusted collaborators, including: Panacea, FL, Alligator Point, FL, Albany, GA, and Folly Beach, SC (Kendrick and McCord, 2018; Bostian, 2023; personal communication: Anna Yellin, Ilse Gebhard, Russ Schipper). We then assigned low confidence to observations that occurred within 2.5 kilometers of an observed juvenile during any winter in the dataset (2019-2025). Finally, we assigned moderate confidence to the remaining non-breeding observations. Individuals of other species misidentified as monarchs were manually removed following review of attached photographs.

b) Site characteristics:

We associated each monarch adult sighting with local habitat characteristics, including land cover composition surrounding the location of the sighting, as well as distance to the coastline, human population density by US Census block group (U.S. Census Bureau, 2025), and winter weather data at the location.

We analyzed land cover data from the 2022 National Land Cover Database (hereafter NLCD) (U.S. Geological Survey (USGS), 2024). Starting from NLCD land cover classifications on a scale of 30m x 30m, we used ArcGIS Pro to calculate the proportion of land cover represented by high-, medium-, and low- density urban development, open urban land (e.g. parks and greenspaces), agricultural pastures, forests, herbaceous grasslands, and wetlands, across the Southeast. Because adult monarchs are mobile, we assessed the proportion of each land cover type in the area surrounding each sighting on two spatial scales – a 1 km radius and a 2.5 km radius (following Majewska et al., 2019). For sightings within a 2.5 km radius of the US-Mexico border, we included Mexican land cover data from the intergovernmental Commission for Environmental Cooperation's (CEC) North American Land Change Monitoring System and Mexico's Instituto Nacional de Estadística y Geografía (INEGI) (Commission for Environmental Cooperation (CEC), 2024; INEGI, 2018). We also calculated the distance from each sighting location to the nearest coastline, using the continent boundary layer from the ESRI location data portal.

Human population density by block group was sourced from the 2020 United States (U.S. Census Bureau, 2025).

We pulled daily weather data for each pair of sighting coordinates from Daymet's Daily Surface Weather Data report (Thornton et al., 2022) using the R package daymetr (Hufkens et al., 2018). We then calculated the average winter high and low temperatures for each site as well as the number of days with lows below freezing during the meteorological winter (Dec 1 to Feb 28) of 2020-2021, 2021-2022, and 2022-2023 (Daymet data was not available past 2023). For further analysis, we averaged the high and low temperatures and freeze days for each site across all three winters. Relative humidity and precipitation as snow were accessed from ClimateNA using the package ClimateNAr and the ClimateNA API (version 7.60) for the period: Normal 1991-2020 for the winter season (Daly, 2008; Hijmans et al., 2005; Wang et al., 2016).

c) Model selection:

Following Fondell et al., 2010, we constructed candidate habitat models in two stages. In the first stage, we considered only land use factors, including land cover and population density. We fit logistic regression models to the data using the full set of land use variable combinations but excluded any models in which correlated variables appeared together (Pearson's correlation coefficient >= 0.5). The 2.5 km radius scale landcover data consistently fit better in single variable landcover models and all subsequent landcover models were fit with the 2.5km scale data only. We fit the models on the 2019 – 2024 training data. All numeric predictors were normalized as part of model preprocessing.

Ranking the models by AIC, we propagated the top 25 models to the next stage of model selection, however, we excluded any models for which the delta AIC fell within +/- 2 of a simpler, nested model, to avoid propagating uninformative variables (Arnold, 2010). In the second stage of model selection, we added climate variables (winter relative humidity, precipitation as snow, average winter high and low temperatures, number of winter days with temperatures below freezing, and distance to the coast) to each of the 25 remaining candidate models, individually and in combination where variables were not correlated.

Out of the set of 513 models considered across both stages, we used all models with a $\Delta AIC \leq 6$ to predict the classification of the winter 2024-2025 observations and calculated the ROC-AUC for each model (Symonds & Moussalli, 2011). Again, we excluded models in which the addition of a variable did not lead to better performance by at least 2 delta AIC.

We performed the same model selection protocol across four subsets of our data:

1. The full set of winter observations in the Southeast from 2019-2024 (n = 6097)
2. The full set of winter observations excluding those observations for which the breeding/non-breeding classification was ranked as ‘low confidence.’ (n = 5589)
3. Temperate zone observations: winter observations from areas of the Southeast with USDA Plant Hardiness Zones of 7b – 9b (n = 3505)
4. Hot zone observations: winter observations from areas of the Southeast with USDA Plant Hardiness Zones of 10a-12a (n = 2592). This dataset included observations from the known South Florida winter resident population (Knight & Brower, 2009) as well as some sites in South Texas and coastal Louisiana.

All models were fit in R version 4.5.1 (R Core Team, 2025) using the packages tidymodels (Kuhn & Wickham, 2020) and multilevelmod (Kuhn & Frick, 2022).

Results:

Monarchs were observed throughout the Southeast during the winters of 2019-2025, with the majority of observations coming from Florida and Texas (Figure 3.1a). Observations appeared to follow the Gulf Coast from Florida to Texas as well as the Atlantic Coast from Florida north into the Carolinas. Observations were assigned to both winter-breeding and non-breeding overwintering throughout the meteorological winter (Figure 3.1b), although reported sightings were more rare after the end of December, especially above 30°N latitude (Figure 3.S1).

Our model selection protocol resulted in 3 competitive models fit to the full dataset, 3 competitive models fit to the dataset with low confidence observations excluded, only 2 competitive models fit to the data from temperate regions, and 7 competitive models fit to the data from hot regions (Table 3.1). The Akiake weight of subsequent models quickly declined in lower ranked models. All competitive models were moderately accurate at predicting the breeding status of the 2024-2025 winter test observations. The models fit on the data that excluded low-confidence observations performed best, with ROC-AUCs values between .748 and 760. The accuracy of the models fit with the full dataset was comparable to that of the models fit to the temperate and hot data subsets (ROC-AUC ranges: .643–.652, .653-.654, and .606-.679, respectively).

Some variables had consistent effects across models and data subsets; however, the models fit with data from hot climates only generally behaved differently from the models fit to either the temperate data or data from across the full climate range. Across all models, the most significant predictors of breeding status were relative humidity, population density, proportion developed landcover of various classes (high density, medium density, and low density), and proportion of landcover occupied by wetlands (Figure 3.3).

Relative humidity was present in all competitive models fit with the full dataset, the data subset excluding observations with low confidence breeding status, and the temperate data subset, and was highly significant in all of these models ($p < 1e-16$) (Figure 3.3). Model coefficient estimates for the effect of relative humidity were consistently positive (Figure 3.4), meaning that higher relative humidity was associated with a greater probability that an observation would be identified as a winter-breeding monarch. Relative humidity was only a predictor in one of the competitive models fit with the ‘hot’ data.

Human population density (by US Census block group) was present as a predictor in 12 out of the 14 models we deemed competitive across the 4 data (sub)sets. Higher population density was always associated with a greater probability of winter-breeding (Figures 3.4, 3.5). Sightings in areas with different population densities were unevenly distributed between temperate and hot regions – the highest density census block groups came from the Miami, FL metropolitan area in USDA plant hardiness zone 11b. Population density had the highest estimated effect size of all the coefficients included in the two models fit with temperate data and was highly significant in these models ($p < 1e-22$).

The effects of landcover development on predicted breeding status varied, but were largely positive, predicting a greater probability of winter-breeding in developed areas. In two out of the three competitive models fit to the full dataset, medium-intensity development was the most significant predictor of breeding status ($p < 1e-34$). High-intensity and low-intensity development were also positively associated with winter-breeding in models fit to the full dataset, to data excluding low confidence observations, and to data from temperate regions. However, landcover development was not strongly predictive of breeding status in observations from hot regions.

The best ranked models fit to data from hot regions all included the proportion of nearby landcover classified as wetland. When considering observations from hot regions only, wetland cover was consistently the most significant predictor of breeding status (p value range: 5.37e-15 to 2.50e-21) and monarchs observed in wetland habitats were less likely to be winter-breeding.

Despite published accounts of overwintering monarchs on maritime islands (Kendrick & McCord, 2018, 2023), and the importance of wetlands in models fit to the hot data subset, distance to the coastline was not a strong predictor of winter-breeding/overwintering status and did not feature in any of the models in our final, competitive set. However, because distance to the coastline was correlated (>.5) with all the climate variables that we considered, the influence of proximity to the coast on meteorological conditions could be reflected in the models that include relative humidity, mean winter high temperature, mean number of days with temperatures below freezing, and precipitation as snow. Counter to our expectations, forest cover was also not a strong predictor of non-breeding overwintering status, appearing in only 3 of 14 competitive models considered across all 4 data subsets.

Interestingly, the proportions of winter-breeding and overwintering observations reported between the two sources of data, Journey North and iNaturalist, were not equal (p = 2.2e-16). Of the two, observations made to Journey North were more commonly classified as winter-breeding monarchs. One possible explanation for this discrepancy is that Journey North users, who are participating in a monarch-specific project, are more interested in monarchs than the typical iNaturalist user and are either more motivated to check for juvenile life stages in the areas where they observe adult monarchs, or are better able to identify juveniles when they find them. Additionally, volunteer monarch observers are also often maintainers and creators of monarch habitat, establishing milkweed patches, protecting natural monarch habitat, and enriching naturally occurring habitat patches with additional host and nectar plants (Lewandowski & Oberhauser, 2017). As a result, Journey North volunteers may be more likely than iNaturalist users to actively create and maintain landscapes which including milkweed that could be used for breeding.

Discussion:

In this study, we used winter sightings of adult monarchs from across the Southeast, submitted by volunteer contributors to Journey North and iNaturalist, as well as publicly available landcover and climate data, to model monarchs' use of habitat for winter-breeding and non-breeding overwintering. Using these data, we developed models that use information about the location of a winter monarch sighting to diagnose the monarch's breeding status. While imperfect, these models perform better than chance. Our results suggest that relative humidity and urbanization are positively associated with winter-breeding, and that wetlands may provide important habitat for non-breeding overwintering monarchs in very warm regions of the southeastern United States. However, there are also caveats to our analysis that highlight the challenges of working with opportunistically collected, presence-only data.

Human population is known to be a common confounding factor in analyses using opportunistic, volunteer-sourced data, as observer effort is not evenly distributed across the region of study (Isaac et al., 2014; Momeni-Dehaghi et al., 2024; Phillips et al., 2009; Tang et al., 2021; Tracy et al., 2022). We attempted to reduce the impacts of uneven observer effort and missing absence data by comparing presence to presence: anywhere where an adult monarch was observed was a location where we knew at least one observer had been present and had made an observation. In other words, rather than asking, 'where are monarchs breeding in the winter,' our models pose a slightly different question: given that someone sees a monarch in the winter, are there habitat factors that predict whether or not that monarch is breeding? This approach is different from and complementary to other recent studies which have used participatory science to address the extent of winter-breeding, including Momeni-Dehaghi et al. (2024), which used larval monarch occurrence data from Journey North and the MLMP and Fyson et al. (2025), which used egg, larval, and pupal observations from Journey North, iNatualist, and Mission Monarch.

Human population density was included as a predictor in 12 out of 14 of our final, competitive models, with higher population densities universally predicting higher probabilities of winter-breeding. This is consistent with the idea that winter-breeding monarchs are generally using anthropogenic resources and rely on humans to provide and maintain their host plants (Batalden & Oberhauser, 2015; Steele et al., 2023). However, it may still be the case that uneven observer effort is biasing our results when it comes to the effects of human population density. Where more observers are present, they have more opportunity to observe juvenile monarchs. Given that we used proximity to observed juveniles in our criteria for assigning breeding status, it's possible that more monarchs were diagnosed as winter-breeding in higher population areas because their offspring were better represented in the data. Conversely, butterflies that we assigned as 'overwintering' in less populous areas could be winter-breeding butterflies with few observers present to find and record their offspring. Overall, our models cannot differentiate winter-breeding and non-breeding overwintering monarchs any better than we can, and our original designations are dependent on observers either catching monarchs in the act of reproduction and taking note of their behavior or observing and reporting juvenile monarchs where they are present. It's very likely that many of our purported 'overwintering' monarchs are winter-breeding monarchs whose offspring and breeding behavior went unobserved. Using the data that we have, it is difficult to disentangle possible real effects of human population density on monarch behavior from observation biases.

Relative humidity was also consistently positively associated with winter-breeding. This aligns with Momeni-Dehaghi et al.'s conclusions from their occupancy modeling work, in which they found that snowfall and relative humidity were the most important variables for predicting winter-breeding monarch occupancy in eastern North America, although, unlike them, we did not find a large impact of precipitation as snow (2024). Desiccation is a danger to overwintering monarchs (Brower et al., 2008), and we had expected high relative humidity to be equally important to both winter-breeding and non-breeding overwintering monarchs. However, nymphalid butterfly eggs have been shown to have greater hatching success under more humid conditions (Clark & Faeth, 1998), so it is possible that wintering monarchs observed in less humid environments are reproductively active but are less likely to produce surviving larvae.

A striking feature of our models was the prominence of wetland landcover as a predictor of non-breeding overwintering in USDA hardiness zones of 10 and above only. Several published accounts of non-breeding overwintering take place in wetland environments in more temperate zones (Brower, 1995; Kendrick & McCord, 2018, 2023), and wetlands have been identified as important roosting habitats for eastern North American fall migrants (Boxler et al., 2024, 2025), but it was unexpected for wetlands to be associated with non-breeding overwintering specifically in warm regions, which, in our study, included southern Florida, southern Louisiana, and southeastern Texas. Field research aiming to locate and assess overwintering monarchs in these regions may benefit from focusing on wetland habitats. Unfortunately, wetlands in the southeast are imperiled by development, as well as sea level rise and extreme weather driven by climate change (Kyzar et al., 2021; White et al., 2022). Our findings suggest that these habitats may be more important to monarch overwintering than previously appreciated and should be prioritized for conservation.

Compared to the monarchs of the large, central flyway, we know relatively little about monarch migration and wintering behavior between the Appalachian Mountains and the Atlantic coast (Boxler et al., 2024, 2025; Kendrick & McCord, 2023). While some of these butterflies may participate in an alternative migration through the Caribbean (Dockx et al., 2023), there is evidence that some butterflies remain in the southeastern United States to overwinter in a non-breeding state (Kendrick & McCord, 2018, 2023; Satterfield et al., 2015). These southeastern overwintering populations could serve as an important redundancy for the Mexican overwintering population, especially in the context of continued concerns about Mexican overwintering numbers and threats to the oyamel fir forest habitat (K. Oberhauser & Townsend Peterson, 2003; Inamine et al., 2016; but see Crossley et al., 2022). Additionally, diversity in overwintering behavior represents potential for monarchs to adapt to changing conditions in the future as climatic conditions and species distributions are predicted to shift (Pérez-Miranda et al., 2017; Zylstra et al., 2022). It is essential for us to better understand monarch overwintering behavior in the southeastern United States if we are to conserve and maintain populations using these alternative wintering sites. Participatory science is a powerful tool for monitoring and investigating these monarchs, even as volunteer-sourced data comes with biases and limitations. In our study, we attempt to use volunteer observations to distinguish between habitat used by non-breeding overwintering monarchs in the southeast and habitat that supports winter-breeding – a recent phenomenon with troubling implications for monarch health (Satterfield et al., 2015, 2016; Steele et al., 2023). While our results have not yet been validated in the field, it is promising that we were able to identify differences in habitat between adult monarchs that were classified as winter-breeding vs. non-breeding and to predict breeding status on the basis of habitat characteristics with better than random success. This work should inform future field studies that will ground test our conclusions. If validated, our findings can help researchers target sites to look for overwintering monarchs, which must be located and identified before they can be researched and conserved.

Table 3.1: Model performance metrics for all models with a ΔAIC ≤ 6 relative to the top performing model for each dataset

Model	**Δ AIC**	**Akaike weight**	**ROC-AUC**
Full dataset			
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, LC_Forest2pt5k, LC_Wetland2pt5k, RH_wt, PAS_wt	0	0.391	0.652
LC_DevMed2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, Temp_AverageHighC, RH_wt, PAS_wt	1	0.237	0.653
LC_DevMed2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, RH_wt, PAS_wt	4	0.053	0.643
Excluding low confidence observations			
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, LC_Forest2pt5k, LC_Wetland2pt5k, RH_wt, PAS_wt	0	0.192	0.748
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_AgPasture2pt5k, LC_Herb2pt5k, LC_Wetland2pt5k, RH_wt, PAS_wt	3	0.043	0.760
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, LC_Forest2pt5k, LC_Wetland2pt5k, Temp_AverageHighC, RH_wt	6	0.010	0.760
Temperate region observations			
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevOpen2pt5k, LC_Herb2pt5k, RH_wt, PAS_wt	0	0.288	0.653
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_DevOpen2pt5k, RH_wt, PAS_wt	5	0.024	0.654
Hot region observations			
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_AgPasture2pt5k, LC_Herb2pt5k, LC_Wetland2pt5k, Temp_meanFreezeDays	0	0.0543	0.679
PopDensitySqmi_2020, LC_DevLow2pt5k, LC_AgPasture2pt5k , LC_Wetland2pt5k	2	0.0200	0.616
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_AgPasture2pt5k, LC_Herb2pt5k, LC_Wetland2pt5k	3	0.0121	0.656
LC_DevLow2pt5k, LC_DevOpen2pt5k, LC_AgPasture2pt5k, LC_Wetland2pt5k	5	0.0045	0.643
PopDensitySqmi_2020, LC_DevLow2pt5k, LC_Wetland2pt5k, RH_wt	5	0.0045	0.622
PopDensitySqmi_2020, LC_DevHigh2pt5k, LC_AgPasture2pt5k, LC_Wetland2pt5k	6	0.0027	0.651
PopDensitySqmi_2020, LC_AgPasture2pt5k, LC_Herb2pt5k, LC_Wetland2pt5k	6	0.0027	0.606

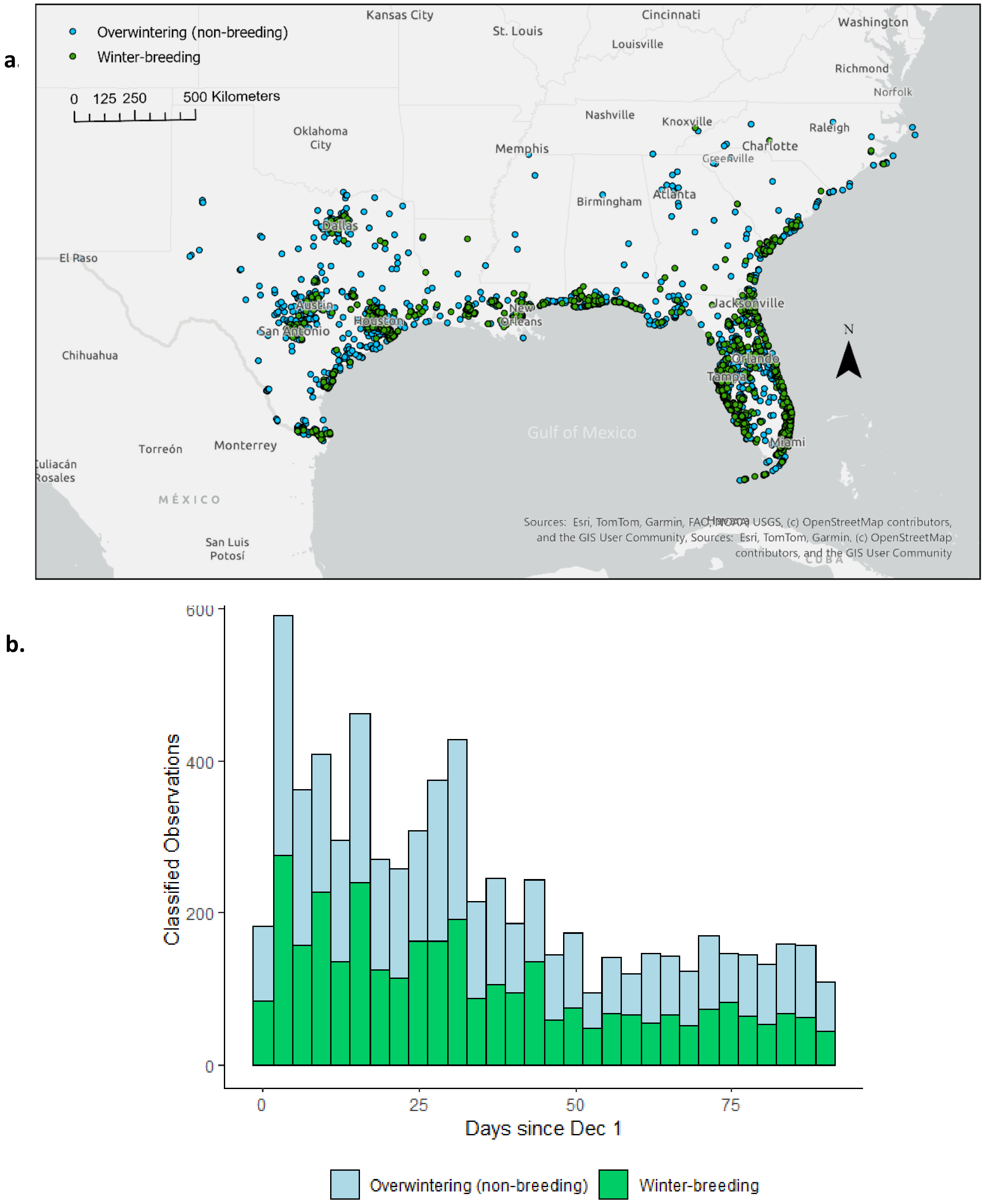


Figure 3.1: Winter monarch observations (2019 – 2025), distributed in space **(a)** across the southeastern US and time **(b)** throughout meteorological winter (Dec 1 – Feb 28/9). Most observations were reported from Florida and Texas as well as the US Gulf Coast. More monarchs were reported early in the winter, but sightings of both non-breeding (blue) and winter-breeding (green) monarchs continued to occur throughout the season.

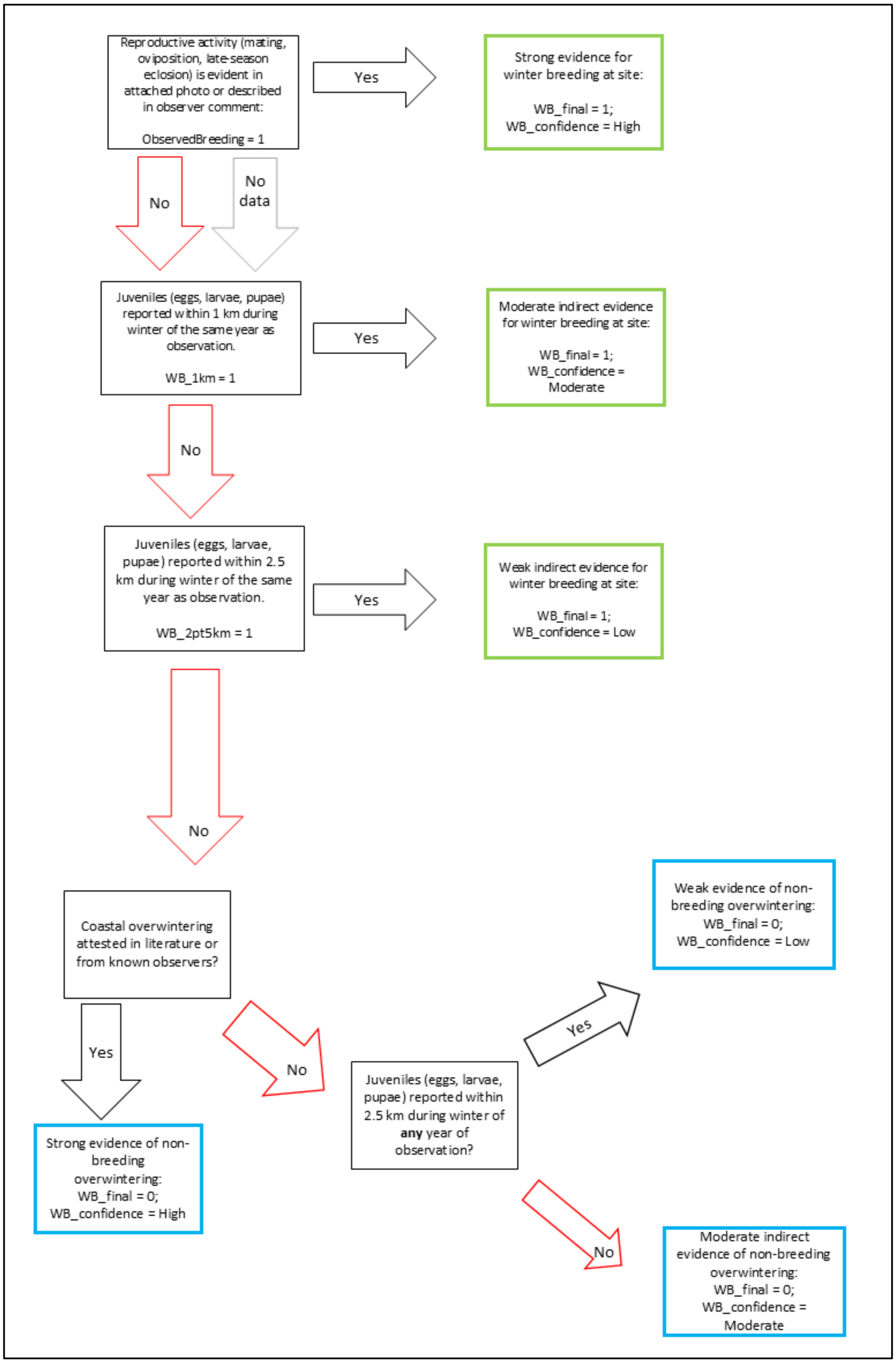


Figure 3.2: Flow chart illustrating criteria used to assign winter-breeding vs. overwintering status (0 = overwintering, 1 = winter-breeding) and confidence (Low, Moderate, High).

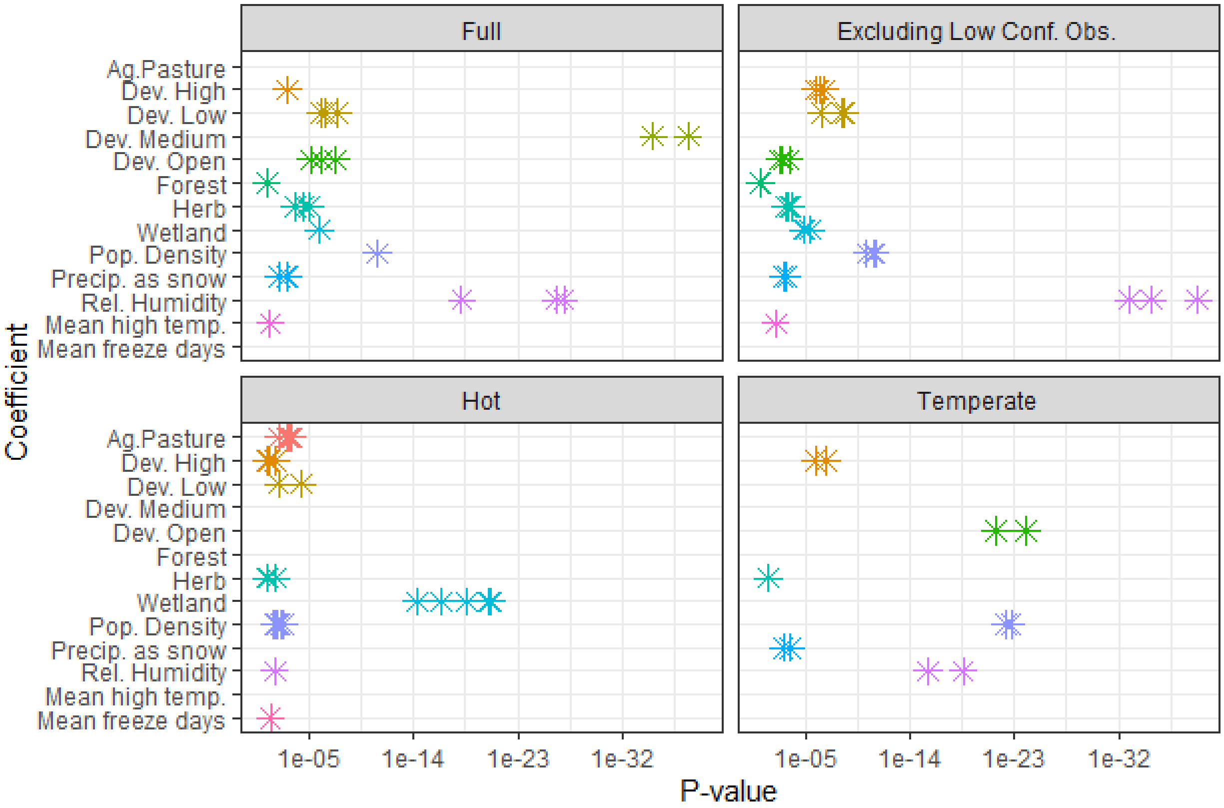
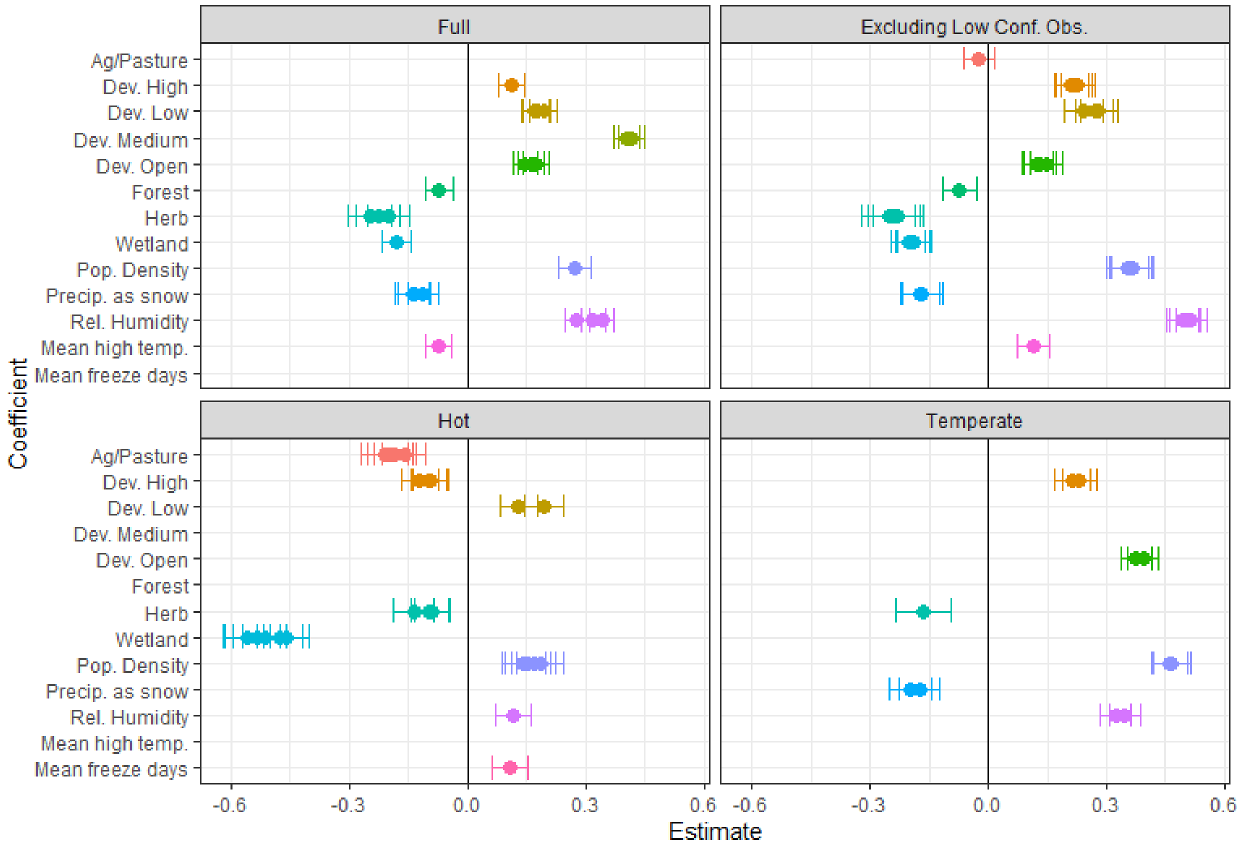


Figure 3.3: Comparing the significance of all significant (p ≤ 0.05) variables included in top-ranking competitive models (ΔAIC ≤ 6) fit to each subset of winter-breeding and overwintering observations.



Winter-breeding: Less probable ⟷ More probable Less probable ⟷ More probable

Figure 3.4: Estimated coefficient values for all variables included in top top-ranking competitive models ($\Delta AIC \leq 6$) fit to each subset of winter-breeding and overwintering observations. Positive values indicate variables that contribute to a greater probability of observed winter-breeding. Error bars represent standard error.

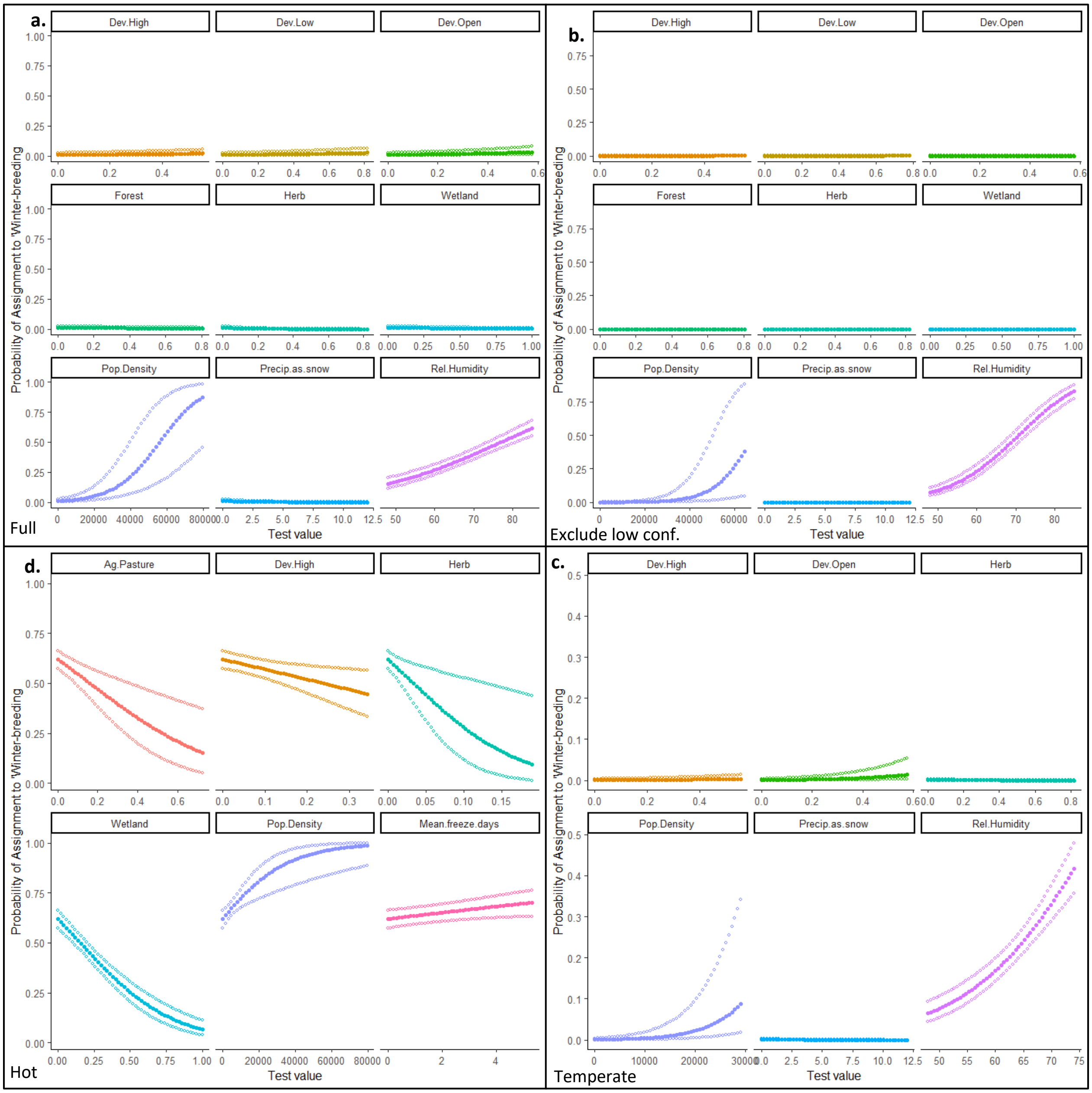


Figure 3.5: Effects of each variable included in the best fitting model fit with each subset of the data, clockwise from top-left: **a)** full dataset, **b)** excluding low confidence observations, **c)** temperate zone observations, **d)** hot zone observations. Variables vary over the range observed within each dataset. Predicted probabilities are plotted along with the upper and lower bounds of a 95% confidence interval.

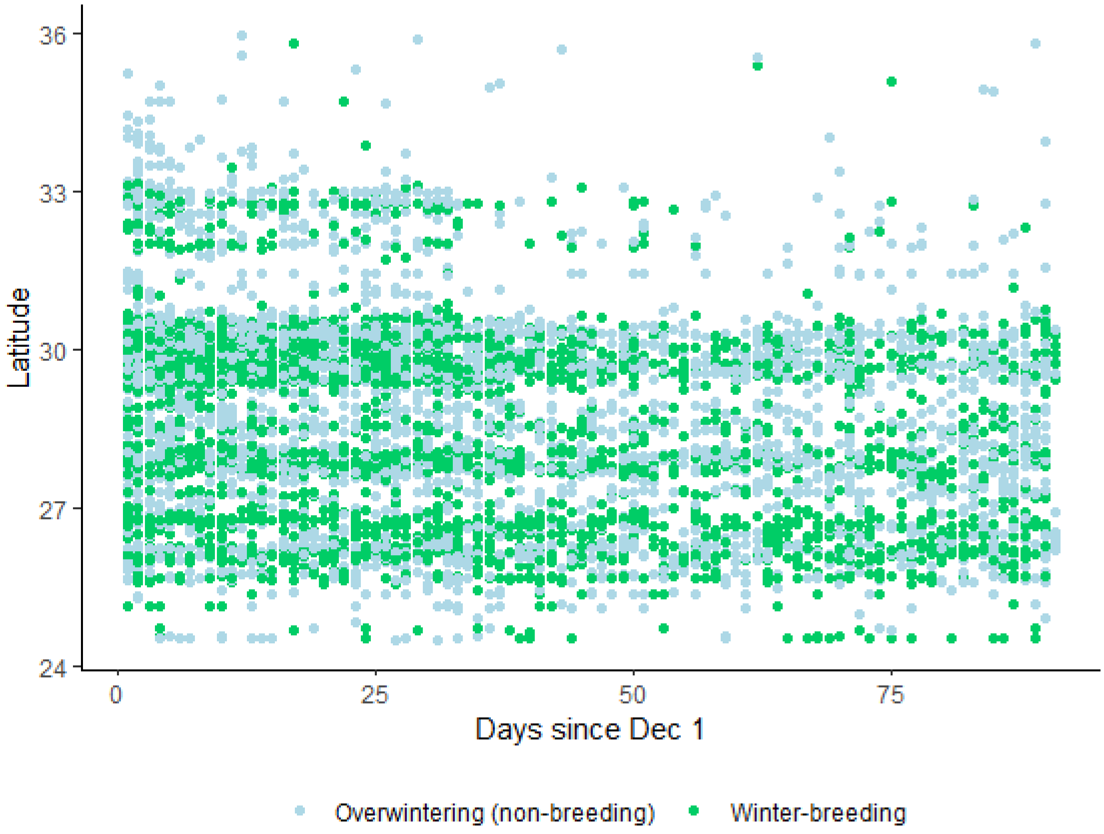


Figure 3.S1: Latitude of individual observations by days since the start of meteorological winter for the Northern hemisphere. Observations from above 30°N become rare after the end of December.

CHAPTER 4:

GENERAL CONCLUSIONS

Although they may not be as visually striking as the clustered overwintering monarchs of Central Mexico, monarchs that spend the winter in the southeastern United States may still influence the persistence of the migration phenomenon. Over the course of the preceding studies, I have used both data analysis and theoretical modeling to explore what monarchs are doing in the winter in the Southeast: breeding, or remaining non-reproductive, and to assess what consequences their winter breeding activity may have for the migratory monarchs in the region.

Through modeling interactions between winter-breeding resident monarchs, returning spring migrants, and their parasites, I found that cohabitating with residents in a simulated milkweed patch depressed migrant recruitment into the next generation. In the model, migrant abundance was negatively impacted both by competition with residents for milkweed resources and by increased parasite prevalence in the presence of residents. These findings support concerns that winter-breeding residents could pose a threat to the health of migratory monarchs, especially as winter-breeding is expected to expand under climate warming (Momeni-Dehaghi et al., 2024). My modeling work allows us to anticipate a time in which many more migrants may share spring breeding habitat with the offspring of winter-breeding populations.

Leveraging volunteer observations from across the Southeast, I identified habitat characteristics that are associated with winter-breeding and with non-breeding overwintering. This analysis carries caveats – our habitat models cannot identify breeding status any more keenly than the original observers whose data they were trained on. However, my findings align with ideas connecting winter-breeding to human occupancy and developed land uses (Batalden & Oberhauser, 2015; Steele et al., 2023) and additionally suggest that wetland habitats may be hotspots for non-breeding overwintering monarchs in the warmest regions of the US Southeast.

Both studies raise new hypotheses that can be put to the trial of further observation. For example: can lower O.E. prevalence be observed in early generation spring monarchs during years when severe winter frosts reduce the population of winter-breeding residents? Or, if we conduct field surveys of targeted Gulf Coast wetlands, might we identify additional alternative overwintering sites for non-reproductive monarchs?

Questions like these fall within a broader need for further research into monarchs in the southeastern United States. In their 2024 proposed ruling on threatened species status for the monarch, the US Fish and Wildlife Service specifically solicited responses regarding the “resident monarchs in southern Florida, the Gulf Coast, the southern Atlantic Coast, and the southern Pacific Coast,” classifying them as a source of uncertainty for the overall status of the species in the US (United States Fish and Wildlife Service, 2024). And, as much as remains to be learned about resident winter-breeding monarchs, even less is known about non-breeding overwintering monarchs in the Southeast. It will take additional research, perhaps with the increasingly advanced monarch tagging and tracking techniques now available, to determine where the monarchs that use these overwintering sites come from and whether they contribute to the spring migration in return. If it is found that habitat in the Southeast can truly provide functional alternative sites for eastern migratory monarch overwintering, these sites should be prioritized for conservation in order to maintain the full richness of monarch behavioral diversity and provide redundancy for the monarch migration in eastern North America.

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APPENDIX A

CHAPTER 2 SUPPLEMENT: SCALING ACROSS A REGION WITH MIXED PATCH TYPES

Introduction: Using the results of our model, we conducted back-of-the-envelope calculations in an attempt to lay some rough bounds on the impact of shared migrant-resident breeding habitat across a regional scale. We made several major simplifying assumptions during this process, and these results should not be understood as earnest infectious disease forecasts, but rather as a starting point for further exploration.

Methods: Assuming that migrant monarchs are equally as likely to visit milkweed patches that are occupied by residents as they are to visit patches without residents, the effect of patch sharing across the spring-breeding range should vary with the proportion of spring-breeding habitat where both resident and migrant monarchs overlap. For different assumed extents of habitat sharing within the range, we projected the effect of habitat sharing on infection prevalence after one generation using the patch-hatched prevalence values from the modeled shared patch and migrant only patch scenarios and the following equation: Predicted Population Prevalence = (Habitat Overlap Proportion)*(Prevalence in Shared Patch) + (1 – Habitat Overlap Proportion)*(Prevalence in Migrant-Only Patch)

Results: A conservative habitat overlap estimate of 0.1% resulted in an estimated increase in population-wide infection prevalence of 0.35% in the 1st spring generation. Assuming 5% habitat overlap, we projected an increase of 17.55%. Finally, at a 20% overlap, where 1 in 5 returning migrants shares habitat with year-round residents, we projected a 70.20% increase in O.E. infection prevalence in the spring generation.

Discussion: Our estimates are approximate and rest on highly reductive simplifying assumptions, but our findings do suggest that sharing patches with resident monarchs, even in relatively small proportions of the migratory monarch spring breeding range, could contribute to increased O.E. prevalence across the eastern North American monarch subpopulation. The monarch winter-breeding range is expected to expand under climate warming and may soon constitute a greater proportion of total monarch spring breeding habitat (Momeni-Dehaghi et al., 2024).

Table 2S1: Predicted Prevalence in Population as Migrant and Resident Habitat Overlap Increases

Habitat Overlap Proportion	Predicted Prevalence in Offspring Gen.*	Increase in Prevalence*	% Increase in Prevalence
0.1 %	0.102	0.0004	0.35 %
0.5 %	0.104	0.0018	1.75 %
1.0 %	0.106	0.0034	3.51 %
5.0 %	0.120	0.018	17.55 %
10.0 %	0.138	0.034	35.10 %
20.0 %	0.174	0.072	70.20 %

Predicted Population Prevalence = (Habitat Overlap Proportion)(Prevalence in Shared Patch) + (1 – Habitat Overlap Proportion)*(Prevalence in Migrant-Only Patch)

*Relative to predicted prevalence at 0% resident-migrant overlap (0.102)