**An atmospheric circulation framework contextualizes swings in monarch butterfly migration success**

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## **Abstract**

Climate change induced shifts in atmospheric circulation such as the Northern Hemisphere Jet Stream (NHJ) result in increased variability of regional and seasonal surface climate, with broad implications for the survival and reproduction of organisms. For migrating insects, which have a body temperature varying in response to environmental conditions and rely on plant resource availability along their migration route, there is a high likelihood that shifts in NHJ generate profound changes in annual population size. Despite the apparent importance of a circulation-centric framework, particularly given a rapidly changing climate, there are few analyses on the effects of atmospheric processes on insect migration and abundance. Here, we compare the interannual variability in monarch butterfly roosts observed at multiple points during the southern fall migration to Mexico, with the latitudinal position of monthly NHJ over North America (NA), to…. NHJ position during summer breeding (August, September), and fall migration (September) influenced roosting numbers along the migratory path annual overwintering acreage. More monarchs return to Mexico when NHJ positions (northern NHJ over eastern NA in August and southern NHJ over western NA in September) lead to warming in the breeding grounds of eastern NA. Southern NHJ over central NA in September increased precipitation along the migration corridor, possibly leading to increased nectar resource availability. Our findings provide evidence for spatially and temporally dynamic impacts of atmospheric circulation on insect migration and help contextualize non-climate related conservation interventions such as habitat restoration and land use in a warming world. The largest impacts of the jet stream are on climate over the summer breeding grounds in the midwestern and Northeastern united states and fall southern migratory path. In

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## **Main**

Global climate change has profound ecological consequences, many of which relate to changes in temperature and precipitation patterns that are critical to resource timing and availability for organismal survival and reproduction. For example, anthropogenic warming moves surface temperature thresholds in both latitude and elevation, influencing both the range and area of species’ distributions (Horton et al., 2015; Lemoine, 2015; Malcolm, 2018), while also leading to trends in plant and animal phenology (Horton et al., 2015, Piao et al., 2019). Beyond warming at breeding and overwintering grounds and along migration corridors, migrating animals will likely continue to be experiencing an increase in the intensity and frequency of extreme weather events (La Sorte et al., 2016), such as heat waves and hurricanes, enhancing droughts, wildfires, and flooding across large spatial scales (Coumou and Rahmstorf, 2012; Abatzoglou and Williams, 2016). In the Northern Hemisphere (NH) midlatitudes, the interannual variability and regional distribution of weather and extreme weather events can be influenced by the Northern Hemisphere Jet stream (NHJ) (Kornhuber et al., 2019), high-speed westerlies in the tropopause. The NHJ forms a barrier between pressure systems, with warm tropical air (high-pressure, anti-cyclonic areas) typically to the south and cool polar air (low-pressure, cyclonic areas) to the north (Belmecheri et al., 2017). Northward and southward NHJ latitude positions designate changes in regional and seasonal temperature and precipitation patterns. In recent decades, the NHJ has shown a more variable, meandering, and sinusoidal pattern, creating conditions for seasonally persistent, unusual weather patterns and extremes that are more widespread and regionally connected (Coumou and Rahmstorf, 2012; Francis and Vavrus, 2012; Francis and Skific, 2015; Horton et al., 2015; Wang et al., 2015; Röthlisberger et al., 2016; Wang et al., 2017; Mann et al. 2017; Mann et al., 2018; Trouet et al., 2018).

Transcontinental animal migrations rely on regionally connected weather conditions (Strong et al., 2015) and are therefore highly likely to be threatened by the impacts of climate change (La Sorte et al., 2016, Malcolm, 2018; Horton et al., 2019). This type of migration is difficult to investigate as animals move through multiple habitats often at low density over months until finally settling together in high density for breeding and/or overwintering. For migrating insects, which have a body temperature varying in response to environmental conditions and rely on plant resource availability along their migration route, there is a high likelihood that shifts in NHJ generate profound changes in annual population size.

The eastern monarch butterfly migration is one of the most iconic and endangered long-distance insect migrations (Voorhies et al., 2019; Fig. 1). In February and March, monarchs leave their overwintering grounds in the forest highlands of central southern Mexico. A small portion of monarchs veer to the west of the North American Cordillera (Lyons et al., 2012; Billings, 2019) while the eastern monarchs begin a multi-generational migration north (Fig. 1). In the fall, the fourth or fifth generation of eastern monarch migrates south from the upper midwest and northeastern US, traveling thousands of miles to return to the overwintering grounds. From 1994 to 2020, there has been a negative trend in the total area occupied by monarch colonies at their overwintering sites in Mexico (Fig. 2C), a key metric in considering monarch population size and migration success. This has prompted organization and implementation of a collaborative monarch conservation effort between Canada, Mexico, and the United States facilitated by public demand (Solis-Sosa et al., 2019). There are many factors contributing to the monarch migration declines, including changes in land use, disease, and pesticide use (Pleasants et al., 2017, Thogmartin et al., 2017). However, the decline is also punctuated by large inter-annual variability which has been linked with climate along the migration route and at breeding and overwintering grounds (Thogmartin et al., 2017; Malcolm, 2018; Saunders et al., 2019; Zylstra et al., 2021). The decline in monarch population numbers is absent in summer population estimates at breeding grounds (Saunders et al., 2019), leading researchers to ask how climate in late summer at breeding grounds and along the fall migration are driving the decline in overwintering acreage (Saunders et al. 2019; Zylstra et al., 2021). [add journey north citizen science roosting products] Both temperature and precipitation are known to affect monarch survival and reproduction at the population level, yet much less is known about how those processes scale to a region, while weather as it relates to climate is seldom included in models of monarch butterfly systems (Grant and Bradbury, 2019). These potentially large swings in population response due to seasonal climate across a continent can mask the success of conservation and restoration efforts of the monarch butterfly (Heffernan et al., 2014; Inamine et al., 2016).

Here, we created an atmospheric circulation-centric framework to describe the inter-annual variability of the eastern monarch migration across North America, towards improving sub-seasonal predictability of annual migration success, and to assist with comprehending the future climate variability monarchs will experience. We hypothesize that the latitude of the monthly NHJ can influence monarch migration success, primarily by driving both surface temperatures and precipitation variability at critical junctures in the migration timeline and locations, such as summer breeding grounds and along spring and fall migration corridors. We correlated three proxies for monarch population throughout the migration (roosting observed in August, September, and overwintering acreage estimates in Mexico) with climate variables: monthly temperatures (maximum, minimum, average), precipitation, ndvi, surface windspeeds, and the NHJ- defined as the latitudinal position of the maximum zonal wind speed at 300hPa at 2.5° longitudinal resolution (See Methods). While these time series currently have a 20-year period of overlap from 2002 to 2021, we found that the strongest relationships between the monarch roosting data and regional climate occurred over the 15-year period 2004-2018, and we move forward using this period. Studies using the same winter population size estimates but different estimates for late-summer populations have also found this period to be strongest (Zylstra et al. 2020). The collection agencies reporting overwintering acreage transitioned in 2004 to the WWF- Telcel Alliance in coordination of the Monarch Butterfly Biosphere reserve.

For spring, summer, and fall, monthly NHJ influences the interannual variability of overwintering acreage (p<0.1, Fig. 1, Table 1). Positive correlations (red polygons in Fig 1b) indicate that northern (southern) NHJ lead to higher (lower) overwintering acreage (Fig.1a), while negative correlations (blue polygons) indicate that southern (northern) NHJ lead to lower (higher) overwintering acreage. In the spring, as monarchs begin to leave their overwintering grounds and migrate North (Fig. S2a), they benefit from northern NHJ in February over western NA (125-100°W), southern NHJ in March over western NA (120-105°W), and northern NHJ in April over eastern NA (77.5°W). Cooler temperatures in March in northern Texas confine egg laying to southern latitudes, which may be ideal for monarchs via egg development because of warmer temperatures, as well as a lower mean age to first reproduction, which typically implies populations will grow quickly. Moving into the summer breeding months (Fig.S2a), monarchs benefit from northern NHJ in June over eastern NA (97.5-77.5°W), southern NHJ in July over western NA (122.5°W), northern NHJ in August over eastern NA (102.5 -72.5°W), and southern NHJ in September over western NA (120-115°W). The fall migration South begins in September and October (Fig. S2b). Monarchs benefit from a southern NHJ in September over central NA (105-97.5°W), and a northern NHJ in October over western NA (122.5-112.5°W) and eastern NA (67.5-65°W) (Fig. 1).

We now focus our attention to the potential mechanisms behind fall (August – October) NHJ position influence on overwintering acreage (Fig. 2, Fig. S2, Fig. 3). We find that late summer and autumn NHJ can lead to high monarch returns to the overwintering grounds by characterizing 1) warmer average and minimum temperatures in August (northern NHJ) and September (southern NHJ) over the breeding grounds of northeastern US and southeastern Canada (Fig. 2), as well as 2) cooler temperatures and more precipitation in September along the migration route in central North America (Fig.3), and 3) warmer temperatures in October in western US and less precipitation along the migration route (Fig. 4).

When we examine the most recent year, 2018, we notice warmer average and minimum temperatures in August and September as well as cooler temperatures along the migration route, contributed to larger overwintering acreage (Fig. S3). Years of low monarch overwintering hectares feature cooler temperatures in the breeding grounds in August and September, and/or drier conditions along the migration corridor in September (e.g. 1997, 2000, 2004, 2009, Fig. S3). Some weather events in one part of the season can negate the positive effects of other months. For example, in 2002, warmer breeding grounds in August in September (which typically indicate higher monarch return) preceded an extremely southern NHJ in October which led to temperatures that were up to 4°C cooler and a low monarch return (Fig. S2).

In August (late summer), Generation 5 monarchs are immature (eggs, larvae, and pupae) and start to prepare for their southern migration (Fig. S2). This generation differentiates from generations 1-4 in a variety of morphological and physiological traits such as wing size, wing strength, lipid reserves, and navigation through a different developmental pathway. As with many insects, temperature and relative humidity have an important influence on the success of this developmental plasticity. We saw a strong influence of NHJ latitude on surface temperatures in August and September in the breeding grounds of northeastern US and Canada and of those surface temperatures on monarch return (Fig. 2; Fig. S1). In August, the NHJ directly above the breeding ground (longitude 102.5-72.5°W) was positively correlated with monarch return and surface temperatures, where a northern (southern) NHJ led to warmer (cooler) temperatures and higher (lower) monarch acreage (Fig. 2a). Warmer August temperatures for a broader northeastern region (Fig. 2a, Fig. S1) may increase the core breeding distribution suitable for monarchs by widening the region of plant availability and survival (Lemoine et al., 2015), as well as monarch physiology and development. Beyond expanding viable habitat, these warmer August temperatures are likely better for monarchs preparing for a southward migration in the next month by providing a longer time window for monarchs to reach adult maturity and migratory status. At this time, the future migrating monarch is viable from 20-30°C, with survivorship steeply declining above or below these temperatures (Zalucki, 1982). Within that range, monarch development is fastest and uniform with warmer temperatures (Zalucki, 1982), with a lower likelihood and frequency of frost events. While correlation values extended above 50°N, it is unlikely that the future migrating monarch can survive the average minimum August temperatures there.

September NHJ position (85-80°W) over the breeding grounds is also positively correlated with monarch overwintering hectares (Pearson’s correlation analysis r = 0.37 to 0.53, p<0.1), although correlations are insignificant using Spearman’s rank correlation analyses (Fig. 2b). Interestingly, latitudinal anomalies over eastern NA are inversely related to the position of the NHJ over western NA (120-115°W) in a clear dipole pattern (Fig. 2b). Northern NHJ position over western NA creates lower minimum temperatures in eastern NA (Fig. 2b) in a ridge-trough pattern across the continent. Monarchs are now predominantly in the late larvae and pupae stages, and cool temperatures can delay eclosion before late fall (Zalucki, 1982). This ridge-trough pattern is evident in September of 2013 (Fig. S2), prefacing a winter of intense drought in California (Wang et al., 2015). Cold snaps are lethal to monarch larvae and pupae which cannot withstand consecutive days of temperatures colder than 12°C (Zalucki, 1982). This ridging pattern may correspond with Rossby waves forming and resonating around a preferred phase (Röthlisberger et al., 2016; Kornhuber et al., 2019) and may become more frequent under anthropogenic warming (Francis and Skific, 2015; Mann et al., 2018). Not only can this ridging pattern become more frequent, this pattern may ‘flip’ more frequently, with California becoming deluged with precipitation corresponding with warm falls and winters in eastern NA, such as in 2017 (Wang et al., 2017). Avian migration studies have found that such ridge-trough configurations can alter migration patterns and success via resource availability such as influencing masting seed production for boreal bird populations (Strong et al., 2015). Ridge-trough patterns across the continental US may lead to situations where NHJ position is good for the western monarch migration and poor for the eastern monarch migration, although more research is needed to fully characterize this potential phenomenon.

Over central NA and the Great Plains (105-97.5°W), the predominant route south, a southern shift in NHJ in September increases migration success by driving cooler maximum temperatures (Fig. 3a), more precipitation events (Fig. 3b), and greater nectar availability (as represented by NDVI (Saunders et al., 2019)) along the fall migration corridor (Fig. 3c). Lower temperatures decrease evaporative demand and higher precipitation leads to moisture delivery at a crucial point in the growing season, staving off drought, and supporting plant growth and reproduction. Temperatures in the southern Great Plains typically exceed 29°C in September and are often too hot for migration. Instead, monarchs are concentrated in their more northern summer breeding grounds for most of September (Howard and Davis, 2009). Cooler maximum temperatures along the southern Great Plains are more related to setting the table for the upcoming migration, increasing nectar plants availability in September and October. For monarchs beginning their migration from the more northern breeding grounds, cooler maximum temperatures are beneficial because they i) physiologically restrain female monarchs from starting oogenesis (Barker and Herman, 1976), ii) reduce the metabolic rate and caloric needs of this regionally heterothermic animal (Masters et al., 1988) and iii) reduce the likelihood a migrating monarch experiences lethal, hot temperatures while flying (Zalucki, 1982). Over the past 25 years, 2004 stands out as dropping to 20% of the overwintering acreage from the year before. In addition to the illegal logging at the overwintering grounds in the preceding spring, and over 50% of agricultural fields using roundup, jet stream driven climate in the late summer months seems to have been involved in this drop. Due to a southward NHJ position in August over eastern North America and a northward excursion in September over the Great Plains, monarchs experienced a particularly cold August in the breeding grounds and warm September temperatures along the migration corridor (Fig. S2).

The timing of weather events becomes very important to migration success in the late autumn (October). Delay of, or lower amounts of, precipitation delivery can potentially lead to phenological mismatch between butterfly and nectar plant, induce phenology of out of season host plants, increase the lethal impacts of freezing, or cause poor flight conditions, all of which could disrupt migration. We find that precipitation along the migration corridor in October is negatively correlated with monarch success (Fig. 4b). Most southern bound migrating monarchs have eclosed at this point in time or will do so soon. Precipitation can be deadly for monarchs during migration: rain and snow increase the likelihood a monarch will freeze to death (Anderson and Brower, 1996), rain and hail can permanently damage monarch wings affecting lift and flight (Calvert et al., 1983), and navigating rain events can lengthen the migration effort and route (Ries et al., 2018). A northern NHJ in October over the western US (122.5-112.5°W) corresponds with fewer precipitation events along the migration corridor and higher monarch return (Fig. 4b). Interestingly, lower precipitation (Fig. 4b) corresponds with lower NDVI (Fig. 4c) suggesting fewer nectar resources for migrating monarchs in October-November. Future research should investigate a trade-off between nectar plant phenology and the challenges of migrating in inclement weather for monarchs, especially during these months. Our study indicates that increased management of nectar plants in September along the central US corridor may assist monarch migration. For example, 2015 was a year of higher monarch overwintering acreage than we would have expected considering the warm September and October migration route (Fig. S2). However, earlier that summer, Tropical Storm Bill caused flooding conditions in the central US. Considering that fall temperatures influence precipitation and drought conditions along the migration route, the extra precipitation in the summer months may have mediated the plant response to warmer temperatures later in the season and would still allow for nectar availability along the migration route.

A northern NHJ in October over the western US (122.5-112.5°W) also corresponds with warmer temperatures in the western US (Fig. 4a). There is mark-recapture (Billings, 2019) and genetic (Lyons et al., 2012) evidence that some western monarchs periodically overwinter in Mexico instead of coastal California. Our results could indicate that warmer temperatures encourage western monarch populations to migrate to Mexico, although the mechanism is uncertain and needs further research.

We have examined the influence of NHJ position on monarch migration and overwintering acreage through pathways of surface temperature and precipitation variability. However, a circulation-centric framework allows us to also include other weather events central to migration, events changing with anthropogenic warming. High-amplitude ridge-trough patterns are projected to occur more frequently and can contribute to developing and steering hurricanes and storms by forming steep pressure gradients, such as with Hurricane Sandy in 2012 (Francis and Skific, 2015). In addition to storms, NHJ can interact with winds lower in the troposphere such as the Great Plains Lower-Level Jet (which flows northwards at 850hPa) to influence migration via wind speed or direction (La Sorte et al., 2014). Model ensembles project changes in the frequency of the GPLLJ in spring and summer along migration routes and breeding grounds and a westward shift of anticyclonic airflow in summer (Tang et al., 2017). These patterns in changing climate can be captured and are reflected with large changes in seasonal latitudinal NHJ position.

Describing when and why monarch migratory numbers are declining is a challenging endeavor. Significant effort has been invested in developing analyses that can improve our understanding and means to describe and predict migratory return numbers and trends in eastern North America. Monarchs vary in space and time as they move through their annual migration and climate driven weather is a strong determinant in how many monarchs will return south to the Mexican overwintering grounds. Here we demonstrate the role jet stream variability plays in monarch migration success, especially during fall migration. Positional changes of the NHJ impact both temperature and precipitation in preparation and during the migration. By better understanding the climate forces behind the large swings in monarch population, and continuing to observe how they seem to be changing with anthropogenic warming, the effects of land cover change as well as the success of numerous conservation efforts may be better contextualized in the face of a low population driven by less than ideal climate that year. Through this macrosystems ecology framework focusing on the role of the NHJ on seasonal surface climate conditions along the migration route, we may better predict the effects of future climate change on the monarch butterfly.

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Flockhart et al. GCB 2017

Zylstra et al. NEE 2021

## **Methods**

### **Data Sources**

Monarch Fall Roost data was collected from Journey North, a citizen science platform, for 2002 to 2020 for the months of August (Fig. 2a) and September (Fig. 2b). The dataset includes the date the roost was observed, the latitude and longitude coordinates to the tenth of a degree, and in some cases, an estimate of number of monarchs in the roost. The number of monarchs in the roost are more prevalent post-2011 and were not used in this study. To access, users can visit<https://maps.journeynorth.org/maps/2020/fall>, click on Monarch Fall Roost, and then View Data for the year of interest. Mexico Winter Acreage is available from 1994 to 2021 (Fig. 1c) and is the total area (in hectares) occupied at overwintering sites in the fir and pine forests of central southern Mexico . From 1994-2003, annual overwintering area data was collected in and around the Monarch Butterfly Biosphere Reserve (MBBR)from the National Commission of Natural Projected Areas (CONANP) in Mexico, while 2004-2020 was collected by World Wildlife Fund Mexico, typically in December. There are annual reports published breaking down the percent contribution to the total acreage at each exact roosting location and the exact methods used to collect those values. Due to this transition in methods in 2004, we moved forward with the analyses only examining 2004-2018.

To visualize the monthly spread of monarch butterflies across the continent, we used the Global Biodiversity Information Facility (GBIF) and accessed every Monarch Watch and iNaturalist observation of *Danaus plexippus* from 1994 to 2020 in North America (GBIF 2021). The orange points are then observations that are east of -105E and excluding Florida, to remove the western Monarch population and non-migratory populations from this visualization.

Monthly NHJ position was calculated for each longitude over the North American continent (125-65°W) as the latitude of monthly maximum zonal wind speed at 300 hPa for latitudes 0 to 90°N using the NCEP/NCAR reanalysis product (at 2.5-degree resolution). A similar definition was used by Belmecheri et al. (2017) to calculate NHJ indices but with the Twentieth Century Reanalysis version 2 product.

Monthly climate data used in this study included surface temperature (maximum, minimum) and precipitation from the CRU TS4.05 observational dataset at 0.5-degree resolution. Daily Normalized Difference Vegetation Index (NDVI) was from NOAA Climate Data Record (CDR) of AVHRR NDVI Version 5<https://www.ncei.noaa.gov/metadata/geoportal/rest/metadata/item/gov.noaa.ncdc:C01558/html> and aggregated to monthly resolution.NDVI is used as a proxy for resource availability.

### **Data Analyses**

The number of roost observations were summed by month and year to produce time series of roosts in August and September from 2002 to 2020.

To focus our analyses on the interannual variability of monarch overwintering acreage, we removed the long-term trends from all time series (monarch roosts in August, September, December; monthly NHJ time series at each longitude, monthly temperature, precipitation, and NDVI fields) by fitting a linear model and extracting the residuals.

To visualize the NHJ across disjointed longitudes we used a smoothing loess filter (Figs. 1 and S2). Fig S2 shows the loess filter of the NHJ across longitudes for each year.

Most longitudes feature a non-normal distribution of NHJ position and may not have a linear relationship with overwintering acreage. We therefore used Spearman rank correlation analyses (Lehmann and D’Abrera, 1998) with a threshold of p<0.1 to examine the relationship (1994-2018) between monthly NHJ position across individual 2.5-degree longitudes over the North American continent (125-65°W) and annual acreage (Table 1). We grouped longitudes of similar correlation values. We then took the average latitudinal position across grouped longitudes to correlate regional NHJ position with climate fields. In three months (February, August and October) there were single 2.5-degree longitudes that were insignificantly (p>0.1) correlated with monarch acreage that we grouped with neighboring longitudes in Fig. 1, as well as in future analyses, because they were similar to neighboring longitudes and did not lower correlation values with overwintering acreage and climate variables.

We also used Spearman rank correlation to examine the relationship of both annual acreage and the grouped latitudinal NHJ position with average temperatures. We used the more conservative Pearson correlation analysis (at similar p<0.1 significance threshold) to compare the annual acreage and latitudinal NHJ position to precipitation, NDVI, and minimum, maximum temperature fields.

The latitudinal NHJ position in September over central NA (105-97.5°W) is significantly correlated with overwintering acreage, however the climatological mean position of the NHJ is in northern central NA (53°N), and significant Spearman rank correlation coefficients with NHJ position and average and maximum surface temperatures are north of the migration corridor (Fig. S2b) and north of viable regions for monarch survival and migration (Zalucki, 1982). To examine whether the NHJ southernmost position influenced monarch overwintering acreage via controls on maximum temperature, we conducted a composite analysis where we took the 7 southernmost years of average NHJ position over central NA and compared the average maximum temperatures and precipitation amounts of those 7 years against all 25 years using a Student’s t-test and p<0.1 significance threshold (similar methods have been used e.g. by Cayan et al., 2001). The 7 southernmost positions of the longitudinally averaged jet stream over the central US for the time frame 1993-2019 ranged from 35°N to 45°N.

### **Code Availability**

R scripts for all analyses can be found at<https://github.com/AmyHudson/MonarchsJetStream>

### **Data Availability**

All data used in this study is open sourced. Some processed data can be found in: <https://github.com/AmyHudson/MonarchsJetStream>/data/processed

### **Additional References**

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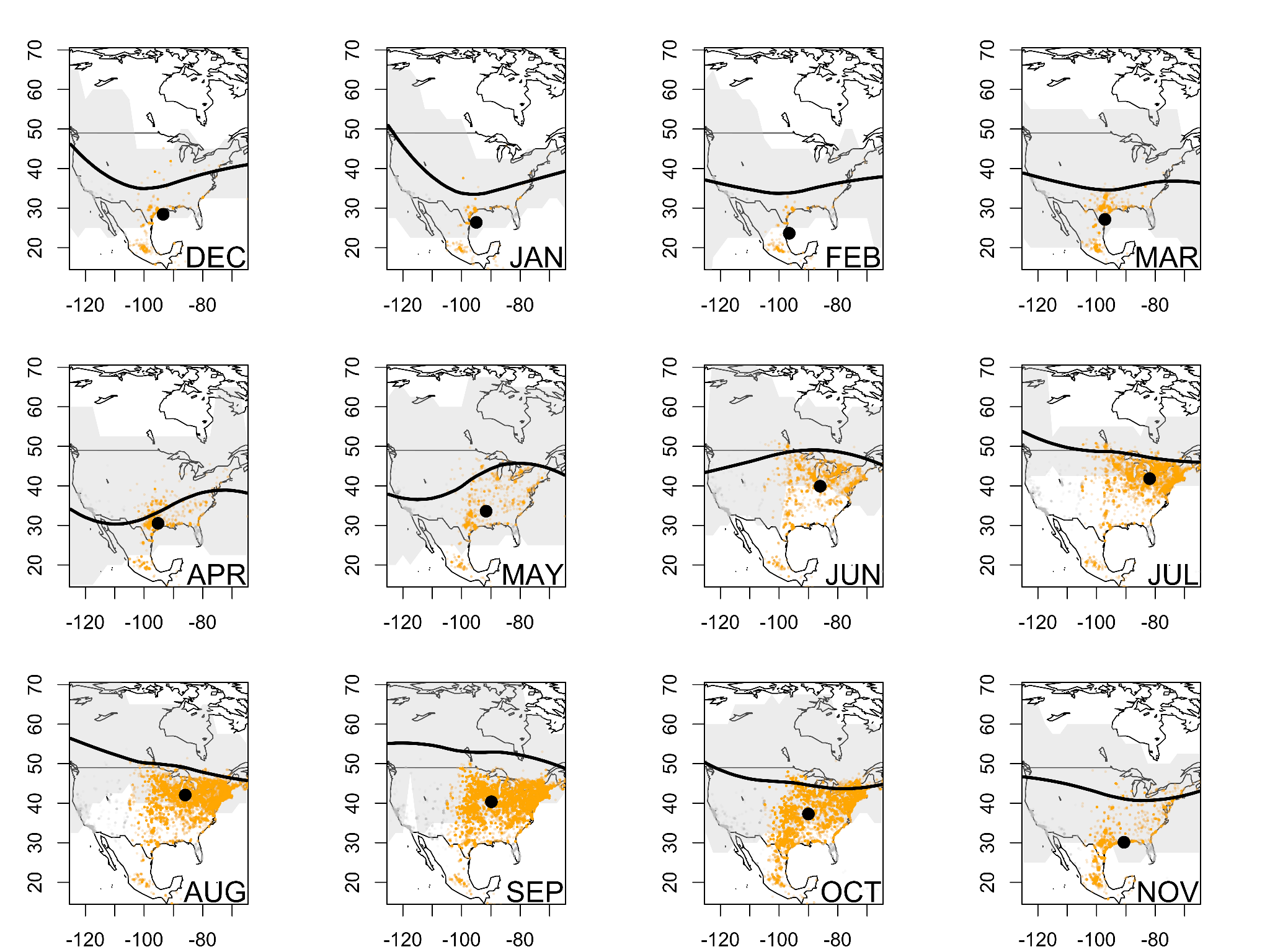
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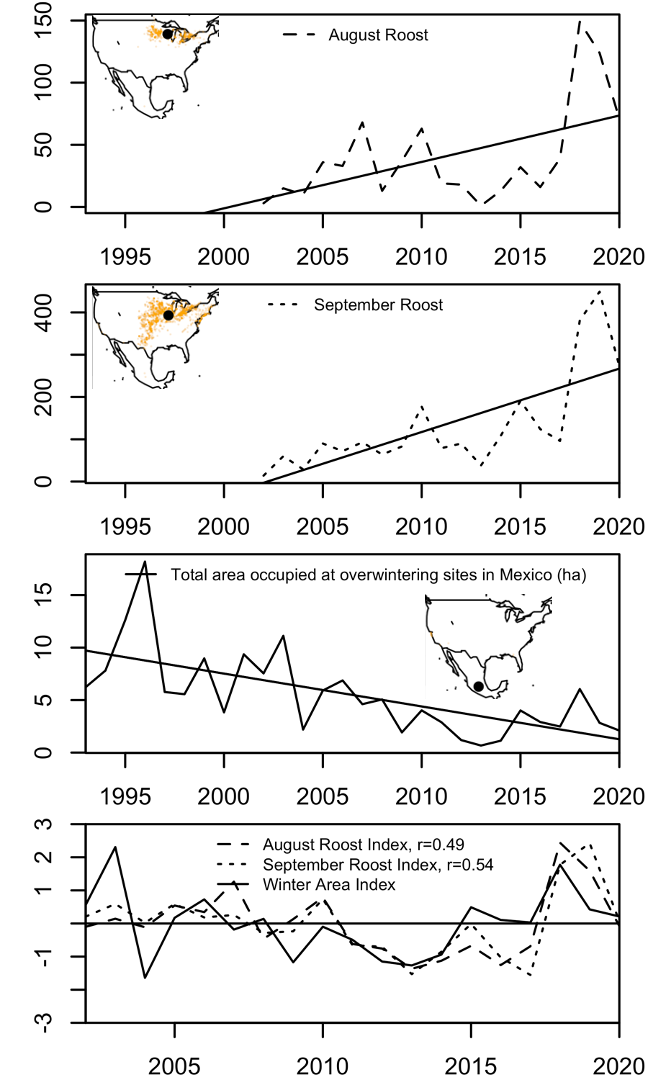
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## **Figures and Tables**

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**Fig. 1: Monthly eastern Monarch butterfly migration and Northern Hemisphere Jet (NHJ) position variability (1994-2020).** Orange points designate monthly observations of monarchs collected in GBIF, the black point is the centroid of these observations. The monthly NHJ latitudinal range is designated by a shaded gray polygon, with the black line representing the median NHJ latitude smoothed across longitudes with a loess filter. Gray points in Florida and the western US designate monarch populations that are unlikely to migrate to Mexico. Monarchs overwinter in the forests of southern Mexico, with an annual census conducted in December. Beginning in February and March, monarchs begin to migrate to various northern breeding grounds, following the seasonal warming of the continent. The NHJ similarly shifts north in its mean state. From April-September, up to 5 generations of Monarchs are produced, and in September, Generation 4-5 begins the southern migration from breeding grounds to overwintering grounds, producing Generation 1 the following spring.

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**Fig. 2: Seasonal monarch roosting indices and interannual relationships.** Raw values of August and September monarch roost counts and total area occupied by monarch colonies at overwintering sites in Mexico. Map insets designate the respective locations of monarch roosts. The residuals from fitted linear models were used to derive indices capturing the interannual variability of the eastern monarch migration. The Winter Area index is significantly correlated with both the August Roost index (r=0.49, p<0.05) and the September Roost index (r=0.54, p<0.05) for the period 2004-2018.

**Fig. 3: The latitudinal variability of the jet stream in summer and fall influences the fall monarch migration. A) Initial fall migration index corresponds positively to May June August and negatively with September. B) Final return overwintering success corresponds positively to June August and negatively with September. A) and B) share windows of overlap.**

**Fig. 4: ​​The jet stream position influences climate at key migration times and places. (A northern jet stream can warm minimum temperatures which benefits monarch migration return)**

**Fig. 5: The jet stream influence on nectar resources and habitat.**

**what is jet doing for plant resources during migration?**

**Greenness NDVI (Saunders et al 2019)**

**Does greenness correspond w Nectar Resources NPN Nectar connectors**

**maybe also look at ndvi and August and September roosting (could show signal over roosting grounds and leading up (May, June, August?)**

**winter correlation w august September etc. ndvi?**

**Northern Hemisphere Jet (NHJ) position increases (decreases) Mexico-bound monarch migration success through warmer (cooler) surface temperatures and warmer (cooler) minimum temperatures in breeding grounds.** Grey masks highlight the longitudinal bands of the NHJ position that are significantly (p<0.1) correlated with annual overwintering monarch numbers shown in Fig.1. (left panel) A, August average temperatures in eastern NA are positively correlated with average NHJ position for 105-75°W (middle panel) and monarch overwintering acreage (right panel), with Spearman’s rank correlation coefficient plotted. B, September minimum temperatures in Western NA are positively correlated with average NHJ position for 120-112.5°W (middle panel) and negatively monarch overwintering acreage (right panel), with Pearson’s correlation coefficient plotted. A dipole pattern is apparent in b, with ridging or troughing of the western NHJ influencing minimum temperatures on both coasts of the continent- in particular the breeding grounds of the eastern monarch.

**Fig. 3: Early autumn (September) Northern Hemisphere Jet (NHJ) southern position increases Mexico-bound monarch migration success through cooler maximum surface temperatures, more precipitation, and greater nectar availability along the migration corridor.** Considering the September NHJ from 105-97.5°W a, the seven southernmost NHJ correspond with cooler maximum temperatures (℃, p<0.1)(left panel) and maximum temperature negatively correlates with monarch acreage (right panel) b, the seven southernmost NHJ correspond with more precipitation (mm, p<0.1)(left panel) and precipitation positively correlates with monarch acreage (r, p<0.1) and c, NDVI (September and October), a proxy for nectar availability, positively correlates with NHJ position (left) and monarch acreage (right panel).

A, Shaded polygons represent the longitudinal bands of NHJ that are significantly (p<0.1) correlated with overwintering monarch numbers, where red (blue) designates positive (negative) ⍴ correlation coefficients (exact values for individual longitudes in Table S1), with the range of jet stream latitudinal position for those longitudes displayed as their vertical extents. The median latitudinal position of the monthly NHJ for the 4 highest (lowest) monarch migration overwintering years (after detrending using a linear regression) are plotted across 2.5 longitudinal bands with a loess filter in purple (orange). B, Monthly NHJ correlations with monarch overwintering acreage in Mexico vary between months. February, April, June, August, and October NHJ are positively correlated with monarchs at the Mexican overwintering grounds while March, July, and September NHJ are negatively correlated. The black dot designates the general centroid of the monarch migration in that month.

**Fig. 4: Autumn (October) Northern Hemisphere Jet (NHJ) northern (southern) position increases (decreases) Mexico-bound monarch migration success through warmer (cooler) surface temperatures in western US and fewer (more) precipitation events along migration corridor.** Considering the October NHJ from 122.5-112.5°W: a, The NHJ positively correlates with average temperatures (left panel) and monarch acreage positively correlates with average temperatures (right panel) (Spearman’s correlation) in western North America. b, The NHJ negatively correlates with precipitation (mm) along the migration route (left panel) and monarch acreage (hectares)(right panel)(Pearson’s correlation) c, NDVI (October-November) negatively correlates with the NHJ (left panel) and monarch acreage(hectares)(right panel) along the southern US migration in the lower midwest/southwest (Pearson’s correlations).

**Table 1: Spearman correlation coefficients between monarch overwintering acreage and NHJ position by longitude over the period 1994-2018.** Select regions are plotted in Figs. 1 and 2 as shaded polygons. Rows are months and columns are longitudes at 2.5°W resolution. Significant correlation values are shown using a threshold of p<0.1. Both overwintering acreage and NHJ position were detrended using linear regression.

**Fig. S3: Late summer (August, September) temperature anomalies and NHJ position 2004-2018.** Linearly detrended temperature anomalies ranging from -6 to 6°C from the CRU dataset are overlaid with loess filter of the monthly NHJ at each 2.5 degree of longitude for August (left), September (middle) and October (right) panels. The annual observed monarch acreage (Fig. 1) is also listed.