Multiscale seasonal factors drive the size of winter monarch colonies

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Monarch butterflies in eastern North America have declined by 84% on Mexican wintering grounds since the observed peak in 1996. However, coarse-scale population indices from northern US breeding grounds do not show a consistent downward trend. This discrepancy has led to speculation that autumn migration may be a critical limiting period. We address this hypothesis by examining the role of multiscale processes impacting monarchs during autumn, assessed using arrival abundances at all known winter colony sites over a 12-y period (2004–2015). We quantified effects of continental-scale (climate, landscape greenness, and disease) and local-scale (colony habitat quality) drivers of spatiotemporal trends in winter colony sizes. We also included effects of peak summer and migratory population indices. Our results demonstrate that higher summer abundance on northern breeding grounds led to larger winter colonies as did greener autumns, a proxy for increased nectar availability in southern US floral corridors. Colony sizes were also positively correlated with the amount of local dense forest cover and whether they were located within the Monarch Butterfly Biosphere Reserve, but were not influenced by disease rates. Although we demonstrate a demographic link between summer and fine-scale winter population sizes, we also reveal that conditions experienced during, and at the culmination of, autumn migration impact annual dynamics. Monarchs face a growing threat if floral resources and winter habitat availability diminish under climate change. Our study tackles a long-standing gap in the monarch's annual cycle and highlights the importance of evaluating migratory conditions to understand mechanisms governing long-term population trends.

Danaus plexippus | gamma-hurdle model | NDVI | annual cycle | migration route

Migration is a difficult period of the annual cycle to investigate (1–3), yet evidence suggests that migration costs can have significant impacts on the survival of individuals and, ultimately, the viability of a population (4, 5). In particular, the autumn migratory period has received little attention, although important ecological conditions and life cycle events occur during this time, such as resource senescence and inductions of hibernation and diapause (6, 7). The annual migration of eastern North American monarch butterflies (*Danaus plexippus*) from their breeding grounds in the United States and Canada to their wintering grounds in Mexico is one of the longest known migrations of any insect (8). Long-term data (9) show a significant decline in winter colony sizes since the beginning of monitoring in 1993 (Fig. 1), with an 84% decrease from peak abundance in 1996 (10). The exact causes of the decline are debated, as a variety of stressors operating at different spatial scales and times of the life cycle threaten monarch butterflies (11). Loss of milkweed host plants during the breeding season due to increased herbicide (glyphosate) use in Midwestern US agricultural fields is hypothesized to be a primary cause of monarch declines (12–17). However, cumulative glyphosate application reached peak levels between 2003 and 2005 and has since remained relatively stable (14–16). Yet, the monarch population continues to decline, despite the fact that milkweed loss has slowed substantially (14, 16). A number of other factors threaten monarchs, including increased temperature and precipitation variability during the breeding and overwintering seasons (15, 18–20); the specialist protozoan parasite *Ophryocystis elektroscirrha* (*OE*), which reduces mass, flight speed, endurance, and life expectancy (21–23); and reductions in winter habitat availability of Oyamel fir (*Abies religiosa*) forests from illegal logging and severe storm events (24–26).

Although the winter data from Mexico reveal a decline in the monarch population since the mid-1990s, a similar pattern has not been consistently observed by monitoring programs of adults in northern regions (27–29), spurring a discussion that has garnered considerable interest among researchers and the public (24, 30–32). Summer indices of adult monarchs generated from three monitoring programs across the northern United States and two early autumn censuses at stopover locations do not show a significant decline in abundance over the same 19-y period (27–29, 33, 34). Summer count data are primarily collected by citizen scientists at nonrandom locations, generally close to urban and suburban areas (31). Thus, summer monitoring programs undersample agricultural fields and other sites where milkweed has

Significance

We address a debate that has spurred scientific and public discourse: whether conditions during autumn migration are contributing to the decline of the eastern monarch butterfly population. Using a multiscale modeling approach, we reveal that continental-scale landscape greenness during migration (proxy for nectar availability) and the amount of forest cover at winter sites significantly influence arrival colony sizes. We also demonstrate a significant demographic connection between summer and winter population sizes. Our results suggest that environmental factors during—and at the culmination of—autumn migration, combined with summer population size, explain a substantial portion of temporal variation in monarch population dynamics during a time frame after which other major putative sources of mortality (host plant and winter habitat loss) have lessened considerably.

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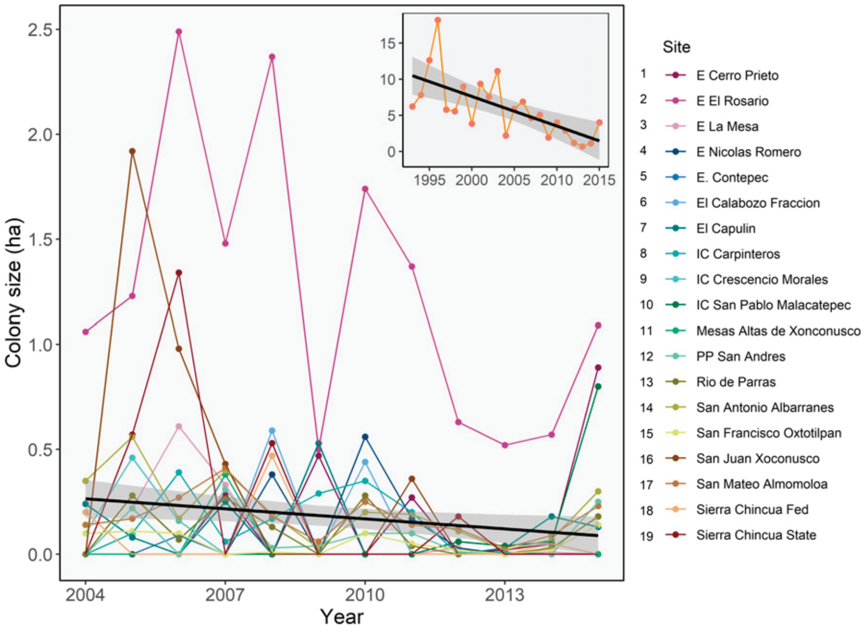

Fig. 1. Monarch butterfly winter colony sizes (ha) at all 19 sites during December 2004–2015. The black line shows a linear trend, and the gray shading is the 95% credible interval (CI). (*Inset*) Total overwintering area (ha) occupied by colonies annually in central Mexico since 1993 (orange circles; ref. 9); linear trend (black line; $y = -0.41x + 10.90$) and 95% CI (gray shading) shown.

traditionally been most abundant, potentially inflating estimates of the breeding population size (32). It is unclear as to whether failure to detect declines in summer breeding indices is a result of data biases (28, 32) or the absence of real trends in the summer population.

The disparity between a decline in total winter population size and a lack of trend in summer indices has led to speculation that the autumn migration may be a primary limiting period of the monarch's annual cycle (28, 29, 33–35). Scarcity of nectar sources (which provide the lipids needed for migration; refs. 36 and 37) along the migration route from either climate or land use changes (38–41) and increased parasitism (42), as well as continued small-scale degradation at wintering sites (43), may be possible drivers preventing monarchs from successfully completing the autumn migration and settling in winter colonies, respectively. We examine the connection between environmental conditions along the autumn migration route and individual winter colony sizes from 2004 (the first year in which individual colony data are available) to 2015 (Fig. 1) using a variable selection approach within a hierarchical modeling framework. To do this, we combine environmental data with researcher-collected and citizen science monarch data to delineate both broad-scale environmental conditions and fine-scale habitat changes influencing the autumn migration. Our study uses long-term monarch data from all 19 individual winter colony sites located within and outside of the Monarch Butterfly Biosphere Reserve, a protected area in central Mexico, to identify continental- and local-scale factors associated with abundances of wintering monarch butterflies at the time of their annual arrival in December (*SI Appendix*, Table S1). Previous analyses that aggregate the winter colony data (28, 29) overlook the influences of potential stressors operating at the local scale (e.g., habitat quality and availability), which may mask important colony-level heterogeneity at winter sites.

To determine whether factors during the autumn migratory period contribute to monarch population declines, we evaluate effects of peak summer population (in the Midwestern United States) and migratory roost indices (a proxy for autumn population size) and annual disease prevalence. We also assess environmental variables, including autumn temperature and an autumn greenness index [Normalized Difference Vegetation Index (NDVI), a surrogate for nectar availability as measured by satellite imagery] along the Midwest migratory corridor, as well as forest habitat availability and previous year dynamics (i.e., presence/size of colonies in the prior year) at colony sites in Mexico (Fig. 2). By starting our analysis in 2004, we investigate the role of autumn environmental variables during a time frame after which other major putative sources of decline (e.g., milkweed and large-scale winter forest loss) have largely diminished (15, 16, 25, 26).

We compare our results to those obtained from two models fit using the aggregated winter colony data (one beginning in 2004 and a second starting in 2000, the first year NDVI data are available) where we estimate total winter population size annually as a function of the variables in our best-supported model. We do this to evaluate whether the demonstrated species-environment relationships hold at both spatial scales (i.e., individual colony and aggregate total winter colony levels) and when including four additional years of data. We calculate residuals from all model runs to compare model fits over time (i.e., trends in the residuals) and assess the amount of temporal variation in monarch population dynamics explained by the various covariates (see *SI Appendix* for more details). We also compare residuals from our models to an aggregated model that includes only a peak summer population index, which we use to evaluate the importance of autumn variables in explaining the winter monarch population decline.

Results

The most strongly supported model describing winter colony sizes includes effects of peak summer population index, autumn greenness during the first half of migration, dense forest habitat availability at colony locations, and whether a colony was located within/outside of the Monarch Butterfly Biosphere Reserve (see *SI Appendix*, Table S2 for a list of the top 10 models and *SI Appendix*, Table S3 for a complete list of parameter estimates from the top-supported model). Random site effects are also strongly supported (*SI Appendix*, Table S3), indicating that colony sizes are, on average, consistent within sites over time (e.g., larger at El Rosario; smaller at San Francisco Oxtotilpan). We did not find support for effects of autumn temperatures (average or minimum), *OE* parasitism, the presence or size of the colony in the previous year, or any two-way variable interactions (*SI Appendix*). Although we detected positive associations of the migratory population index (measured mainly in the US portion of the migration), greenness during the second half of migration, and amount of total forest cover (open and dense forest cover combined), these variables were not included in the final model

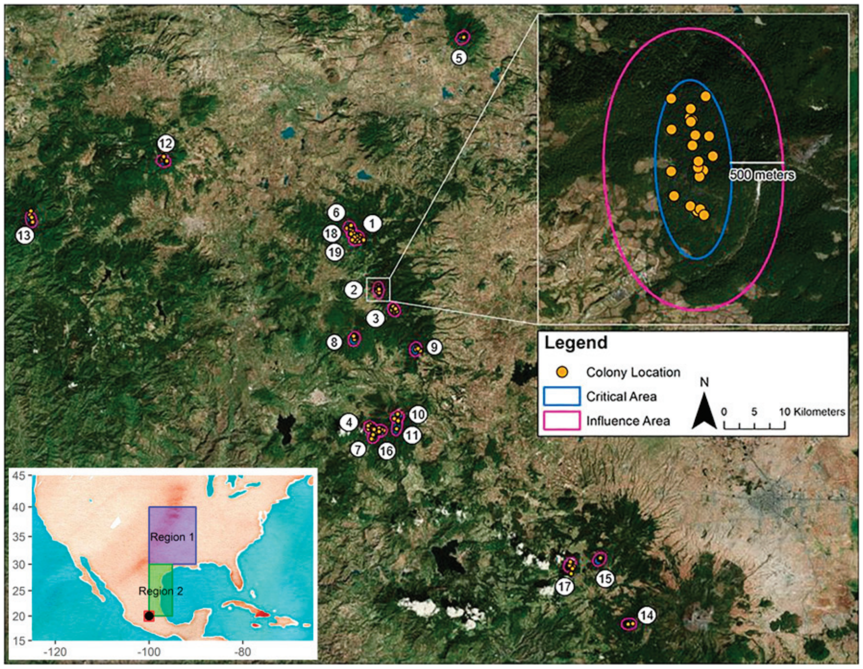

Fig. 2. Map of wintering monarch colony locations (orange circles) within and outside of the Monarch Butterfly Biosphere Reserve in central Mexico (shown as the black circle within the red area in *Bottom Left Inset*) during 2004–2015. Blue ellipses denote 100 ha critical areas around colonies, and pink ellipses denote 500 m influence areas around each critical area. Forest cover covariates were calculated within the critical area + influence area. The numbers in the white circles refer to the colony names in Fig. 1. (*Bottom Left Inset*) Geographic regions used to calculate environmental covariates (*SI Appendix*, Table S1) along the monarch butterfly's Midwest migration route during the first half (Region 1 during 15 Sept–15 Oct; blue box) and second half of the autumn migration (Region 2 during 15 Oct–15 Nov; green box).

because of high correlations with more strongly supported variables (*SI Appendix*).

The index of peak summer monarch abundance in the Midwestern United States, a factor that is correlated ($r = 0.73$) with total winter population size (i.e., aggregated colony data) but does not exhibit a significant trend over time (Fig. 3*A*), has the strongest effect of the continental-scale variables on arriving colony sizes [Fig. 3*B*, mean (95% credible interval) estimates from the top-supported model: −0.423 (−0.690, −0.217); negative values indicate a positive effect due to the inverse-logarithmic link function]. The greenness index (as measured by NDVI where higher values indicate greener landscapes and presumably increased nectar availability) during the first half of migration (15 Sept–15 Oct; Fig. 2), a factor that is moderately correlated ($r = 0.37$) with winter population size but does not exhibit a significant negative trend (Fig. 3*C*), also has a strong positive association with winter colony sizes [Fig. 3*D*; −0.351 (−0.647, −0.056)].

Location within the Monarch Butterfly Biosphere Reserve has the greatest effect [Fig. 4; −1.389 (−2.772, −0.084)] of the local-scale variables. The amount of local dense forest cover surrounding

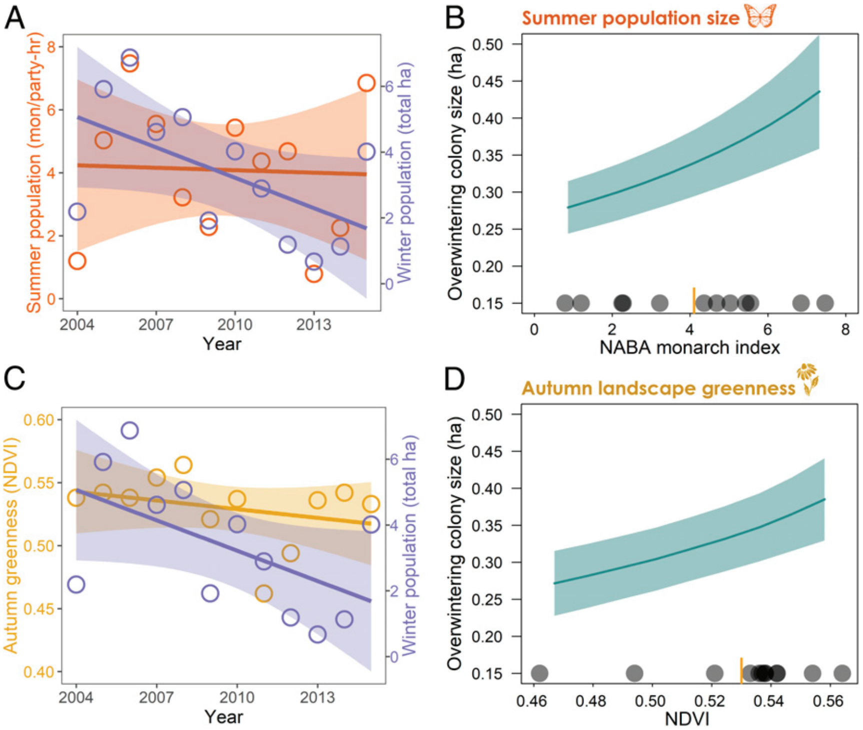

Fig. 3. Raw continental-scale covariate values and their effects on winter colony sizes (ha) during 2004–2015. (*A*) Data showing the peak annual summer monarch population abundance index (orange circles) and annual total winter population (purple circles); associated linear trends (solid lines) and 95% CIs (shading) shown. Note there is no decline in the summer population index [slope (β) = −0.03 (−0.40, 0.034), estimated with separate linear regression]. (*B*) The marginal effect (solid line; 95% CI shaded) of peak summer population index (NABA) on winter colony sizes (estimated from the top-supported model) for colonies located inside the Monarch Butterfly Biosphere Reserve ($n = 14$) when all other covariates are held at mean values. The gray circles show the raw annual values of NABA indices (the vertical orange line is the mean). (*C*) Annual landscape greenness index data (NDVI; proxy for nectar availability) in Region 1 (Fig. 2; yellow circles) and annual total winter population (purple circles). Note there is not a significant decline in the autumn greenness index [$\beta = -0.002$ (−0.007, 0.002)]. (*D*) The marginal effect (solid line; 95% CI shaded) of NDVI during the first half of autumn migration on winter colony sizes (estimated from the top-supported model) for colonies located inside the reserve when all other covariates are held at mean values.

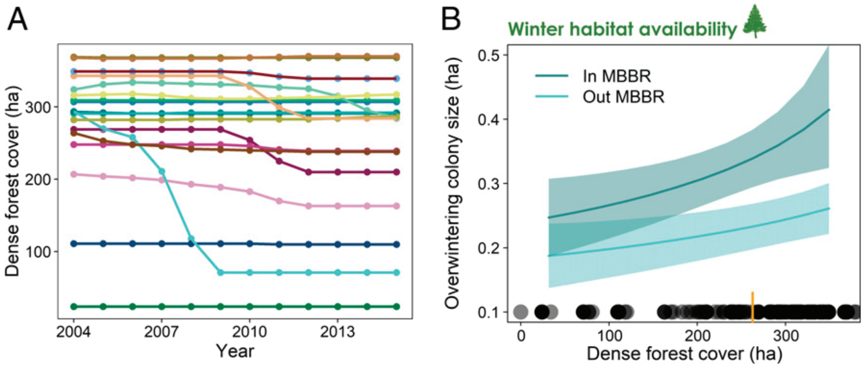

Fig. 4. Local-scale covariate effects (estimated from the top-supported model) on individual winter colony sizes (ha) during December 2004–2015. (*A*) Raw data showing the amount of dense (>70% canopy cover) forest (ha) surrounding each of 19 colony sites during 2004–2015 as measured within a 100 ha ellipse + 500 m buffer (Fig. 2). Color coding of colony sites matches that of Fig. 1. (*B*) The marginal effects of dense forest cover (ha) surrounding colony sites (solid lines with 95% CIs shaded) and colony presence within (dark blue) and outside (light blue) of the Monarch Butterfly Biosphere Reserve when all other covariates are held at their mean values. The gray circles show the raw annual values of forest cover (the vertical orange line is the mean).

individual winter colony site locations (Fig. 2), a factor that varies spatially and, to a lesser extent, temporally (i.e., five sites exhibited forest loss, whereas the remaining 14 had constant values; Fig. 4*A*), also positively affects annual monarch colony sizes [Fig. 4*B*; −0.530 (−1.332, 0.145)]. Mean residual estimates from our best-supported colony-level model are minimally variable (*SI Appendix*, Fig. S1) and do not show a significant temporal trend [$\beta = -0.01$ (−0.02, 0.005), estimated post hoc; *SI Appendix*, Fig. S1], indicating that top-supported covariates explain temporal variation in fine-scale colony dynamics well during 2004–2015.

Our colony-level results are consistent with those from analyses of the aggregated (sum total) winter colony data [i.e., positive effects of peak summer index, autumn greenness, and dense forest cover (summed across colonies); *SI Appendix*, Fig. S2], regardless of whether we begin the time series in 2000 or 2004, although covariate effects are generally smaller because local-scale variation is overlooked with aggregate models (*SI Appendix*, Table S4). Estimated residuals (posterior means) from the aggregate full (summer index + autumn greenness + winter forest) models exhibit small negative linear trends [$\beta_{2000} = -0.07$ (−0.14, −0.003), $\beta_{2004} = -0.06$ (−0.16, 0.004), estimated post hoc; *SI Appendix*, Fig. S3 *A* and *B*], suggesting that full models capture most, but possibly not all, factors influencing colony dynamics (albeit the residual decline is not significant when starting from 2004).

In comparison, residuals from models including only the peak summer index (starting in 2000 and 2004 with no environmental variables) exhibit significantly large negative trends [$\beta_{2000} = -0.22$ (−0.33, −0.11), $\beta_{2004} = -0.17$ (−0.29, −0.06); *SI Appendix*, Fig. S3 *C* and *D*], indicating poor fit and an inability to explain the decline in the winter monarch data. We calculated the standard deviation (SD) of residuals from each model to assess the amount of variation explained by predictor variables. The variation in residuals from summer-only models ($SD_{2000} = 1.46$, $SD_{2004} = 0.95$) is higher compared with models that additionally incorporate the significant autumn covariates ($SD_{2000} = 0.70$, $SD_{2004} = 0.60$; *SI Appendix*, Fig. S3). Together, these residual analyses highlight the importance of autumn greenness and the amount of local dense forest cover at colony sites in explaining both annual fluctuations and declines in the winter monarch population.

Discussion

Our results reveal that winter arrival dynamics of monarch butterflies from 2004–2015 are a product of summer breeding population size, autumn greenness along the Midwest migratory route, and forest cover at colony sites. Although the peak size of the summer population has a significant influence on the subsequent winter population, colony sizes are also positively associated with landscape greenness (a proxy for nectar availability as measured by NDVI) and the amount of local dense forest cover at individual winter sites. Taken together, these two variables significantly decrease the amount of unexplained temporal variation in residuals compared to a model including only the peak summer index (*SI Appendix*, Fig. S3). Hence, conditions experienced during, and at the culmination of, autumn migration impact annual dynamics during a time frame (2004–2015) after which other major putative sources of population decline (e.g., milkweed and large-scale winter forest loss) have lessened. Interestingly, disease rates are not associated with arrival colony sizes and do not appear to have contributed to the population decline during this period. Several researchers have hypothesized that autumn migratory conditions, specifically nectar availability and disease prevalence, may be the leading source of monarch declines (28–30, 33, 35). Our results provide empirical evidence for only one of the factors posited as a source of autumn mortality, landscape greenness (i.e., surrogate for nectar limitation), but also support an important demographic connection between the winter and the summer populations.

It is difficult to quantify the influence of the autumn migration on the long-term monarch decline relative to other seasonal factors without a full annual cycle model, yet our study demonstrates the importance of live plant biomass in autumn to winter monarch abundance. Nectar resources along the migration route, particularly floral corridors located in the southern United States (e.g., central Texas; Region 1 in Fig. 2) where monarchs enter arid climates midmigration, are critical to migratory success (36, 40). Climate projections of autumn/winter drought conditions in south–central Texas (44) suggest that nectar resources in this region may be reduced because of decreased precipitation in the future. Indeed, the three least green (driest) autumns of our study period (2009, 2011, and 2012) coincided with 3 y of below average colony sizes (12-y avg: 3.37 ha) in Mexico (Figs. 1 and 3*C*; albeit the summer population index was also low in 2009). Although there is a causal mechanism relating monarch abundance with our proxy for available nectar resources (45–48), the NDVI metric could also be capturing other environmental variables (e.g., precipitation and wind) that may influence monarch migratory success. Ascertaining the critical corridors where monarchs build up lipid reserves during migration is crucial, especially as autumn migration conditions may become more constraining if nectar resources are depleted from ongoing climate change.

Our results demonstrate a significant relationship between peak summer population index and arriving winter colony sizes, highlighting the importance of breeding conditions on monarch population dynamics (15, 19, 20). This result is consistent with past studies that have shown a correlation between summer and winter population indices, but an incongruence of long-term trends—an inconsistency that has been attributed to either biased sampling designs (28, 31, 32) or the lack of migratory success during autumn (28, 35). Severe reduction of milkweed during summer breeding has been proposed as a main stressor on the monarch population (12–14), yet monarchs continue to decline even as milkweed loss has slowed since 2003–2005 (16). Other environmental conditions, such as summer and, especially, spring climates are critical to summer monarch population growth

(15, 19, 20) and may contribute to the declines. Presumably, the influences of spring and summer environmental conditions, including milkweed availability, landscape greenness, and precipitation/temperature, are captured in our index of peak summer abundance [North American Butterfly Association (NABA) counts], although the metric is imperfect. For instance, aggregate models that included the NABA covariate differed slightly in terms of model fit (*SI Appendix*, Fig. S3) depending on the period examined (2000–2015 vs. 2004–2015). We speculate that NABA surveys may not have been as effective at capturing the summer monarch population size before 2004 as post-2004, after glyphosate use had leveled off and milkweed was largely eliminated from agricultural fields. NABA counts may have underestimated the summer population when milkweed was present in large numbers in corn and soybean fields because volunteers primarily monitor in nonagricultural areas (32). Moreover, cross-scale interactions among potential drivers (e.g., availability vs. distribution of suitable habitat and local weather vs. regional climate events) and carryover effects across regions and seasons likely contribute to monarch dynamics in ways that are difficult to ascertain (15). These interactions, as well as heterogeneity in summer sampling schemes and annual variations in ecological processes, may also lead to inconsistent species-environment relationships across different temporal scales (20).

Local-scale environmental variables additionally contribute to early winter colony sizes. Location within the designated Monarch Butterfly Biosphere Reserve and the amount of dense forest cover surrounding individual sites are positively associated with colony sizes (Fig. 4*B*). Reserve boundaries were originally drawn to ensure protection of the largest colonies, so the positive relationship with location in the reserve is not surprising. Intact forests maintain the microclimate required by monarch aggregations and provide freeze protection (49). Enhanced protection of critical areas inside and outside of the reserve likely contributes to higher habitat quality. Logging is prohibited within the core zones (research activities and low-scale ecotourism are allowed), and only sustainable land use management (low-impact harvesting) is allowed in buffer zones with special permits (43). However, five of the colonies substantially lost dense forest cover over the study period (Fig. 4*A*), four of which also exhibited declines in monarch population size. Our colony-level analysis allowed us to tease apart the local-scale factors from the regional drivers influencing monarch dynamics, as aggregating forest cover and winter colony data to annual values masks important colony-level variation (*SI Appendix*). Maintenance of available habitat and minimization of anthropogenic disturbance (e.g., tourism and pest control measures, which can cause colony dispersal and expenditure of lipid reserves) within colony locations could help ensure continued colony presence (25).

We did not find support for an effect of *OE* infection on monarch colony sizes (in both colony-level and aggregate analyses; *SI Appendix*), as has been observed in another recent study which analyzed data starting from 1993 (16). *OE* infection rates increased from about 1–8% during 1998–2005, but were more stable during the time frame of our analysis (most values were around 10%; ref. 16). Future work quantifying the relationship between *OE* infection rates during summer breeding and subsequent autumn/winter monarch abundances will help elucidate the role of parasitism across the full annual cycle. Neither did we find evidence for an important effect of autumn temperature on colony sizes (*SI Appendix*). No study has yet shown an effect of autumn temperatures on monarch abundance, possibly because temperatures during autumn only influence adult activity, and not breeding and development as in the summer months.

Migratory periods are notoriously difficult to study due to technological, statistical, and data limitations, yet incorporating conditions experienced by animals during these critical phases is necessary to understand and evaluate population trajectories. In this paper, we shed light on a scientific debate about the extent to which autumn migratory success and winter colony establishment is contributing to monarch population declines during a time frame after which other cited sources of mortality have leveled off (15, 16, 25, 26). Our results reveal that landscape greenness (a proxy for broad-scale nectar availability) during autumn migration and forest habitat cover at colony sites contribute to temporal population dynamics and declines in winter colony sizes, in addition to conditions at northern breeding locations. The recent surge in popularity of citizen science monitoring programs and implementation of the Integrated Monarch Monitoring Protocol has the potential to provide critical data across the eastern US breeding grounds, including in undersampled agricultural regions (28). This increased focus on random survey placement may soon lead to robust continental-wide assessments during spring and summer breeding seasons. Future work should integrate data across the monarch's entire annual cycle and continental range to scale up local processes and simultaneously evaluate the putative causes of decline for this iconic insect.

Materials and Methods

Winter Monarch Data Collection. Our analyses use monarch abundance data as measured by the surface area (ha) of the wintering habitat occupied at 19 unique sites when individuals congregate in high-elevation Oyamel fir forests within and outside of the Monarch Butterfly Biosphere Reserve in Mexico (Fig. 2). The combined occupied area is used as a proxy for total population size (16), as the vast majority of individuals congregate in the colonies. Each colony is named after the property where the colony is located (hence we use colony and site interchangeably). We used data collected on colony sizes when they were well established in mid-December from 2004–2015 (14 Dec–31 Dec, except 2004 when data were collected 1 Dec–15 Dec), as measured by tracing a polygon around trees with butterfly clusters (see ref. 25 and *SI Appendix*).

Covariate Data Summary. We incorporate the following variables in our models of winter colony sizes: peak summer population index (North American Butterfly Association counts), migratory roost index (i.e., a proxy for the autumn population size; as measured by Journey North count data), autumn temperature and landscape greenness (NDVI, a proxy for broad-scale nectar availability) along the northern and southern portions of the migration route (Fig. 2), annual *OE* disease prevalence, winter forest habitat availability, and previous year dynamics (i.e., presence and sizes of colonies in prior year) at local sites in Mexico. See *SI Appendix* for additional details on how each covariate was measured and calculated.

Data Analysis. Approximately 50% of the colony data (site-year combinations) were zeros during December surveys (i.e., <0.01 ha of area occupied), resulting in a strongly right-skewed distribution of colony sizes (*SI Appendix*, Fig. S4). We thus applied a hierarchical hurdle model to separately estimate the probability that monarchs used a colony site in a given year and the size of the colony conditional on use (50). Our model is composed of two submodels: (*i*) a binomial mixed model (logistic regression) based on the presence/absence of monarchs (i.e., colonies) at surveyed sites each year, and (*ii*) a zero-truncated gamma model to estimate the effects of environmental variables on colony sizes (*SI Appendix*, Table S1). We used a gamma distribution because colony sizes are positive skewed (many small colonies and a few large ones) and an inverse-logarithmic link function to model the covariate effects, which were site or year specific or both.

We evaluated the effect of a single variable on the occurrence probability of monarchs at individual colony locations (the first part of the hurdle model): presence/absence of a colony in the previous year. We tested all other variables (*SI Appendix*, Table S1) in the second part of the hurdle model (gamma submodel). Because we had no a priori hypotheses for which environmental factors would predict the occurrence of colonies vs. their sizes, we opted to assess covariate effects on the size of colonies. It is generally acknowledged that covariates should be added to the count component of hurdle models because occurrence is fundamentally a function of abundance (51). To account for pseudoreplication of colony sites as well as unexplained site-specific factors that may influence colony occurrences and abundances, we incorporated site-level random effects in both parts of the model (15, 52). To minimize autocorrelation and overfitting, we used a forward selection approach to select the environmental variables (fixed effects) for inclusion in the final set of models. All continuous covariates were standardized to have a mean of zero and a SD of one, which allows for straightforward comparison of the effect sizes of the different variables (see *SI Appendix* for the model code and implementation details).

We also fit a gamma mixed model to the total annual winter population size [i.e., aggregated (summed) colony size data] using the variables in our best-supported model (aggregating where appropriate, i.e., total dense forest cover), as well as a random effect of year (see *SI Appendix* for more details). We fit two versions of this model: (*i*) using data beginning in 2004 (the same as the colony level analysis), and (*ii*) using data beginning in 2000, the first year NDVI is available. We compared the direction and magnitude of parameter estimates for all covariates from both model runs with those obtained from our individual colony-level analysis. Additionally, we fit models (starting from 2000 and 2004) using aggregated colony data and including only the peak summer population index as a predictor to compare the amount of variation explained by the summer index alone vs. the full (summer index + autumn greenness + winter forest) models. We calculated residuals (fitted values subtracted from observed values) from all model runs and conducted post hoc regressions (in a Bayesian framework) on residual values as a function of year to examine model fit and any remaining temporal trends in residuals after accounting for covariate effects.

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