



Multiscale seasonal factors drive the size of winter monarch colonies

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Edited by May R. Berenbaum, University of Illinois at Urbana–Champaign, Urbana, IL, and approved February 15, 2019 (received for review April 4, 2018)

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 under-sample 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.

Author contributions: S.P.S., L.R., and E.F.Z. conceived of the research; S.P.S. designed the analysis with E.F.Z.; N.N., M.I.R., E.G.-S., and E.R.-S. collected and extracted data; S.P.S. conducted analyses; S.P.S., L.R., and E.F.Z. wrote the paper with editorial contributions from all authors.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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See Commentary on page 8093.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1805114116/-DCSupplemental.

Published online March 18, 2019.

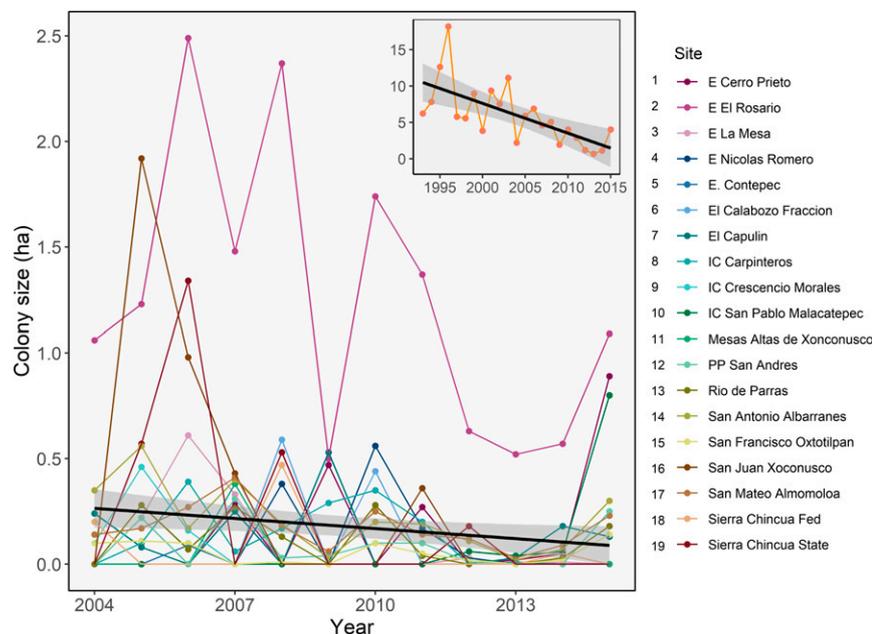


Fig. 1. Monarch butterfly winter colony sizes (ha) at all 19 sites during December 2004–2015. The black line shows a linear trend, and the gray shading is the 95% credible interval (CI). (Inset) Total overwintering area (ha) occupied by colonies annually in central Mexico since 1993 (orange circles;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

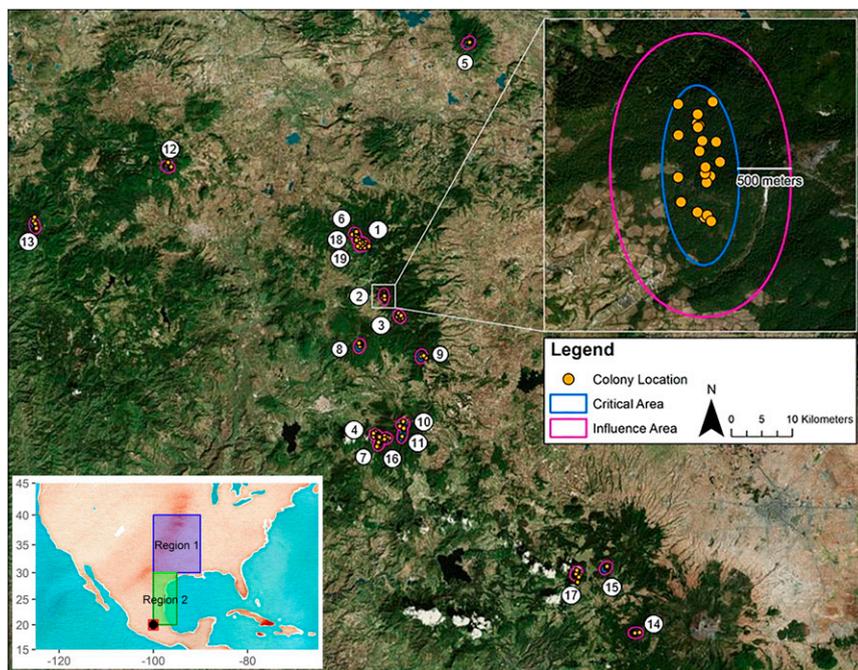


Fig. 2. Map of wintering monarch colony locations (orange circles) within and outside of the Monarch Butterfly Biosphere Reserve in central Mexico (shown as the black circle within the red area in *Bottom Left Inset*) during 2004–2015. Blue ellipses denote 100 ha critical areas around colonies, and pink 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. 3A), has the strongest effect of the continental-scale variables on arriving colony sizes [Fig. 3B, 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. 3C), also has a strong positive association with winter colony sizes [Fig. 3D; -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

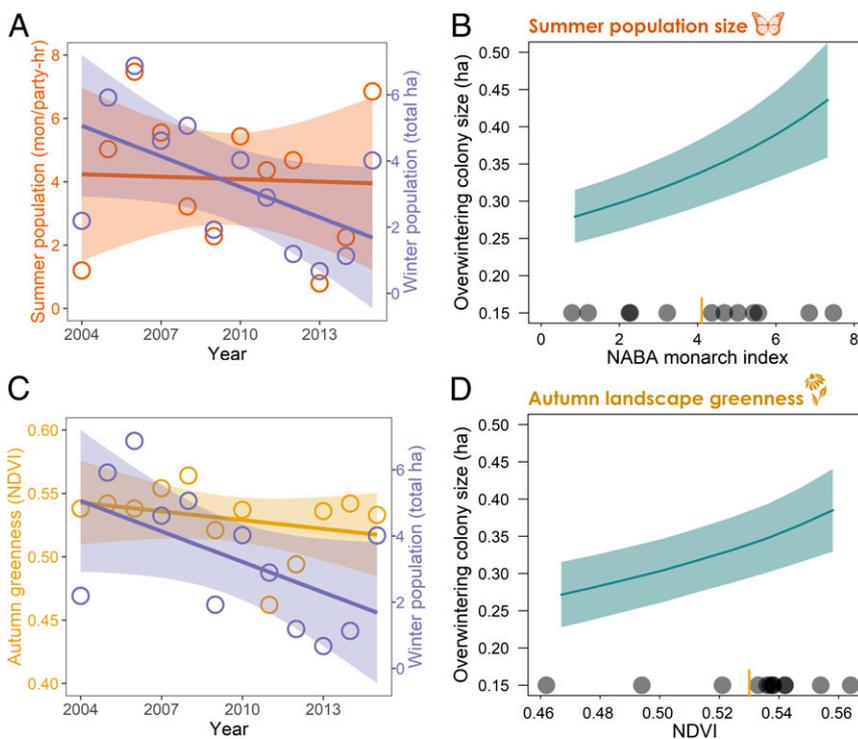


Fig. 3. Raw continental-scale covariate values and their effects on winter colony sizes (ha) during 2004–2015. (A) Data showing the peak annual summer monarch population abundance index (orange circles) and annual total winter population (purple circles); associated linear trends (solid lines) and 95% 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.

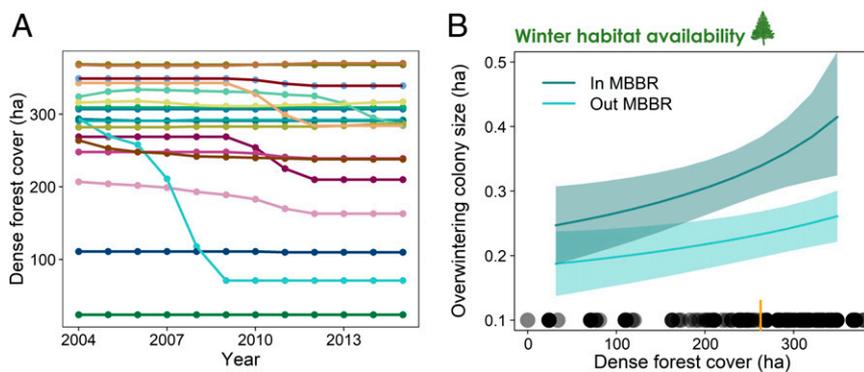


Fig. 4. Local-scale covariate effects (estimated from the top-supported model) on individual winter colony sizes (ha) during December 2004–2015. (A) Raw data showing the amount of dense (>70% canopy cover) forest (ha) surrounding each of 19 colony sites during 2004–2015 as measured within a 100 ha ellipse + 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. 4A), also positively affects annual monarch colony sizes [Fig. 4B; -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 3C; 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. 4B). 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. 4A), 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 sub-models: (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.

ACKNOWLEDGMENTS. We are grateful to the local communities within and around the Monarch Butterfly Biosphere Reserve for permission to conduct research on their properties and to the World Wildlife Fund for financial support to monitor colonies. We thank North American Butterfly Association volunteers, E. Howard for access to Journey North data, A. Sussman and J. G. López-Sánchez for creating the map of colonies, M. Farr and M. Plummer for statistical support, and N. Haddad and E. Zylstra for feedback on the paper. We also appreciate the insightful comments provided by G. Mitchell and an anonymous reviewer. This work was supported by the National Science Foundation (Awards EF-1702635 and EF-1702179) and PAPIIT-UNAM (Award IN 301215).

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SI Appendix – Saunders et al.

Monarch population biology

The eastern North American monarch butterfly population extends from the east coast of the United States to the Rocky Mountains during summer breeding, and overwinters in dense colonies in forests on a limited number of mountain peaks at the boundary of the Mexican states of Michoacán and México (1). Each spring (February and March), individuals fly from Mexico into Texas and surrounding areas where they lay eggs on milkweed (2, 3). Adult butterflies resulting from those eggs fly to northern breeding grounds throughout the central and eastern U.S. and southern Canada, arriving in May and June, and reproduce. An additional two to three generations are produced throughout the summer with the bulk of recruitment occurring in the Midwestern U.S. (4, 5). Individuals in the final generation migrate back to Mexico after entering reproductive diapause by late August.

Winter monarch data collection and covariate data

Winter monarch data collection.—To collect individual winter colony size data, a team of experienced individuals from the National Commission on Protected Areas (CONANP) of the Secretariat of the Environment and Natural Resources (SEMARNAT) and the World Wide Fund for Nature (WWF), accompanied by at least one local forest owner, visit all sites annually. Throughout the main text, we refer to a colony as aggregations of clustering butterflies relatively close to each other that exhibit a clear preference for a particular area of forest over time (6). Estimating the number of butterflies within colonies is virtually impossible due to the compact nature of their clusters and the complex architecture of the tree branches where they congregate.

NABA counts. – The North American Butterfly Association (NABA) compiles butterfly counts from citizen scientists through the Seasonal Count Program at approximately 450 established count circle locations (7, 8). Each point count location consists of a circle with a diameter of 25 km. One to several people survey the circle during a given day and report all individuals of all butterfly species observed. Effort is accounted for by multiplying the amount of time spent by the number of parties (groups of individuals) that searched during the survey (party-hours). We calculated the average number of monarchs per party-hour for all collection efforts conducted in the Midwestern United States (above 40° latitude band) during the period from 19 July – 15 August, which we used as a proxy for annual peak summer abundance ($NABA_t$, subscripted to indicate year t) during 2004 – 2015.

Journey North roosts. – Journey North citizen science participants report observations of nocturnal roosts, which monarchs form during their autumn migrations (9, 10). All reported roost observations are verified by Journey North staff and archived in an online database. Journey North sightings begin around 15 Aug and continue until 31 Oct each year across the United States and Mexico. We used an annual index of the number of reported autumn roosts from 2004 – 2015 ($Roosts_t$) and included only those roosts found in the central monarch flyway (i.e. Midwest migratory corridor; ref. 9, 11), since monarchs from Atlantic coastal locations constitute only a small fraction (approx. 23%; ref. 5) of the wintering cohort in Mexico (7, 12). We excluded roosts reported to be ≤ 50 butterflies (8% of sightings) because small roosts are over-reported under the current protocols (11). Additionally, we omitted repeat observations of the same roost by the same individual (i.e. only the first observation of a roost was used). These criteria (including omitting roosts found within states bordering the Atlantic coast) resulted in a total of 993 roost observations over 12 years. Because of a high correlation between $NABA_t$ and

$Roosts_t$ ($r = 0.58$), we independently tested their effects and retained the most strongly supported index (i.e. models with lowest Deviance Information Criterion [DIC]; see below) in subsequent models (13).

Autumn climate—We defined two annual temperature variables (average temperature and minimum temperature) at distinct spatiotemporal scales along the autumn migratory route. The time periods and regions of interest were determined via timing and location of sightings by citizen scientists over the 12-year period (10), as well as by monarch phenology (14). We restricted our calculation of autumn environmental variables (climate, NDVI) to within the central flyway (Fig. 2 in main text) because the majority of monarchs in the overwintering grounds likely use this region during migration. A smaller fraction of monarchs originating in the northeast use an eastern corridor to migrate, but they constitute less than a quarter of the overwintering population (5, 9). First, we acquired daily minimum and average temperatures throughout the first half of the migration route (Region 1) between 105°W, 40°N and 90°W, 30°N (Fig. 2 in main text) during 15 Sept – 15 Oct from Daymet (daymet.ornl.gov), which interpolates data from weather stations to produce spatially gridded estimates of daily weather (15). Second, we acquired daily minimum and average temperatures throughout the second half of the migration route (Region 2) between 105°W, 30°N and 95°W, 20°N (Fig. 2 in main text) during 15 Oct – 15 Nov. For both measures, we used daily minimum and average temperatures in a grid of points separated by 1 degree across the specified region, and averaged the values across each region to yield a single mean temperature ($avgTemp.R1_t$, $avgTemp.R2_t$) and minimum temperature ($minTemp.R1_t$, $minTemp.R2_t$) for each year t in each region (R1 and R2). Because regional values were highly correlated ($r = 0.86$ for min temp; 0.88 for mean temp), we independently tested the effects of the two temperature covariates for each region and retained the regional pair of covariates that was most strongly supported in subsequent models.

Normalized Difference Vegetation Index. – To assess the influence of nectar availability along the migration route on arrival abundances at the wintering grounds (and hence the ability to build up lipid reserves for successful migration; ref. 16), we used the Normalized Difference Vegetation Index (NDVI; lta.cr.usgs.gov/noaa_cdr_ndvi), which quantifies the density of green vegetation by calculating the visible and near-infrared light reflected by vegetation. Most of the energy (i.e. lipids) that adult butterflies use to fuel their activity is obtained from flower nectar (17, 18). Monarchs arrive at Mexican wintering sites with high lipid levels, suggesting that they accumulate lipid reserves in the southern U.S. and northern Mexico (14). NDVI is commonly used as an indicator of drought, primary biomass production, and herbivore resource availability on large spatial scales (19-21). Bottom-up effects resulting from drought can greatly reduce Lepidoptera resource availability (22, 23), and the relationship between plants and available moisture has been identified as a primary driver of population dynamics for a number of herbivorous insects (24-26).

In this study, we use the NDVI greenness index as a proxy for vegetation productivity/phenology (i.e. nectar resource availability), as has been done in several prior studies which assess NDVI associations with the distribution, abundance, and migratory condition of nectar-reliant organisms. For example, NDVI has been used as a proxy for: resource availability for butterflies (23); nectar flow for honeybees (27); vegetation heterogeneity in resources for butterfly species (19); and resource availability for migrating hummingbirds (28). NDVI has also been correlated with mosquito abundance (for those species that feed on nectar; 29) and giant honeybee abundance (16). Further, a recent study demonstrated a link between remotely-sensed productivity (EVI, enhanced vegetation index) and nectar abundance using

ground-truthed data from flowers (30). Taken together, these studies indicate that NDVI can accurately represent broad-scale nectar availability in the context of our analyses.

We defined NDVI at the same two spatiotemporal scales as the temperature covariates ($NDVI.R1_t$, $NDVI.R2_t$). We averaged these data across the two regions (Fig. 2 in main text) at monthly timescales during the autumns of 2004 – 2015. Because of a high correlation between regions ($r = 0.80$), we tested their effects individually and retained the most strongly supported covariate of the two measures. NDVI data were collected from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua (Instrument: MOD13Q1)/ Terra (Instrument: MYD13Q1 product) satellite at a 250 m spatial and 8-day temporal resolution.

OE parasitism rate—Monarchs infected by the protozoan parasite *Ophryocystis elektroscirrha* have reduced survival, flight speed, and flight endurance (31). The prevalence of infection in the population accumulates over the course of the breeding season such that monarchs of the final generation that are infected by *OE* are less likely to complete the autumn migration (32, 33). We included the annual proportion of the eastern migratory population (i.e. during the autumn migratory/early wintering period) infected with *OE* ($OEInfect_t$) from 2004 – 2014 (32, 34) with an imputed missing value for 2015 (using the mean value from 2004 – 2014; 35) because data were not available for that year (34).

Forest habitat availability.— To identify changes in forest area and condition between 2004 and 2015, we used a map series (36-38) generated for a long-term land cover monitoring project of the Monarch Butterfly Biosphere Reserve and its surrounding area (286,993 ha). We used maps which show land cover for the years of 2003, 2006, 2009, and 2012 generated at a 1:40,000 scale. To update the map series for 2015, we used Landsat ETM+ images 27/46-47 (glovis.usgs.gov), SPOT images (ERMEX-SPOT), and high resolution GeoEye images (Google Earth Pro). On-screen visual interpretation and map analysis were carried out using ArcGIS 9.0. We extracted polygons of dense forest (canopy cover > 70%, indicative of well-preserved forests) and open forest (canopy cover 40 – 70%) from the available land cover maps. We defined two covariates related to forest habitat availability at each of j individual colonies: the amounts of (1) dense forest cover ($DForest_{j,t}$) and (2) dense + open forest cover ($DOForest_{j,t}$) at individual colony sites. Dense forest cover provides the optimal microclimate for wintering monarchs, whereas open forest cover represents habitat that is usable but sub-optimal. Each covariate was measured in hectares and calculated annually around individual colony sites within a 100 ha critical area (i.e. historical perching area, 1994 – 2015) with an additional 500 m out from the perimeter of the critical area (i.e. adjacent areas where monarchs fly in search of water). The 500 m buffer distance was selected based on the average proximity of the critical areas to water, as well as the maximum distance monarchs typically travel from roost edges. To best capture microclimate conditions, critical area ellipses were oriented downhill and accounted for both the microbasin and the known ravine each colony used for movement.

Colony locations are not random over time; rather, monarchs tend to congregate in the same general areas year after year, which are represented by the critical area designations. All ellipses were the same area but differed in shape (Fig. 2 in main text) depending on the spatial distribution of colony location points (39, 40). Because the shape of critical area ellipses varied, the size of the buffer areas also varied depending on the area/perimeter ratio (Fig. 2 in main text), thus accounting for the total potential habitat used by monarchs at each site. Two colony sites (El Calabozo Fracción and Sierra Chincua State) shared an ellipse due to close geographical proximity. Land cover data were not available in every year of the study period, so we used linear extrapolation between available years to obtain missing estimates. Because of a high

correlation ($r = 0.85$) between $DForest_{j,t}$ and $DOForest_{j,t}$, we independently tested their effects and retained the most strongly supported forest cover covariate in subsequent models.

Previous year dynamics—In addition to wintering habitat availability, we considered two autoregressive covariates in our models: (i) presence/absence of individuals at a colony site ($ColPres_{j,t-1}$) in the previous year (evaluated on the first part of the two-part model; see modeling details below), and (ii) colony size ($ColSize_{j,t-1}$) at each site in the previous year (tested on the second part of the two-part model). We incorporated these variables to test for a potential spatiotemporal effect between colony occurrence and monarch abundances from year to year.

Colony presence within/outside of Monarch Butterfly Biosphere Reserve—We included a site-specific categorical variable indicating whether the colony was located within ($Reserve_j = 1$, $n = 14$ sites) or outside ($Reserve_j = 0$, $n = 5$ sites) of the Monarch Butterfly Biosphere Reserve. The reserve is known to hold the largest aggregations of monarchs, and therefore the majority (~70%) of the wintering population (39, 40).

Rationale for use of gamma zero-altered hurdle model

Two-part (or ‘zero-altered hurdle’) models applied to ecological and biological questions are useful when observational data show overdispersion and excessive zero values (41-45; Fig. S4). These models are referred to as ‘hurdle’ models because, regardless of the mechanisms causing an increase in the response variable, a hurdle must first be crossed before the data are observed (46, 47). Ecologically, it is relevant to consider these two processes separately because predictors that determine the presence-absence of colonies can be different from those describing abundance (conditional on presence). Statistically, ignoring the large number of non-detections (i.e. areas occupied < 0.01 ha) is problematic as it could result in exaggerated estimates of variance and biased estimates of parameters and standard errors (48, 49).

We chose a zero-altered model, as opposed to a zero-inflated mixture model, to deal with the high number of zeros in the data because we were interested in the probability of not measuring any detectable colony/area occupied versus measuring any size colony/area occupied (i.e. probability of occurrence). In contrast, the aim of zero-inflated mixture models is to discriminate between false and true zeros (i.e. count process allows for zeros). When modeling continuous data that has too many zeros, a distribution with inflated error is needed. However, the gamma distribution, which accurately captures the long tail in the colony size data, does not allow for zero values, so modeling the zeros separately from the non-zeros in a binomial-gamma hurdle model is recommended (41, 42). To account for pseudoreplication of sites, as well as any unaccounted for site-specific variation, we included colony site as a random effect on both parts of the hurdle model (46).

We estimated parameter values for all models using a Bayesian approach with JAGS (50) called from program R (R package jagsUI; 51) using flat normal priors on all of the parameter values (see below for model code). We ran three chains for 150,000 iterations after a burn-in of 100,000 iterations and adaptation phase of 5,000 iterations, and thinned the chains by five. Model convergence was assessed with the Rhat statistic (52) and visual inspection of chains.

Additional details on model selection procedure and results

We started our analyses with 14 environmental variables described in Table S1. Given the high correlation in many variables (see covariate descriptions), we used a forward selection approach to model fitting. In the first step, we evaluated support for univariate models using the Deviance Information Criterion (DIC). While DIC has limitations, model selection and parameter

estimation with DIC have been effectively applied in hierarchical analyses and demonstrated to be useful for inference (53, 54). To the null model (which included random site effects), we added each of the covariates individually and discarded any uninformative covariates that led to increased DIC values after each step. If multiple covariates yielded a reduction in DIC compared to the null model, the model with the lowest DIC was used as a base model for considering additional covariates. If two or more covariates were selected, we also considered biologically reasonable interaction terms (i.e. within the same spatial scale; see below). When additional covariates no longer led to a reduction in DIC, the best-supported model from the previous step was retained as the top-supported model.

Of the 14 covariates (i.e. univariate models) tested, the following eight covariates lowered DIC as compared to the null model: peak summer abundance index ($NABA_t$), autumn migratory roost index ($Roosts_t$), greenness in Region 1 (see Fig. 2 in main text) during the first half of migration ($NDVI.R1_t$), greenness in Region 2 (see Fig. 2 in main text) during the second half of migration ($NDVI.R2_t$), whether the colony was located within the Monarch Butterfly Biosphere Reserve ($Reserve_j$), average autumn temperature in Region 1 during the first half of migration ($avgTemp.R1_t$), dense forest cover surrounding colony locations ($DForest_{j,t}$), and dense + open forest cover surrounding colony locations ($DOForest_{j,t}$).

Given that $NDVI.R1_t$ and $NDVI.R2_t$ were highly correlated with each other ($r = 0.80$), we retained $NDVI.R1_t$ in all subsequent models because it led to a greater reduction in DIC ($\Delta DIC = 8.1$). However, support for both greenness indices (proxy for nectar availability) indicate an association between nectar availability throughout the migration route with arrival abundances on overwintering grounds. Similarly, $DForest_{j,t}$ and $DOForest_{j,t}$ were strongly correlated ($r = 0.85$); $DForest_{j,t}$ led to a greater reduction in DIC ($\Delta DIC = 6.3$) so was retained in all subsequent models. Stronger support for $DForest_{j,t}$ over $DOForest_{j,t}$ in our models reinforces previous evidence that forest thinning should be prevented within and adjacent to overwintering sites to minimize exposure of butterflies to inclement conditions that increase winter mortality. Finally, $NABA_t$ and $Roosts_t$ were both supported yet were correlated ($r = 0.58$); $NABA_t$ was retained in subsequent models given that it led to a greater reduction in DIC ($\Delta DIC = 13.2$). Support for both summer/autumn indices provides further evidence of a link in population dynamics across the autumn period, although the weaker support for $Roosts_t$ over $NABA_t$ suggests that our roost index does not fully capture the autumn migratory population (i.e. the index may be too coarse).

We carried the five remaining supported covariates forward in selection of multivariate models (ensuring that correlated predictors were not included in a model simultaneously) and tested two-way interaction terms between covariates within the same spatial scale that were included in the same model. Thus, we tested the following interactions: $DForest_{j,t} \times Reserve_j$, $NABA_t \times NDVI.R1_t$, $NABA_t \times avgTemp.R1_t$, and $NDVI.R1_t \times avgTemp.R1_t$. Inclusion of these interaction terms did not yield models with lower DIC values, so interactions were not included in subsequent models. The ten most strongly supported models are provided in Table S2; note that the top model, which included only main effects of $NABA_t$, $NDVI.R1_t$, $Reserve_j$, and $DForest_{j,t}$, clearly provides the best fit to the data (with $\Delta DIC = 4.5$ for the second ranked model).

Results on colony occurrence probabilities

The probability of annual monarch colony occurrence at each of the 19 overwintering sites ranged between 0.15 and 0.91 on average (Table S3). Mean probabilities of colony occurrence were highest at El Rosario, San Antonio Albarranes, and San Mateo Almomoloa (Table S3).

Mean colony sizes, conditional on occurrence, ranged between 0.01 and 1.25 ha for average covariate values, with the largest expected colony sizes at El Rosario (see Fig. 1 in main text).

Models fit with additional years of data at the aggregate colony level

To ensure that our estimated relationships with autumn temporal covariates in our top-supported model (i.e. NDVI, dense forest cover, NABA counts) were not a product of beginning our analysis in 2004, we fit a gamma mixed model using the aggregated colony sizes (i.e. total overwintering abundance) during 2000 (the first year NDVI data are available) to 2015 as a function of annual measures of NDVI, total dense forest cover (summed across all colony sites), NABA counts, and a random effect of year (to account for possible dependence due to temporal autocorrelation). Fig. S2 illustrates the estimated relationships between each variable and total overwintering population size – all of which follow the same trend as that of our colony-level analysis beginning in 2004. Parameter estimates for each covariate were in the same direction, albeit the effect sizes were smaller and 95% credible intervals overlapped zero (see Table S4 below). We fit the same aggregate model starting with data from 2004 to demonstrate that these species-environment relationships exist at both fine and broad spatial scales (Table S4).

Comparison of linear trends and total variation in residuals among models

We calculated residuals to evaluate model fit and to examine any trends in the residuals. Comparison of trends in the residuals (via post-hoc Bayesian linear regression with year as the explanatory variable) allowed us to assess how well our models fit over time. Comparison of variation (standard deviation [SD]) in residuals among models allowed us to assess the amount of variation explained by the predictors in each model. Greater variation in the residuals during a given time period (i.e. higher SD) represents greater variability in the response (i.e. more remaining unexplained temporal variation), indicating that the predictors in the model poorly explain fluctuations in colony sizes. If the residuals are minimally variable (i.e. lower SD), the predictors account for more of the temporal variation in colony sizes. For example, there is a much greater spread (i.e. higher SD) of residual values in the bottom row of Fig. S3 versus the top row.

We fit models using aggregate colony data starting in 2000 (the first year NDVI data are available) and 2004 (timeframe of colony-level analysis). We included the top-supported temporal covariates from our colony-level analysis in these models (peak summer index, greenness index in region 1, dense forest cover summed across colonies, and a random effect of year). Posterior means of residuals from these two models exhibited slight declines over time (top row of Fig. S3), whereas mean residuals from a model fit with only peak summer index (since 2000 and 2004) exhibited statistically significant negative trends (bottom row of Fig. S3). In comparison, mean residuals from our colony-level top model do not show a significant trend over time (Fig. S1), demonstrating adequate fit with the fine-scale model throughout the timeframe of our analysis.

Although our colony-level model underestimated certain colony sizes (i.e. the consistently large colonies) early in the time series, our fine-scale model has the lowest variation (SD range: 0.03 – 0.57) of mean residual values compared to the aggregate models. Note that we compare the mean and range of the 19 colony-specific SDs from our colony-level model (Fig. S1) with the SDs from the aggregate models for a more equivalent comparison than simply the SD of all 228 mean residual values. These results suggest that (i) summing colony-level data masks important local-scale variation and (ii) accounting for spatial heterogeneity of individual

colony sizes is key to explaining temporal variation in monarch abundances. Importantly, failure to consider effects of both autumn greenness (i.e. proxy for broad-scale nectar availability) and dense forest cover on winter population sizes results in significantly more unexplained temporal variation in residuals compared to summer-only models.

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```

R/JAGS code for the most strongly supported hierarchical gamma hurdle
model
#-----
# Hierarchical zero-altered gamma hurdle model for estimating
# overwintering monarch butterfly colony sizes at 19 sites in central
# Mexico during December 2004 - 2015.
# Author of code: Sarah Saunders (2017 - 2018)
#-----
sink("fall_model_best")
cat("
model{

# Priors
a1 ~ dnorm(0,0.01)
a2 ~ dnorm(0,0.01)
a3 ~ dnorm(0,0.01)
a4 ~ dnorm(0,0.01)
a5 ~ dnorm(0,0.01)

tau.a8 <- pow(sigma.a8, -2)
sigma.a8 ~ dunif(0, 10000)
tau.a9 <- pow(sigma.a9, -2)
sigma.a9 ~ dunif(0, 10000)

g0 ~ dnorm(0, 0.01)
sd ~ dgamma(2,2)

# For the ones trick
C <- 100000

for (j in 1:usite){
  # Random effect of site on both model parts
  a8[j] ~ dnorm(0, tau.a8)
  a9[j] ~ dnorm(0, tau.a9)

for (t in 1:year){
  # Define logistic regression model, w is probability of occurrence
  # Use the logistic transformation  $\exp(z)/(1 + \exp(z))$ 
  logit(w[j,t]) <- zeta[j,t]
  zeta[j,t] <- g0 + a9[j]

  # Define gamma regression model for the mean using inverse link
  mu[j,t] <- pow(eta[j,t], -1)
  eta[j,t] <- a1 + a2*naba.st[t] + a3*nectar.st1[t] +
a4*forestd.st[j,t] + a5*reserve[j] + a8[j]

  # Redefine mu & sd of continuous part into shape & rate parameters
  shape[j,t] <- pow(mu[j,t], 2) / pow(sd, 2)
  rate[j,t] <- mu[j,t] / pow(sd, 2)

  # For readability, define log-likelihood of gamma
  logGamma[j,t] <- log(dgamma(y[j,t], shape[j,t], rate[j,t]))

```

```

# Define total likelihood, where likelihood is (1 - w) if y <
# 0.0001 (z = 0) or likelihood is w * gammadik if y >= 0.0001 (z =
# 1). So if z = 1, then first part must be 0 and second part must
# be 1. Use 1 - z, which is 0 if y > 0.0001 and 1 if y < 0.0001.
# Z matrix is data and consists of dummy variable of 0s where y >
# 0.0001 and 1s where y < 0.0001.

logLik[j,t] <- (1 - z[j,t])*log(1 - w[j,t]) + z[j,t]*(log(w[j,t])
+ logGamma[j,t])

Lik[j,t] <- exp(logLik[j,t])

# Use the ones trick (matrix of ones fed in as data)
p[j,t] <- Lik[j,t] / C
ones[j,t] ~ dbern(p[j,t])
}
}
}
sink()

## PREP JAGSUI DATA ##
bugsdata <- list(uyear=length(uyear), usite=length(usite),
y=data.matrix(fallmonarchs), z=data.matrix(non_zero),ones=ones,
naba.st=naba.st, nectar.st1=nectar.st1, reserve=reserve,
forestd.st=forestd.st)

inits <- function(){
list(a1=runif(1,1,10),a2=rnorm(1),a3=rnorm(1),a4=rnorm(1),a5=rnorm(1),
g0=rnorm(1))
}

parameters<-c('a1', 'a2', 'a3', 'a4', 'a5', 'g0', 'sigma.a8',
'sigma.a9', 'w')

## RUN BUGS MODEL IN JAGSUI ##
fall.model.best <- jags(data = bugsdata, inits = inits,
parameters.to.save = parameters, model.file = 'fall_model_best.txt',
n.chains = 3, n.adapt = 5000, n.iter = 150000, n.burnin = 100000,
n.thin = 5, parallel = TRUE, store.data = TRUE)

```

Table S1. Continental- and local-scale environmental variables evaluated in our models.

Covariate category	Covariate abbreviation	Description
Continental-scale		
Monarch population size	$NABA_t$	North American Butterfly Association index of monarch counts from 19 July – 15 Aug in Midwestern U.S. [peak summer population]
	$Roosts_t$	Journey North index of roosts migrating through central flyway from 15 Aug – 31 Oct [autumn migratory population]
Autumn climate	$avgTemp.R1_t$	Daily mean temperatures averaged in Region 1 (Fig. 2) during 15 Sept – 15 Oct [first half of migration]
	$avgTemp.R2_t$	Daily mean temperatures averaged in Region 2 (Fig. 2) during 15 Oct – 15 Nov [second half of migration]
	$minTemp.R1_t$	Daily minimum temperatures averaged in Region 1 (Fig. 2) during 15 Sept – 15 Oct
	$minTemp.R2_t$	Daily minimum temperatures averaged in Region 2 (Fig. 2) during 15 Oct – 15 Nov
Greenness index	$NDVI.R1_t$	NDVI measured in Region 1 (Fig. 2) during 15 Sept – 15 Oct [proxy of nectar availability]
	$NDVI.R2_t$	NDVI measured in Region 2 (Fig. 2) during 15 Oct – 15 Nov
Parasitism	$OEInfect_t$	Proportion of larvae infected with protozoan parasite <i>Ophryocystis elektroscirrha</i>
Local-scale		
Previous year dynamics	$ColPres_{j,t-1}$	Presence/absence of a colony at each site in previous year
	$ColSize_{j,t-1}$	Size of a colony at each site in previous year
Forest habitat availability	$DForest_{j,t}$	Amount of dense forest (> 70% canopy cover) surrounding each colony, measured within 100 ha ellipse + 500 m buffer
	$DOForest_{j,t}$	Amount of dense + open forest (40 – 70% cover) surrounding each colony, measured within 100 ha ellipse + 500 m buffer
Reserve location	$Reserve_j$	Indicator of whether a colony was located within (1) or outside of (0) the Monarch Butterfly Biosphere Reserve

Subscripts t and j refer to year and colony site, respectively; covariate abbreviations in main text.

Table S2. The ten most strongly supported models of winter monarch butterfly colony sizes at all known sites in central Mexico during December 2004 – 2015. The null model is also shown.

Model	DIC	Δ DIC	Number of parameters
$NABA_t + NDVI.RI_t + DForest_{j,t} + Reserve_j$	5457.8	0.0	6
$NABA_t + NDVI.RI_t + DForest_{j,t}$	5462.3	4.5	5
$NABA_t + NDVI.RI_t + Reserve_j$	5462.8	5.0	5
$NABA_t + NDVI.RI_t$	5464.1	6.3	4
$NABA_t + DForest_{j,t}$	5467.4	9.6	4
$NABA_t + NDVI.RI_t + avgTemp.RI_t$	5467.5	9.7	5
$NABA_t + Reserve_j$	5467.9	10.1	4
$NABA_t + NDVI.RI_t + DForest_{j,t} + avgTemp.RI_t$	5468.1	10.3	6
$NABA_t$	5468.4	10.6	3
$NABA_t + avgTemp.RI_t$	5472.1	14.3	4
Null model	5500.8	43.0	2

Models were ranked according to differences in the Deviance Information Criterion (Δ DIC). All covariates shown were included on the gamma submodel only. Models also included an intercept term and colony site as a random effect on each part of the hurdle model (i.e. logistic and gamma submodels). See Table S1 for covariate descriptions.

Table S3. Parameter estimates from the most strongly supported model estimating winter monarch butterfly colony size at all 19 sites in central Mexico during 2004 – 2015.

Parameter	Mean	95% CI	85% CI	50% CI
NABA [gamma submodel]	-0.423	-0.690, -0.217	-0.607, -0.263	-0.498, -0.339
NDVI [gamma]	-0.351	-0.647, -0.056	-0.563, -0.138	-0.448, -0.252
Dense forest [gamma]	-0.530	-1.332, 0.145	-1.087, -0.028	-0.757, -0.277
Reserve [gamma]	-1.389	-2.772, -0.084	-2.388, -0.402	-1.827, -0.938
Intercept [gamma]	4.389	3.221, 5.780	-	-
Random site effect SD [gamma]	0.938	0.527, 1.578	-	-
Intercept [logistic submodel]	0.108	-0.757, 1.044	-	-
Random site effect SD [logistic]	1.701	0.984, 2.810	-	-
<i>w</i> E. Contepec	0.217	0.051, 0.456	-	-
<i>w</i> IC Carpinteros	0.647	0.386, 0.866	-	-
<i>w</i> Sierra Chincua Fed	0.287	0.091, 0.540	-	-
<i>w</i> Sierra Chincua State	0.358	0.137, 0.618	-	-
<i>w</i> E. Cerro Prieto	0.502	0.251, 0.751	-	-
<i>w</i> El Calabozo Fracción	0.218	0.052, 0.461	-	-
<i>w</i> IC Crescencio Morales	0.288	0.091, 0.542	-	-
<i>w</i> E. Nicolás Romero	0.358	0.138, 0.619	-	-
<i>w</i> E. El Rosario	0.914	0.729, 0.996	-	-
<i>w</i> E. La Mesa	0.429	0.191, 0.687	-	-
<i>w</i> E. San Juan Xoconusco	0.359	0.137, 0.619	-	-
<i>w</i> El Capulín	0.575	0.319, 0.812	-	-
<i>w</i> Mesas Altas de Xoconusco	0.151	0.022, 0.372	-	-
<i>w</i> IC San Pablo Malacatepec	0.358	0.136, 0.615	-	-
<i>w</i> PP San Andrés	0.647	0.385, 0.867	-	-
<i>w</i> Río de Parras	0.647	0.387, 0.866	-	-
<i>w</i> San Francisco Oxtotilpan	0.718	0.465, 0.913	-	-
<i>w</i> San Antonio Albarranes	0.913	0.729, 0.996	-	-
<i>w</i> San Mateo Almomoloa	0.913	0.728, 0.996	-	-

The 95% credible intervals (CI) for all parameters are shown; 85% and 50% CIs for covariate effects on gamma submodel also shown for reference. NABA = $NABA_t$, NDVI = $NDVI.RI_t$, Dense forest = $DForest_{j,t}$, Reserve = $Reserve_j$, w_j = probability of colony occupancy at each site j (estimated from logistic submodel), SD = standard deviation; see Table S1 for covariate descriptions. Negative mean values indicate a positive effect due to the use of an inverse-log link function for the gamma distribution abundance submodel (i.e. all four covariates in the top-supported model had a positive association with winter colony sizes).

Table S4. Parameter estimates from the most strongly supported model (with random year effect) fit using total winter monarch butterfly colony sizes annually (i.e. aggregated colony-level data) in central Mexico during 2000 – 2015 and 2004 – 2015.

Parameter	Mean	95% CI	85% CI
<i>2000 – 2015</i>			
NABA	-0.075	-0.181, 0.004	-0.145, -0.017
NDVI	-0.086	-0.225, 0.015	-0.173, -0.010
Dense forest	-0.119	-0.227, -0.036	-0.191, -0.057
Intercept	0.321	0.240, 0.431	0.258, 0.394
Random year effect SD	0.107	0.030, 0.224	0.046, 0.181
<i>2004 – 2015</i>			
NABA	-0.174	-0.322, -0.070	-0.270, -0.095
NDVI	-0.180	-0.439, 0.054	-0.359, -0.006
Dense forest	-0.215	-0.556, 0.066	-0.437, -0.021
Intercept	0.381	0.197, 0.609	0.250, 0.522
Random year effect SD	0.091	0.007, 0.282	0.019, 0.203

The 95% and 85% credible intervals (CI) for all parameters are shown. Negative mean values indicate a positive effect due to the use of an inverse-log link function (i.e. all three covariates had a positive association with total winter population size). SD = standard deviation.

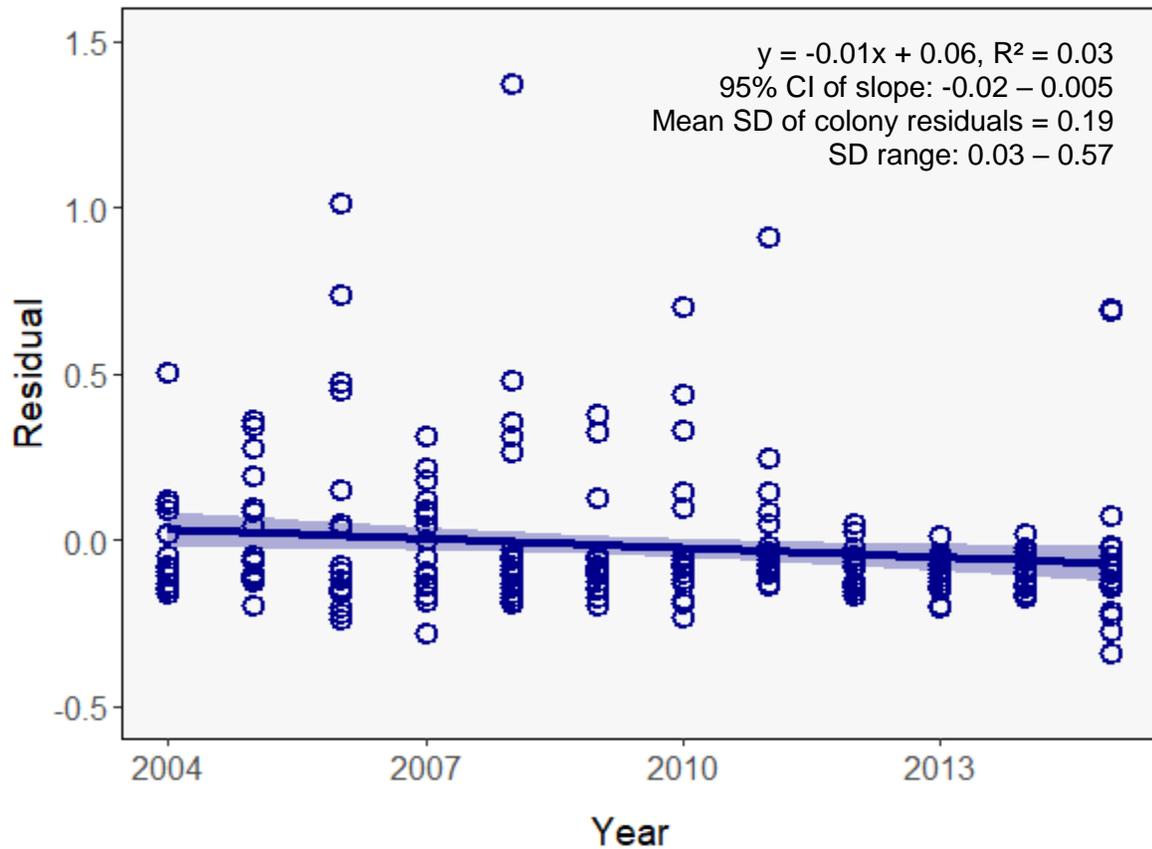


Figure S1. Posterior means (from 30,000 MCMC simulations) of estimated residuals from our top-supported hierarchical gamma hurdle model using colony-level size data (from all 19 known winter colonies) during 2004 – 2015 as a function of peak summer index (NABA counts), autumn greenness in region 1 (NDVI), dense forest cover surrounding colony locations, whether a colony was located inside/outside of the reserve, and random site effects on both parts of the hurdle model. The linear trend (solid line) and associated 95% credible interval (shading) are shown. Text indicates linear equation (for a post-hoc Bayesian regression), R^2 (amount of variance explained by year), 95% credible interval of slope, and standard deviation (SD, mean and range) of residual values.

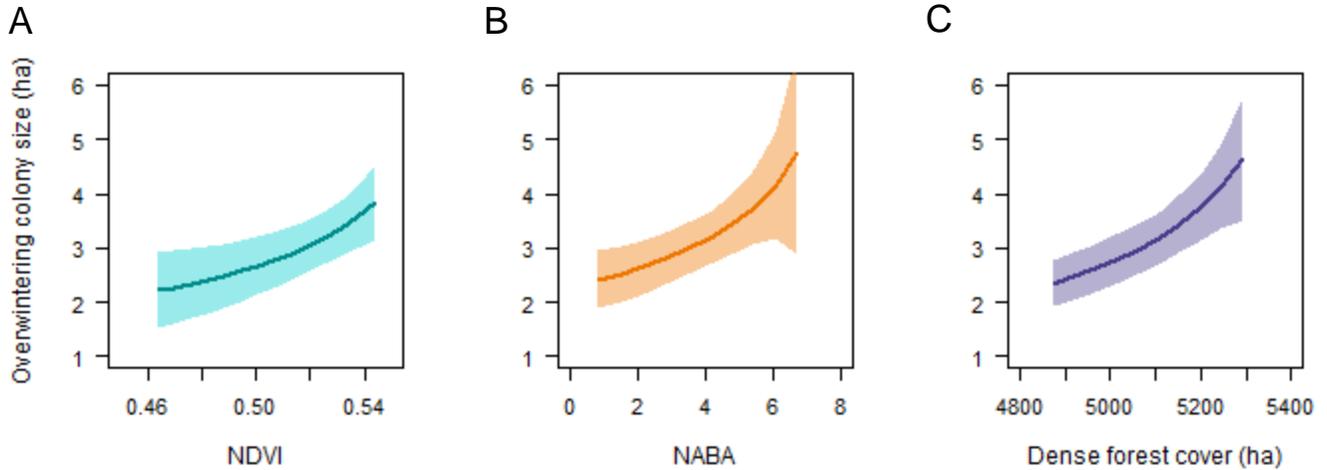


Figure S2. Covariate effects of (A) NDVI during the first half of autumn migration, (B) NABA counts (peak summer index), and (C) dense forest cover (ha; summed across colonies) on total overwintering colony size during 2000 – 2015, as estimated using a model with aggregated winter colony data. Solid lines show the marginal effect (with 95% credible intervals shaded) when all other covariates are held at their mean values.

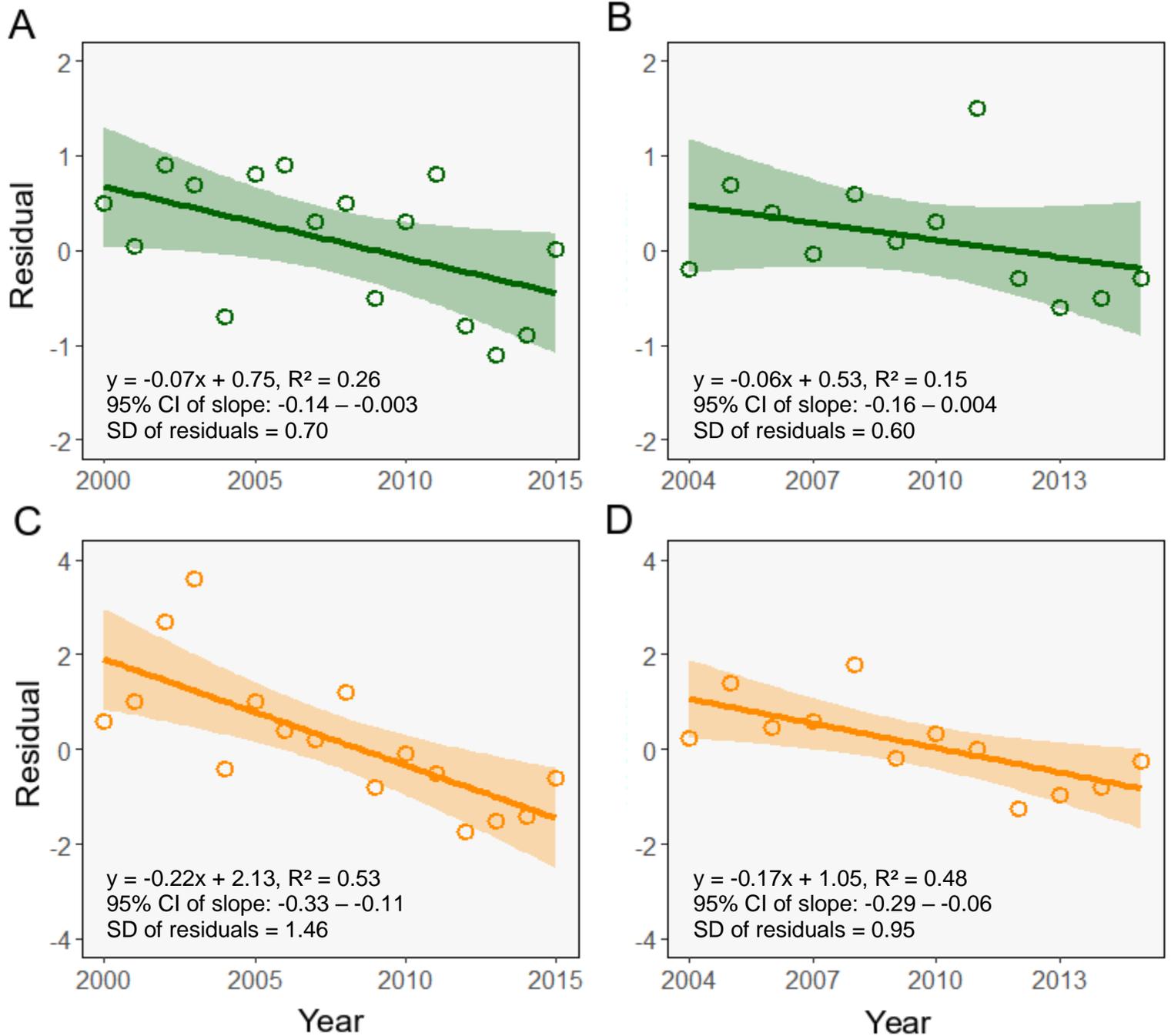


Figure S3. Estimated residuals (posterior means from 30,000 MCMC simulations) from gamma mixed models fit using aggregate colony data during 2000 – 2015 (A & C) and 2004 – 2015 (B & D). In A & B, models included peak summer index (NABA counts), autumn greenness in region 1 (NDVI), total dense forest cover surrounding colony locations (summed across colonies), and a random effect of year. In C & D, models included only peak summer index (NABA counts) and a random effect of year. The linear trend (solid line) and associated 95% credible interval (shading) are shown for post-hoc Bayesian regressions of the residuals. Text indicates linear equation, R^2 (amount of variance explained by year), 95% credible interval of slope, and standard deviation (SD) of residual values.

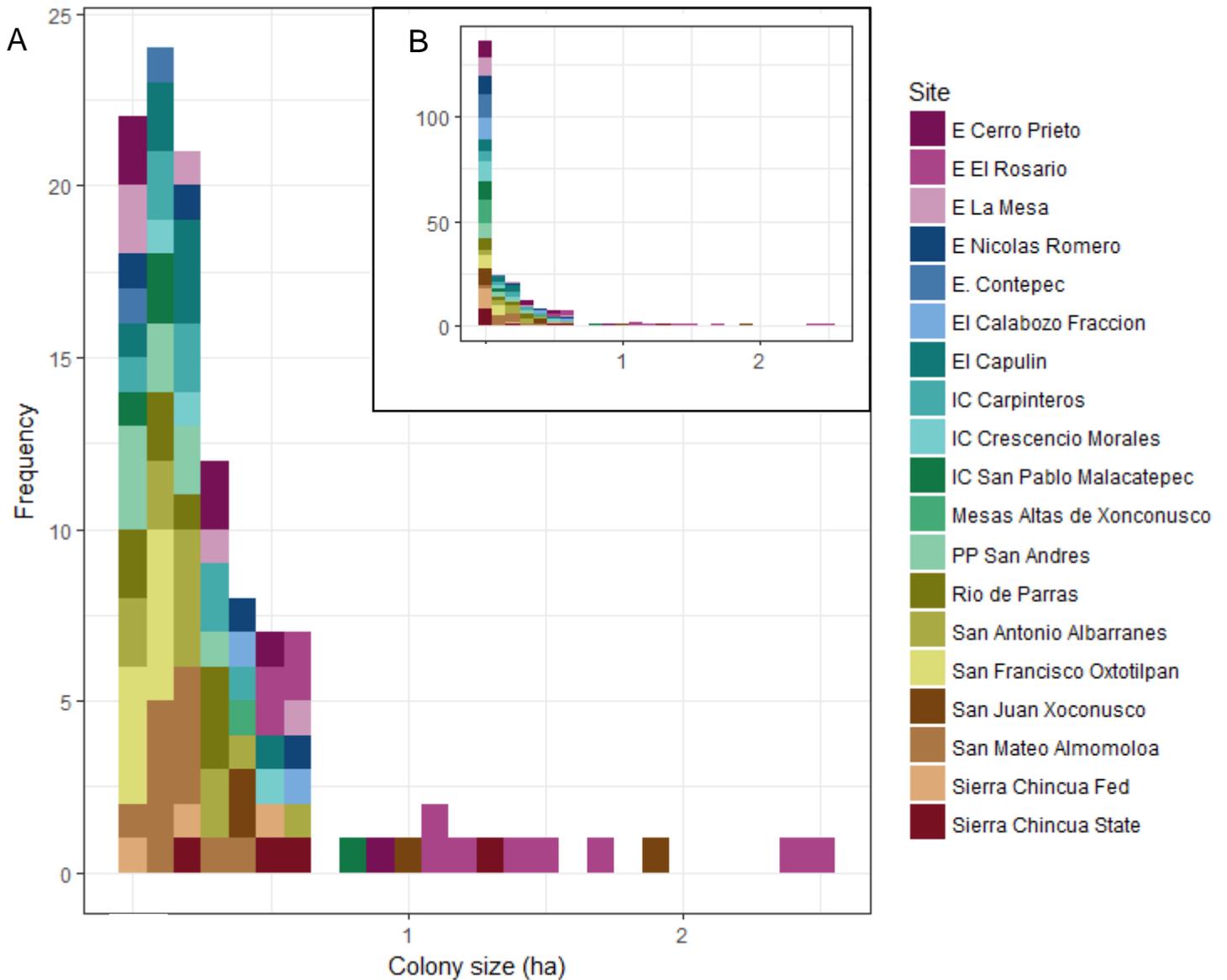


Figure S4. Histograms of monarch butterfly wintering colony sizes (hectares). (A) Annual observations across all 19 colony sites during December 2004 – 2015, excluding zero values (i.e. ≥ 0.01 ha; $n = 114$ or 50% of site-years). (B) Total annual observations, including zeros ($n = 228$). Color coding represents the colony site and matches that of Fig. 1 in main text. E. El Rosario, San Antonio Albarranes, and San Mateo Almomoloa had a colony detected every year during the study period.