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Three decades of declines restructure butterfly communities in the Midwestern United States

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Insects are declining worldwide. These declines have been documented across taxonomic groups and are worrisome given ecosystem services provided by insects. Long-term data have illuminated butterfly declines across geographic regions. However, critical questions remain on how butterfly declines are distributed across species and functional groups, limiting effective conservation. Here, we show unprecedented changes in butterfly biodiversity resulting from 32 y of species levels declines throughout the Midwestern United States. No species increased over the three-decade study period and abundance declined across every functional group (e.g., rare, common, migratory, resident; annual mean trend: −0.9 to −2.3% per year). Species richness declined across all but one functional group, with concomitant increases in evenness (e.g., abundance among species) in several groups resulting from steeper losses in abundance for common species (abundance: −1.9% per year; richness: −0.04% per year) as compared to rare species (abundance: −0.9% per year; richness: −1.33% per year). Our results paint a bleaker picture than other butterfly studies likely due to our long time series of data and ability to include rare species. Such widespread declines undoubtedly affect other trophic levels and ecosystem services. Focusing risk assessments and management interventions only on rare species is likely to be insufficient given broad declines across species, which have fundamentally restructured butterfly communities in the region. As such, conservation efforts should shift focus to species assemblages and entire communities when possible.

biodiversity | insect decline | integrated community model | Lepidoptera

Insects are declining worldwide across taxonomic groups and ecosystems (1–4). Losses have been documented in human-dominated landscapes as well as protected areas (5, 6), and in both common and rare species (7). Insects provide innumerable ecosystem services including pollination, herbivory, prey for other animals, and decomposition; they also supply humans with silk, wax, dyes, and food (8, 9). Continued insect declines could lead to loss of essential, irreplaceable services to humans (10) and other animals (11). For example, caterpillars (larval butterflies and moths) transfer energy from plants to other animals (12) and are the primary food for the offspring of breeding birds in North America, even those that generally do not feed on insects as adults (13, 14). Despite the important roles that insects fulfill, critical questions about which species are declining most rapidly, where such declines occur, and how species-level declines are distributed among taxonomically and functionally similar community members remain largely unanswered, limiting conservation efforts.

Butterflies are the most extensively surveyed insects, thanks to monitoring programs that harness the enthusiasm of volunteer scientists worldwide (15, 16). These monitoring programs have cataloged long-term declines in different countries, including losses of 50% in the United Kingdom and the Netherlands since 1976 and 1990, respectively (4). In the United States, a recent analysis found a 22% decline in the total abundance of butterflies from 2000 to 2020 (17). However, data limitations and challenges in interpreting long-term trends have restricted the spatial, taxonomic, and temporal extent at which insect declines are documented (18, 19). Single-species research tracking trends of flagship species such as the monarch butterfly have been important for identifying environmental stressors connected to population dynamics (20, 21), but these trends and drivers may not be indicative of the responses of other butterfly species (22, 23). Some datasets provide coarse snapshots (16, 24) over regional or nation-wide spatial extents, while others provide repeated site-level monitoring across smaller geographic extents (25, 26). No single data source provides the ideal information: data on the entire butterfly community across a regional spatial extent with structured surveys over a long time series. Yet, by combining data sources and using hierarchical community modeling approaches, we

Significance

Insects are declining worldwide, yet gaps remain in our understanding of how declines are distributed across species within communities. Using three decades of butterfly monitoring data aggregated from the Midwestern United States, we found that no butterfly species increased in abundance from 1992 to 2023. 59 out of 136 species declined (annual mean trend: −1.2 to −6.9% per year) with losses distributed across all functional groups including residents, migrants, rare, and common species. Community composition changed such that abundance is now more even across species, driven by more severe losses in abundance—but not richness—of common species compared to rare species. These widespread declines are likely cascading across ecosystems. Conservation efforts that focus on entire communities could mitigate butterfly biodiversity loss.

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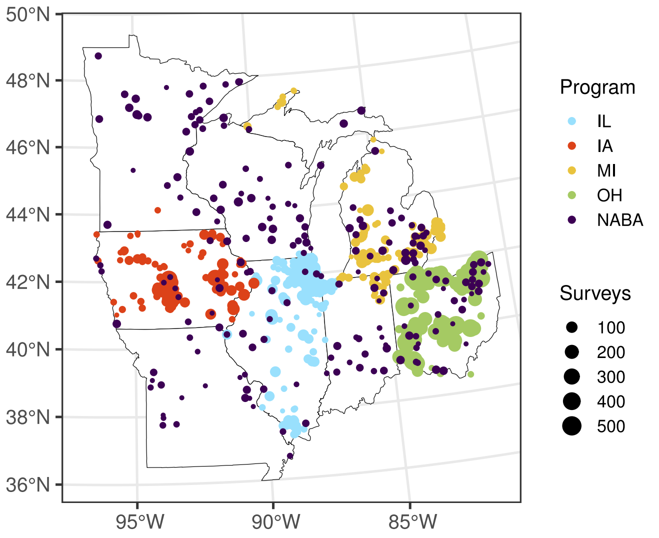

Fig. 1. Total number of surveys within the Midwestern United States from 1992 to 2023. Data come from five volunteer-based monitoring programs: 1) Illinois Butterfly Monitoring Network (IL); 2) Iowa Butterfly Survey Network (IA); 3) Michigan Butterfly Network (MI); 4) Ohio Lepidopterists (OH); and 5) North American Butterfly Association (NABA).

leveraged data from multiple monitoring programs to obtain a holistic view of the Midwestern US butterfly community.

Here, we document unprecedented changes in 136 species within the Midwestern US butterfly community by integrating data from five distinct participatory science programs. The data come from more than 90,000 h of surveys with >4.3 million butterfly observations collected between 1992 and 2023 (Fig. 1). Using an integrated community model (27), we estimate both single species and community-wide relative abundance indices for Midwestern butterflies over the 32-y time frame. Our model estimates both species and community-level abundance parameters at the county-level across each growing season of the study period, borrowing power from common species to obtain estimates of rare species that elude single-species modeling efforts. Through post hoc analyses, we derive annual relative abundance indices for every species based on their activity curve throughout each growing season (the annual time period that butterflies are active in the study area). We use these indices as the basis for calculating trends for individual species and functional groups, as well as community metrics including species richness and evenness, all while propagating uncertainty within a Bayesian framework.

Butterfly biodiversity declined precipitously in the Midwestern United States over the three-decade study period. We found no species or group of species that increased in abundance or species richness (the total number of species), shifting communities to greater uniformity of abundance among member species. Within counties, richness declined by −0.3% per year (95% credible interval [CI] of the trend estimate does not overlap zero, Fig. 2), resulting in a median decrease in species of −9.1% over the study period. We estimated a concomitant increase in species evenness [via (28), Fig. 2]. We calculated trends for species groups based on their prevalence (common vs. rare) and functional traits (specialist vs. generalist [one or >1 host plant family], number of generations per year, migratory vs. resident, overwintering strategy). Migratory species did not change in richness (trend = 0.00 species per year, −0.02% per year, 95% CI: [−0.02, +0.01]), while all other groups declined in county-level richness (−0.01 to −0.15 species per year; −0.04 to −1.33% per year, *SI Appendix*, Table S1). We saw declines in evenness for rare species and species overwintering as eggs, which can be driven by losses in species richness as well as abundance becoming more uneven through time across species in these groups; however, most other groups increased in evenness (*SI Appendix*, Table S2). Resident and rare species declined in richness more than migratory and common species, respectively. We did not find a difference in richness declines between univoltine (1 generation per year) and multivoltine (2+ generations per year) species but multivoltine species increased more in evenness than univoltine species. Declines in evenness or richness did not differ between specialists and generalists. Across overwintering strategies, species overwintering as eggs lost the highest percent of species (−0.72% per year, compared to −0.12 to −0.34% per year for other groups). Species overwintering as larvae experienced moderate increases in evenness that did not differ from other groups, while those overwintering as eggs declined in evenness compared to those overwintering in later life stages.

Abundance declined in every functional group (0.98 to 1.00 probability of decreasing; Fig. 2 and *SI Appendix*, Table S3). The most common species declined (−1.9% per year) more than the rarest species (−0.9% per year, *SI Appendix*, Fig. S1). In pairwise comparisons, generalist species (−1.9% per year) had more negative trends than specialist species (−1.4% per year), as did univoltine species (−2.1% per year) compared to multivoltine species (−1.5% per year). We found less of a difference between migratory (−1.1% per year) and resident species (−1.7% per year). Species overwintering as eggs had the most negative trends (−2.3% per year), while species overwintering as pupae had the least negative trend (−0.9% per year).

We were surprised to find that no species increased in abundance. Fifty-nine out of 136 species (43%) declined, while the remaining 77 had no clear trend (95% CI contained zero; Fig. 3; *SI Appendix*, Table S4). The 59 species with decreasing trends had annual mean trend estimates between −1.2 to −6.9%. Over one quarter of species ($n = 36$) declined by −2% per year or more, with 19 species declining by −3% per year or more. Six of the seven species with declines of more than −4% were resident species from the family Nymphalidae. Of the species with no clear trend, only 7 (0.5% of the total species analyzed) had positive mean trend estimates. These seven species had a mixture of functional traits with annual mean trend estimates from +0.1 to +1.4%, with only one species above +0.4%. No species had support for an increasing trend (probability of individual species increasing in abundance ranged from 0.56 to 0.69). Our results are bleaker than other studies on butterflies in the United States, likely because of our comparatively longer time series (32 y) and our inclusion of rare species, with many other studies having 20 y of data or less and forced to exclude species that were detected infrequently (1, 17, 29, 30).

The changes in butterfly biodiversity are large and unmistakable. For every 10 species and 100 individuals present at a county at the beginning of our study period, there are now only 9 species and 60 individuals, amounting to a −40% loss in the total number of butterflies over three decades. These losses have profoundly changed the composition of the butterfly community in the Midwest. Abundances across species have become more similar, driven by steeper declines for common species compared to rare ones. We see fewer individuals across all groups and fewer species in groups (except for migratory butterflies). A county with three rare species at the beginning of the study would only have two by the end, but abundance of those species would still be relatively high—about 75% of the original. In contrast, a county that had 20 to 30 common species at the start of the study would likely still have all those species present at the end of the study, but with about half of the original abundance. Because it takes the loss of many individuals over many generations before a common species is gone altogether,

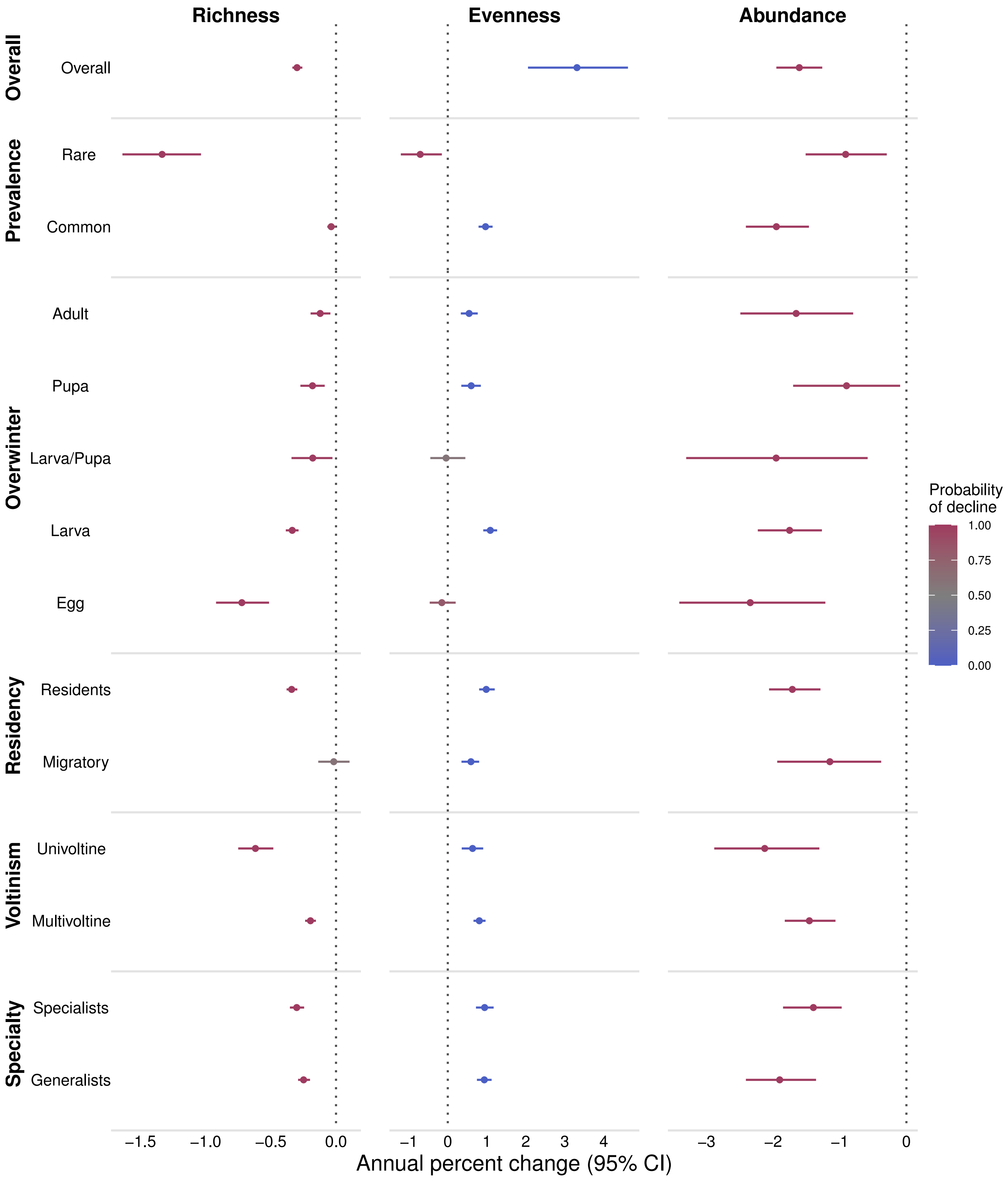

Fig. 2. Annual percent change (95% CI) in richness, evenness (Shannon diversity), and abundance for butterfly communities in the Midwestern United States from 1992 to 2023. We calculated trends for the entire community (overall), as well as species groups based on their prevalence (common vs. rare) and functional traits (specialist vs. generalist [1 or >1 host plant family], number of generations per year, migratory vs. resident, overwintering strategy). Line color shows the posterior probability of declining—red indicates higher certainty of declining trend and blue indicates higher certainty of increasing trend, with gray representing stable or uncertain trends.

species richness metrics may be less meaningful for common species. Conversely, rare species, which experienced less severe declines in abundance, are more susceptible to local extinction due to their initial lower population sizes. Several of the rare species we observed are formerly common species that underwent severe declines in the mid-20th century from conversion of grassland habitat into agriculture (26). These results highlight the importance of evaluating both rare and common species using a holistic perspective.

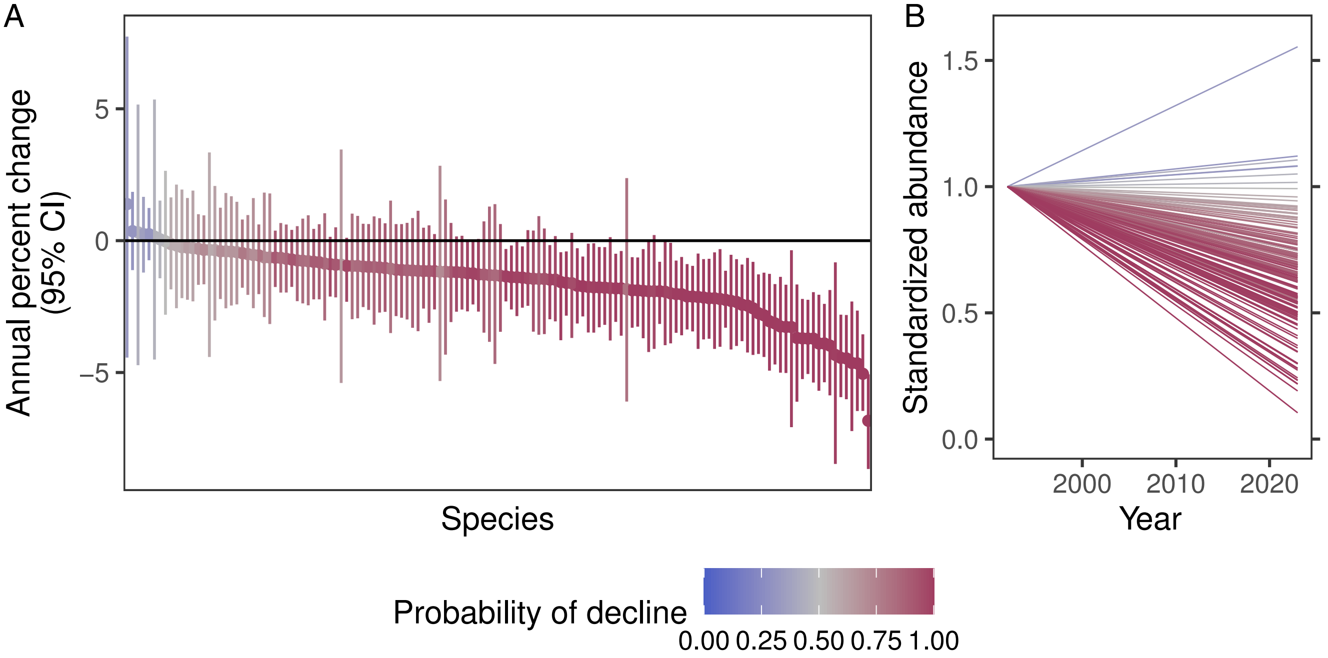

Fig. 3. Population declines for 136 butterfly species in the Midwestern United States from 1992 to 2023. (*A*) Trend over time (percent change per year; 95% CI) for each species. (*B*) Standardized changes in relative abundance for each butterfly species over the 32-y study period. All species start with a standardized abundance of one and change based on their annual trend rates for 32 y, resulting in a final population size described as a proportion of the original population size. Each line represents one species and is colored based on their posterior probability of declining—red indicates higher certainty of declining trend and blue indicates higher certainty of increasing trend, with gray representing stable or uncertain trends. Note that no species had a high probability of increasing (i.e., none are bright blue).

We found that functional traits were linked to rates of decline within the Midwestern US study area. Unsurprisingly, the Midwest lost a higher proportion of univoltine species and individuals compared to multivoltine species; multivoltine species are generally considered to be more adaptable to climate changes and other environmental stressors (1, 17, 31). Declines in species and individuals that winter as eggs outpaced those that overwinter as larvae, pupa, or adults. One mechanism explaining the large declines in species overwintering as eggs is that these species enter the growing season with limited energy reserves, which make them more vulnerable to phenological mismatch with hostplants and extreme weather events (24). The more negative trends detected in generalists compared to specialists may mask a history of declines in specialists that preceded the start of our study, as many prairie specialist butterflies saw concomitant declines of their hostplants and changes in land cover during the 20th century (26). Migrants fared better than residents, with no changes in richness and 68% of the original abundance, while residents declined in richness and had 58% of the original abundance. However, the substantial decline in migratory species abundance highlights the Midwest's potential role in exacerbating population challenges for migrants, reflecting broader global concerns regarding their conservation (32, 33).

Many hypotheses have been put forth as to the causes of global insect and butterfly declines primarily related to climate change and habitat loss (19, 34–36). Although we did not evaluate the causes of butterfly declines in our study, our failure to find any species that increased over the 32-y study period provides important clues. Even in the face of overall declines, species generally have heterogeneous responses to environmental stressors like climate and land use change, such that there is usually a mix of winners and losers (37, 38). For example, climate change negatively affects butterfly populations overall, yet some species show increasing trends through expansion at the northern edge of their range (29), upward shifts in elevation (39), and increased voltinism (40). Changes in land-use such as conversion to agriculture, agricultural intensification, and urban development have been prevalent in most regions globally, both recently (41) and historically (42, 43). Most of the original conversion to agriculture in the Midwestern United States happened from 1850 to 1920 (43). As with climate change, butterfly responses to land-use change are typically variable, including some species that subsequently increase in abundance (34, 44). Despite examining nearly all butterflies within the Midwestern community (37), we did not find evidence that any species increased.

We thus suspect that insecticide use is a key driver of the declines estimated in our study (45). Insecticides are used widely throughout the Midwest in agricultural fields (45). Neonicotinoids are a high-impact class of insecticides that are widely used as prophylactic seed coatings, persist in the environment, and affect nontarget insect species in surrounding areas (45–47). Even sublethal doses of these chemicals cause changes in behavior, reproduction, and development affecting survival of nontarget species (48). Neonicotinoids were first introduced in 1994 and rapidly increased in use after 2003 (49). Neonicotinoids, along with other insecticides, are known to be a stronger driver of declines in butterfly species richness than land use and climate change within the Midwestern United States (45). Studies in California and the United Kingdom have also found strong associations between butterfly declines and neonicotinoid use (50, 51). Our 32-y time series of butterfly data from 1992 to 2023 may be capturing neonicotinoid-driven trends that have not been detected in other studies, as our initial years of data precede the use of these insecticides and long time series are known to produce different results compared to analyses conducted with fewer years of data (6).

Insect declines, including the loss of butterflies in the Midwestern United States, are substantial and concerning. Insects are linked with ecosystem services and functions, and their widespread declines are likely having cascading effects on both higher and lower trophic levels (52–54). Similar to other recent studies, our results reveal considerable declines in individual species. However, we also show that no butterfly species has increased in the Midwest in the last three decades, leading to sizable changes in richness and evenness of the remaining butterfly community. In light of the broad extent of the problem, conservation efforts should shift focus to protection of groups of functionally similar species, and even entire communities, rather than a few focal species (22, 55, 56). Conservation focused on only rare and endangered species is likely insufficient because most species, rare and common, are declining and may soon be vulnerable to local extirpation.

Methods

Butterfly Data. We integrated count data from five participatory monitoring programs in which volunteers collect data: the North American Butterfly Association (NABA; initiated in 1975), Illinois Butterfly Monitoring Network (1987), Iowa Butterfly Survey Network (2006), Michigan Butterfly Network (2011), and Ohio Lepidopterists (1995; see *SI Appendix*, Table S5 for program-specific survey information). The NABA data are semistructured count data from surveys in which multiple observers visit locations within a 25-km diameter circle, recording the number and species of all butterflies observed (57). Historically, these counts occurred once per year in late June or early July but, as of 2008, counts can now occur multiple times per year in spring, summer, and fall (16). NABA data are gathered across the United States; we used only data from the US Midwest, including from Michigan, Iowa, Ohio, Illinois, Missouri, Minnesota, and Indiana.

The other four datasets come from statewide structured surveys in which trained volunteers regularly conduct Pollard walks on prespecified transects throughout the spring, summer, and fall, and record all butterflies observed (25). Exact protocols vary by program (e.g., width of survey, time of day, time of year). Surveys typically occur up to once a week, with <0.2% of surveys occurring as replicate surveys within a week. Each transect is surveyed by a single observer, often the same individual for many years. Surveys from state monitoring programs include some transects in adjacent states. As such, we included Pollard and NABA data from surveys conducted in Indiana, Minnesota, Missouri, and Wisconsin, as well as Illinois, Iowa, Michigan, and Ohio where the state programs were based (Fig. 1). Although systematic butterfly data are available from as early as 1975, we conducted our analyses with data from 1992 onward because available data prior to that year were quite sparse. Only 0.9% of all records between 1975 and 2023 were collected prior to 1992 (*SI Appendix*, Table S6). While not all state monitoring programs had begun by 1992, NABA surveys occurred in all states by 1992 or 1993 (MN, MO), ensuring spatial coverage for the entire 32-y time series. We further restricted our dataset to surveys occurring in the "growing season," defined as 1 May to 30 September as this period is the peak time of butterfly activity in the Midwestern United States and few butterflies were observed on the rare surveys conducted outside this timeframe. Survey locations were selected nonrandomly; as such, the data from these participatory science programs tend to be biased in terms of land use (e.g., surveys did not occur in parking lots, agricultural areas were underrepresented).

There were 136 species in the dataset with ≥50 observations, the minimum number of observations we required for inclusion in our integrated community model. The species with <50 observations generally included stray individuals from species that were not established in the Midwestern United States. We considered the remaining species as the "Midwest butterfly community," defined as the populations of butterfly species that occur together in the Midwestern United States. While this group could arguably be called an "assemblage" (58), we use community to connect to hierarchical and integrated community modeling (27, 59). Due to the long computing time for fitting models, we split butterfly species into groups of 11 to 24 species based on migratory status, voltinism, host plant breadth, and phylogeny. We used the LepTraits database to assess voltinism (univoltine, multivoltine; bivoltine was lumped with multivoltine) as well as host plant breadth (one or multiple host plant families) (60). LepTraits does not include migratory status (migrant or resident), so we used field guides and expert opinion to define this trait (61, 62). We grouped species from Papilionidae and Hesperiidae (the two most ancestral families) and species from the other families (Pieridae, Nymphalidae, Riodinidae, and Lycaenidae) (63). We ended up with seven functional and family groups (*SI Appendix*, Table S7). While this a priori grouping of species could in theory influence individual species results, numerous exploratory analyses revealed species-specific estimates varied minimally across different groupings, suggesting that our approach is robust to this grouping structure (59).

Functional traits can affect butterfly trends due to interactions between life history and drivers of change (1, 4, 29, 64–66) As such, we ran post hoc comparisons on groups of butterflies based on their traits. Specifically, we compared resident species to migratory species, univoltine to multivoltine species, host plant family specialists to generalists, the rarest quartile of species to the most common quartile of species, and pairwise comparisons on overwintering stage (*SI Appendix*, Table S7).

Combined, we have >90,000 h of surveys with a total of 4,345,483 butterfly observations, a median of 4,500 observations per species and a range of 56 to 730,426 observations per species (*SI Appendix*, Table S8).

Statistical Analysis.

Model structure. We adapted the monarch butterfly summer breeding season model from a previous study (21), which integrates data from the five different butterfly monitoring programs. We extended the single species version to a community framework that simultaneously models individual species abundances by linking species-level parameters through a hierarchical approach (27). We modeled activity curves (i.e., weekly abundance estimates through the growing season) for each butterfly species in each year, with species, year, and county effects estimated as random variables drawn from shared, community-level distributions. We then generated a yearly relative abundance index for each species by calculating the area under the species and year-specific activity curves (67, 68). This approach allowed us to estimate annual, species-specific relative abundance indices at the county-level accounting for variability in phenology and abundance as well as uneven sampling. We subsequently used these relative abundance indices to estimate species-specific temporal trends from 1992 to 2023.

Let $y_{i,c,j,t,k}$ denote the number of observed individuals of species $i = 1, 2, \ldots, I$ in county $c = 1, 2, \ldots, 262$ at site $j = 1, 2, \ldots, 1236$ in week $k = 1, 2, \ldots, 23$ of year $t = 1, 2, \ldots, 32$. Replicate surveys $l = 1, 2, \ldots, 13$ within a week were occasionally conducted.

We model $y_{i,c,j,t,k}$ using a negative binomial distribution such that

$$y_{i,c,j,t,k} \sim \mathrm{NegBin}\left(\lambda_{i,c,j,t,k}, \kappa_i\right),$$

where $\lambda_{i,c,j,t,k}$ is the expected number of individuals of species i observed within county c at site j in year t and week k. κ_i is a species-specific dispersion parameter to account for overdispersion in observed counts.

We assumed that the expected species count, $\lambda_{i,c,j,t,k}$ was a function of week within season as well as survey- and site-level covariates. More specifically, we modeled $\lambda_{i,c,j,t,k}$ according to

$$\begin{aligned}\log\left(\lambda_{i,c,j,t,k}\right) = {} & \beta_{0_i} + \beta_{1_i} \cdot \mathrm{week}_k + \beta_{2_i} \cdot \mathrm{week}_k^2 + \beta_{3_i} \cdot \mathrm{open}_c + \beta_{4_i} \cdot \\ & \mathrm{open}_j + \alpha_{1_i} \cdot \mathrm{IA}_j + \alpha_{2_i} \cdot \mathrm{IL}_j + \alpha_{3_i} \cdot \mathrm{MI}_j + \alpha_{4_i} \cdot \mathrm{OH}_j + \alpha_{5_i} \cdot \\ & \log\left(\mathrm{effort}_{t,k(l)}\right) + \epsilon_{0_{i,c}} + \epsilon_{1_{i,t}} + \epsilon_{2_{i,t}} \cdot \mathrm{week}_k + \epsilon_{3_{i,t}} \cdot \mathrm{week}_k^2.\end{aligned}$$

The β parameters are variables related to the biological process (i.e., seasonal abundance patterns) while the α parameters account for variations among the monitoring programs. The ϵ parameters are zero-centered random effects to address spatial and temporal variation. The intercept, β_{0_i}, is the average count (on the log scale) for species i during a single NABA survey. Parameters β_{1_i} and β_{2_i} are linear and quadratic effects of week, respectively, to account for species-specific differences in seasonal activity (e.g., refs. 68 and 69). We calculated the percentage of open land cover (defined as unforested, nonurban, and nonwater land cover) at both the county (open_c) and site [open_j; 12.5 km radius for NABA or 2.5 km radius for Pollard walk programs (24)] levels using the 2011 National Land Cover Database (70), as many butterfly species are associated with open habitat. Week and open land cover covariates were standardized to have a mean of zero and SD of one.

The parameters α_{1_i}, α_{2_i}, α_{3_i}, and α_{4_i} are species-specific effects accounting for differences in the expected counts between Iowa (IA), Illinois (IL), Michigan (MI), and Ohio (OH) statewide surveys, respectively, from the NABA survey (which is used as the baseline). Each of the survey covariates are indicator variables (e.g., where $\text{IA}_j = 1$ if the survey at site j was conducted by the Iowa Butterfly Survey Network and zero otherwise). We included α_{5_i} to account for variability in effort, measured in the number of hours for Pollard walks and party-hours (1 h per person for each hour of surveying) for NABA surveys. Some surveys (0.02% of surveys) had an effort of zero (i.e., were inaccurately or not recorded), so we inputted the median value. We capped effort at 5 h for Pollard walks and 15 party-hours for NABA surveys to remove infrequent large values. We centered the effort to have a mean of one and modeled it as the log of the number of search hours. This approach resulted in model predictions of relative abundance at average survey effort.

The ϵ terms are random effects coming from normal distributions centered around zero with a variance that is estimated in the model. We include random species-specific intercepts for county ($\epsilon_{0_{i,c}}$) and year ($\epsilon_{1_{i,t}}$) and random slopes for linear ($\epsilon_{2_{i,t}}$) and quadratic effects ($\epsilon_{3_{i,t}}$) of week for each species and year.

We modeled all β and α parameters as random variables arising from common, community-level normal distributions with mean and variance hyperparameters (71, 72). For example, we modeled the species-specific intercept, β_{0_i}, as

$$\beta_{0_i} \sim \text{Normal}\left(\mu_{\beta_0}, \tau^2_{\beta_0}\right),$$

where μ_{β_0} is the mean value (on the log scale) across species in the community and $\tau^2_{\beta_0}$ is the variation in species-specific parameters across all members of the community.

Relative abundance indices. After fitting the model, we calculated mean relative abundance (λ) and predicted relative abundance (y) for each species, week, year, and county. We then computed the area under the curve for both types of relative abundance [trapezoidal integration from the pracma package (73)] to calculate $\theta_{i,c,t}$, the mean relative growing season abundance index, and $N_{i,c,t}$, the predicted relative growing season abundance index, for each species in each year of every included county (68).

Determining common and rare species. We extracted the median $\theta_{i,c,t}$ value for each year. We then computed the area under the curve to obtain one relative abundance value for each species. We ranked species by these abundance values and selected the quartile ($n = 34$) of species with the largest abundances (common) and smallest abundances (rare). We used these groups for trait-based analyses and comparisons.

Abundance. We used $\theta_{i,c,t}$ to estimate a log-linear trend for the mean relative abundance index for each individual species (θ_i). We fit models for each species separately.

Richness. We used the predicted relative abundance index $N_{i,c,t}$ to calculate species richness by adding together the number of species with at least one individual predicted at the county across the entire growing season within a given year (i.e., in which $N_{i,c,t} \geq 1$) such that

$$R_{c,t} = \sum_{i=1}^{I} \text{I}\left(N_{i,c,t} \geq 1\right),$$

where $R_{c,t}$ is the number of species in the county and year, I is the total number of species in the model, and $\text{I}()$ is an indicator function returning value 1 if $N_{i,c,t} \geq 1$ and 0 otherwise.

Evenness (Shannon diversity [H′]). We added the predicted relative abundance indices together such that

$$T_{c,t} = \sum_{i=1}^{R_{c,t}} N_{i,c,t},$$

where $T_{c,t}$ is the total number of individuals in county c during year t. We calculated the proportion of individuals $p_{i,c,t}$ belonging to each species as

$$p_{i,c,t} = N_{i,c,t} / T_{c,t}.$$

We used these values to calculate Shannon diversity ($H'_{c,t}$) for each county in each year as

$$H'_{c,t} = -\sum_{i=1}^{R_{c,t}} p_{i,c,t} \log p_{i,c,t}.$$

Trend estimation. We estimated log-linear trends for abundance, richness, and diversity with post hoc linear regressions such that

$$\log\left(\text{Response}_{c,t}\right) \sim \text{Normal}\left(\mu_{c,t}, \sigma^2_{Response}\right),$$

$$\mu_{c,t} = \gamma_0 + \gamma_1 \cdot \text{year}_{c,t} + \epsilon_c,$$

where $\mu_{c,t}$ is the mean response of abundance, richness, or diversity for a given year, γ_0 is an intercept, γ_1 is the effect of year, and ϵ_c is a normally distributed random effect for county with a mean 0 and SD τ^2_c. We fit these post hoc regressions using a Bayesian framework to propagate all uncertainty (i.e., using the full posterior distribution for each response variable). For each response, we provide the annual percent change in the response ($[\exp(\gamma_1) - 1] \cdot 100\%$), 95% CI, and proportion of the CI that is less than zero (indicating a declining trend).

Trait-based trend comparison.

Abundance. We extracted the effect of year ($\gamma_{1,i}$) from the abundance trends for each species. We fit a post hoc regression using the specific-specific $\gamma_{1,i}$ values as the response value and group as a fixed effect. We did pairwise comparisons of groups to assess differences in responses among traits. We used a Bayesian framework to propagate all uncertainty. We modeled $\gamma_{1,i}$ as

$$\gamma_{1,i} = \zeta_{0,i} + \zeta_{j,i} \cdot \text{group}_i + \varepsilon_i,$$

$$\varepsilon_i \sim \text{Normal}\left(\gamma_{1,i}, \sigma^2_{\gamma_1}\right).$$

Richness and evenness. We calculated the richness and evenness ($\text{z}_{c,t}$) of each trait-based group of butterflies, following the same calculations as for the richness and evenness of the whole community. We compared trait-based groups using a fixed effect for trait interacting with year to assess differences in trend over time such that

$$\text{z}_{c,t} \sim \text{Normal}\left(\omega_{c,t}, \sigma^2_z\right),$$

$$\omega_{c,t} = \eta_{g,i} \cdot \text{trait}_i + \gamma_{g,i} \cdot \text{year}_{c,t} \cdot \text{trait}_i + \epsilon_c,$$

where $\eta_{g,i}$ is the intercept for each trait, $\gamma_{g,i}$ is the interaction of year and each trait, and ϵ_c is a random effect for county coming from a normal distribution with a mean 0 and SD of τ^2_c.

We compared the posterior distributions from each $\gamma_{g,i}$ to determine whether the trends for the paired traits differ from each other. For all $\gamma_{g,i}$, we provide the annual percent change as $\frac{\gamma_{g,i}}{initial_{g,i}}$, where $initial_{g,i}$ is the median richness or evenness for the first 5 y. We provide the annual percent change and CI, as well as the proportion of the CI that is less than zero (indicating a declining trend).

Model implementation. We implemented the model using a Bayesian framework with the msAbund function in the spAbundance package (74) in the R statistical environment (75). We provided vague priors for all parameters. We specified normal priors with a mean of zero and a variance of 100 for all mean hyperparameters. We assigned inverse gamma priors to all variance and hypervariance parameters, with shape and scale parameters set to 0.1. We used independent uniform priors for κ_i; while κ_i varies by species, the species-specific κ_i values are not drawn from a community distribution like other species-specific parameters. We ran models for multiple chains (4 to 5 chains depending on computational limitations). We assessed model convergence using the Gelman–Rubin R-hat diagnostic (76) and visual assessment of trace plots using the coda package (77). Total number of iterations varied across groups depending on run time and length needed to achieve convergence, ranging from 160,000 to 1,040,000 iterations. A small number of species-specific parameters had poor convergence (i.e., R-hat > 1.1) for some very common species due to difficulties in separately identifying multiple random effect parameters. This behavior is not uncommon for complex, high-dimensional models when random effect parameters are highly correlated. This did not have any impact on the convergence of the estimated abundance values nor the estimated trends. We used the spOccupancy package to conduct the post hoc linear regressions (78).

Data, Materials, and Software Availability. Covariate data and data describing butterfly names and groupings are available at this Zenodo repository (79). Butterfly data are proprietary and were obtained from the

North American Butterfly Association (https://www.naba.org/), the Iowa Butterfly Survey Network (https://reimangardens.com/insects#IBSN), the Illinois Butterfly Monitoring Network (https://bfly.org/), the Michigan Butterfly Network (https://naturecenter.org/michiganbutterfly/), and the Ohio Lepidopterists (https://www.ohiolepidopterists.org/). These data may be available upon reasonable request to LR and with permission from the aforementioned programs. Code needed to run analyses (R scripts) is available at this Zenodo repository (79).

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1. T. Wepprich, J. R. Adrion, L. Ries, J. Wiedmann, N. M. Haddad, Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS ONE* **14**, e0216270 (2019).
2. R. Van Klink *et al.*, Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420 (2020).
3. M. L. Forister *et al.*, Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science* **371**, 1042–1045 (2021).
4. M. S. Warren *et al.*, The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2002551117 (2021).
5. C. A. Hallmann *et al.*, More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* **12**, e0185809 (2017).
6. R. M. Dalton, N. C. Underwood, D. W. Inouye, M. E. Soulé, B. D. Inouye, Long-term declines in insect abundance and biomass in a subalpine habitat. *Ecosphere* **14**, e4620 (2023).
7. R. Van Klink *et al.*, Disproportionate declines of formerly abundant species underlie insect loss. *Nature* **628**, 359–364 (2024).
8. E. O. Wilson, The little things that run the world (the importance and conservation of invertebrates). *Conserv. Biol.* **1**, 344–346 (1987).
9. A. Y. Kawahara, L. E. Reeves, J. R. Barber, S. H. Black, Eight simple actions that individuals can take to save insects from global declines. *Proc. Natl. Acad. Sci. U.S.A.* 118, e2002547117 (2021).
10. P. Cardoso *et al.*, Scientists' warning to humanity on insect extinctions. *Biol. Conserv.* **242**, 108426 (2020).
11. D. W. Tallamy, W. G. Shriver, Are declines in insects and insectivorous birds related? *Ornithol. Appl.* **123**, duaa059 (2021).
12. D. L. Wagner, A. C. Hoyt, "On being a caterpillar: Structure, function, ecology, and behavior" in *Caterpillars in the Middle: Tritrophic Interactions in a Changing World*, R. J. Marquis, S. Koptur, Eds. (Springer International Publishing, Cham, Switzerland, 2022), pp. 11–62, 10.1007/978-3-030-86688-4_2.
13. R. T. Holmes, J. C. Schultz, P. Nothnagle, Bird predation on forest insects: an exclosure experiment. *Science* **206**, 462–463 (1979).
14. J. Jones, P. J. Doran, R. T. Holmes, Climate and food synchronize regional forest bird abundances. *Ecology* **84**, 3024–3032 (2003).
15. C. A. M. Van Swaay, P. Nowicki, J. Settele, A. J. Van Strien, Butterfly monitoring in Europe: Methods, applications and perspectives. *Biodivers. Conserv.* **17**, 3455–3469 (2008).
16. D. Taron, L. Ries, "Butterfly monitoring for conservation" in *Butterfly Conservation in North America: Efforts to Help Save Our Charismatic Microfauna*, J. C. Daniels, Ed. (Springer, Dordrecht, The Netherlands, 2015), pp. 35–57, 10.1007/978-94-017-9852-5_3.
17. C. B. Edwards *et al.*, Rapid butterfly declines across the United States during the 21st century. *Science* **387**, 1090–1094 (2025).
18. R. K. Didham *et al.*, Interpreting insect declines: Seven challenges and a way forward. *Insect Conserv. Divers.* **13**, 103–114 (2020).
19. D. L. Wagner, E. M. Grames, M. L. Forister, M. R. Berenbaum, D. Stopak, Insect decline in the anthropocene: Death by a thousand cuts. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2023989118 (2021).
20. W. E. Thogmartin *et al.*, Monarch butterfly population decline in North America: Identifying the threatening processes. *R. Soc. Open Sci.* **4**, 170760 (2017).
21. E. R. Zylstra *et al.*, Changes in climate drive recent monarch butterfly dynamics. *Nat. Ecol. Evol.* **5**, 1441–1452 (2021).
22. F. Pilotto *et al.*, Meta-analysis of multidecadal biodiversity trends in Europe. *Nat. Commun.* **11**, 3486 (2020).
23. S. A. Blowes *et al.*, Local biodiversity change reflects interactions among changing abundance, evenness, and richness. *Ecology* **103**, e3820 (2022).
24. E. A. Larsen *et al.*, Overwintering strategy regulates phenological sensitivity and consequences for ecological services in a clade of temperate North American insects. *Funct. Ecol.* **38**, 1075–1088 (2024).
25. E. Pollard, A method for assessing changes in the abundance of butterflies. *Biol. Conserv.* **12**, 115–134 (1977).
26. S. R. Swengel, D. Schlicht, F. Olsen, A. B. Swengel, Declines of prairie butterflies in the midwestern USA. *J. Insect Conserv.* **15**, 327–339 (2011).
27. E. F. Zipkin *et al.*, Integrated community models: A framework combining multispecies data sources to estimate the status, trends and dynamics of biodiversity. *J. Anim. Ecol.* **92**, 2248–2262 (2023).
28. C. E. Shannon, A mathematical theory of communication. *Bell Syst. Tech. J.* **27**, 379–423 (1948).
29. G. A. Breed, S. Stichter, E. E. Crone, Climate-driven changes in northeastern US butterfly communities. *Nat. Clim. Change* **3**, 142–145 (2013).
30. C. A. Halsch *et al.*, Insects and recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2002543117 (2021).
31. T. Wepprich, E. Henry, N. M. Haddad, Voltinism shifts in response to climate warming generally benefit populations of multivoltine butterflies. *Ecol. Lett.* **28**, e70018 (2025).
32. UNEP-WCMC, State of the World's migratory species (2024). https://www.cms.int/sites/default/files/publication/State%20of%20the%20Worlds%20Migratory%20Species%20report_E.pdf. Accessed 16 April 2025.
33. N. B. Kucherov, E. S. Minor, P. P. Johnson, D. Taron, K. C. Matteson, Butterfly declines in protected areas of Illinois: Assessing the influence of two decades of climate and landscape change. *PLoS ONE* **16**, e0257889 (2021).
34. D. Maes, H. Dyck, Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biol. Conserv.* **99**, 263–276 (2001).
35. F. Sánchez-Bayo, K. A. G. Wyckhuys, Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
36. C. L. Outhwaite, P. McCann, T. Newbold, Agriculture and climate change are reshaping insect biodiversity worldwide. *Nature* **605**, 97–102 (2022).
37. M. Dornelas *et al.*, A balance of winners and losers in the Anthropocene. *Ecol. Lett.* **22**, 847–854 (2019).
38. R. Fox *et al.*, Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *J. Appl. Ecol.* **51**, 949–957 (2014).
39. M. L. Forister *et al.*, Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 2088–2092 (2010).
40. F. Altermatt, Climatic warming increases voltinism in European butterflies and moths. *Proc. R. Soc. B.* **277**, 1281–1287 (2010).
41. P. Jaureguiberry *et al.*, The direct drivers of recent global anthropogenic biodiversity loss. *Sci. Adv.* **8**, eabm9982 (2022).
42. E. C. Ellis, K. Klein Goldewijk, S. Siebert, D. Lightman, N. Ramankutty, Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecol. Biogeogr.* **19**, 589–606 (2010).
43. X. Li, H. Tian, C. Lu, S. Pan, Four-century history of land transformation by humans in the United States (1630–2020): Annual and 1 km grid data for the HIStory of LAND changes (HISLAND-US). *Earth Syst. Sci. Data* **15**, 1005–1035 (2023).
44. M. Lütolf, A. Guisan, F. Kienast, History matters: Relating land-use change to butterfly species occurrence. *Environ. Manage.* **43**, 436–446 (2009).
45. B. Deynze, S. M. Swinton, D. A. Hennessy, N. M. Haddad, L. Ries, Insecticides, more than herbicides, land use, and climate, are associated with declines in butterfly species richness and abundance in the American Midwest. *PLoS ONE* **19**, e0304319 (2024).
46. D. Goulson, Review: An overview of the environmental risks posed by neonicotinoid insecticides. *J. Appl. Ecol.* **50**, 977–987 (2013).
47. L. M. Guzman *et al.*, Impact of pesticide use on wild bee distributions across the United States. *Nat. Sustain.* **7**, 1324–1334 (2024).
48. L. Gandara *et al.*, Pervasive sublethal effects of agrochemicals on insects at environmentally relevant concentrations. *Science* **386**, 446–453 (2024).
49. M. R. Douglas, J. F. Tooker, Large-scale deployment of seed treatments has driven rapid increase in use of neonicotinoid insecticides and preemptive pest management in U.S. field crops. *Environ. Sci. Technol.* **49**, 5088–5097 (2015).
50. M. L. Forister *et al.*, Increasing neonicotinoid use and the declining butterfly fauna of lowland California. *Biol. Lett.* **12**, 20160475 (2016).
51. A. S. Gilburn *et al.*, Are neonicotinoid insecticides driving declines of widespread butterflies? *PeerJ* **3**, e1402 (2015).
52. E. M. Grames, G. A. Montgomery, C. Youngflesh, M. W. Tingley, C. S. Elphick, The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecol. Lett.* **26**, 658–673 (2023).
53. L. C. Evans, M. D. Burgess, S. G. Potts, W. E. Kunin, T. H. Oliver, Population links between an insectivorous bird and moths disentangled through national-scale monitoring data. *Ecol. Lett.* **27**, e14362 (2024).
54. Y. Zhou *et al.*, Long-term insect censuses capture progressive loss of ecosystem functioning in East Asia. *Sci. Adv.* **9**, eade9341 (2023).
55. M. W. Belitz *et al.*, A case for assemblage-level conservation to address the biodiversity crisis. *Nat. Rev. Biodivers.* **1**, 134–143 (2025).
56. C. Boyd *et al.*, Spatial scale and the conservation of threatened species. *Conserv. Lett.* **1**, 37–43 (2008).
57. A. B. Swengel, Monitoring butterfly populations using the fourth of july butterfly count. *Am. Midl. Nat.* **124**, 395 (1990).
58. J. E. Fauth *et al.*, Simplifying the jargon of community ecology: A conceptual approach. *Am. Nat.* **147**, 282–286 (1996).
59. K. Pacifici, E. F. Zipkin, J. A. Collazo, J. I. Irizarry, A. DeWan, Guidelines for a priori grouping of species in hierarchical community models. *Ecol. Evol.* **4**, 877–888 (2014).
60. V. Shirey *et al.*, LepTraits 1.0: A globally comprehensive dataset of butterfly traits. *Sci. Data* **9**, 382 (2022).

61. J. Glassberg, *Butterflies through Binoculars: The East* (Oxford University Press, New York, NY, 1999).
62. J. P. Brock, J. P. Brock, K. Kaufman, *Kaufman Field Guide to Butterflies of North America* (Houghton Mifflin Harcourt, 2003).
63. A. Y. Kawahara *et al.*, A global phylogeny of butterflies reveals their evolutionary history, ancestral hosts and biogeographic origins. *Nat. Ecol. Evol.* **7**, 903–913 (2023).
64. A. Eskildsen *et al.*, Ecological specialization matters: Long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Divers. Distrib.* **21**, 792–802 (2015).
65. J. C. Habel, W. Ulrich, P. Gros, M. Teucher, T. Schmitt, Butterfly species respond differently to climate warming and land use change in the northern Alps. *Sci. Total Environ.* **890**, 164268 (2023).
66. S. Whipple, G. Bowser, The buzz around biodiversity decline: Detecting pollinator shifts using a systematic review. *iScience* **26**, 108101 (2023).
67. P. Rothery, D. B. Roy, Application of generalized additive models to butterfly transect count data. *J. Appl. Stat.* **28**, 897–909 (2001).
68. E. B. Dennis, S. N. Freeman, T. Brereton, D. B. Roy, Indexing butterfly abundance whilst accounting for missing counts and variability in seasonal pattern. *Methods Ecol. Evol.* **4**, 637–645 (2013).
69. S. P. Saunders, L. Ries, K. S. Oberhauser, W. E. Thogmartin, E. F. Zipkin, Local and cross-seasonal associations of climate and land use with abundance of monarch butterflies *Danaus plexippus*. *Ecography* **41**, 278–290 (2018).
70. C. Homer *et al.*, Completion of the 2011 National Land Cover Database for the conterminous United States–Representing a decade of land cover change information. *Photogramm. Eng.* **81**, 345–354 (2015).
71. R. M. Dorazio, J. A. Royle, Estimating size and composition of biological communities by modeling the occurrence of species. *J. Am. Stat. Assoc.* **100**, 389–398 (2005).
72. A. E. Gelfand *et al.*, Modelling species diversity through species level hierarchical modelling. *J. R. Stat. Soc. Ser. C, Appl. Stat.* **54**, 1–20 (2005).
73. H. W. Borchers, pracma: Practical numerical math functions (2023). https://CRAN.R-project.org/package=pracma. Accessed 16 April 2025.
74. J. W. Doser, A. O. Finley, M. Kéry, E. F. Zipkin, SpAbundance, an R package for single-species and multi-species spatially explicit abundance models. *Methods Ecol. Evol.* **15**, 1024–1033 (2024), 10.1111/2041-210X.14332.
75. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2024).
76. S. P. Brooks, A. Gelman, General methods for monitoring convergence of iterative simulations. *J. Comput. Graph. Stat.* **7**, 434–455 (1998).
77. M. Plummer, N. Best, K. Cowles, K. Vines, CODA: Convergence diagnostics and output analysis for MCMC. *R News* **6**, 7–11 (2006).
78. J. W. Doser, A. O. Finley, M. Kéry, E. F. Zipkin, spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods Ecol. Evol.* **13**, 1670–1678 (2022).
79. W. Leuenberger, J. W. Doser, M. W. Belitz, ButterflyCommunityTrends. Zenodo. https://doi.org/10.5281/zenodo.15270052. Deposited 23 April 2025.