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Shifting Baselines in North America's Longest Running Butterfly Monitoring Program

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ABSTRACT

Eroding perceptions of biodiversity present a significant challenge for conservation. If younger generations see current degraded states as "natural," goals for conservation actions may not be ambitious enough, and public support may be compromised. Historical data can provide context for fully appreciating the extent of biodiversity loss. We utilize the most species-rich day of each year in North America's longest running butterfly monitoring program's most diverse site to examine how perceptions of peak butterfly richness could shift over time. In early monitoring years, days with over 50 observed species were standard, but now peak richness days have shifted over time, such that these days now see ten fewer species. High-diversity days shape perceptions of biodiversity, and we provide an example of how long-term monitoring data can be utilized to study shifting baselines in observer perceptions of biodiversity and to contextualize current observations.

1 | Introduction

Numerous studies have documented reductions in biodiversity over the past century (Dirzo et al. 2014; Rosenberg et al. 2019; Forister et al. 2021; Habel et al. 2016); however, the ways in which this loss is perceived differ among generations of observers. Without a transfer of knowledge, younger generations may accept contemporary degraded conditions as the standard (Pauly 1995; Soga and Gaston 2018). This "shifting baseline syndrome" can impede conservation efforts because the rate and magnitude of biodiversity loss are consistently underestimated as the frame of reference shifts, distorting the historical baseline through generational amnesia (Papworth et al. 2009). Acceptance of such degraded states as "natural" can lead to distorted conservation goals and future generations that are less likely to consider conservation actions necessary (Jones et al. 2020). Building a better picture of the historical baseline can thus lead to more consistent support for conservation actions and more ambitious goals for restoration efforts.

Historical data are one of the best resources for counteracting shifting baseline syndrome, as they can align perceptions of biodiversity across generations (Soga and Gaston 2018). However, datasets that begin before large-scale anthropogenic degradation are few and increasingly precious. The butterflies of Donner Pass, California, are one such resource from which we can gain insight into the extent to which these losses potentially impact human perceptions of biodiversity. The first checklist of butterflies in this montane landscape was published in 1914 (Shapiro 1998), though the community was first rigorously documented in 1956 and 1960 by John and Thomas Emmel (Shapiro 1998; Emmel and Emmel 1962). In part because of this history, Dr. Arthur Shapiro began walking a transect in this same location in 1973 as part of his butterfly monitoring program across Northern California, which has become one of the most temporally intensive records of butterflies worldwide (Shapiro 2024). This work has shown that Donner Pass is one of North America's most species-rich butterfly faunas on record, especially for a latitude of 39° N.

In this study, we utilize 50 years of species-rich day (or "peak day") records as proxies for perceptions of biodiversity to inform our understanding of generational amnesia. Generational amnesia involves both a change in the state of the environment and a shift in perceptions, such that older generations recognize the change, whereas younger generations do not (Papworth et al. 2009). The peak number of species observed is a memorable and relatable index of diversity, serving as a key motivator for interaction with nature (Kaufman 2006; Dunn et al. 2005; Goldstein et al. 2024). Surveys of people have found that observing wildlife is a primary reason for visiting green spaces (Schipperijn et al. 2010; Dallimer et al. 2012), and that observing new species is especially important for informing perceptions of biodiversity (Ganzevoort and van den Born 2019). Some participatory monitoring programs may even suffer from bias due to an enthusiasm for recording rare species over common species (Dunn et al. 2005). At Donner Pass, declines in butterfly populations are well documented (Forister et al. 2010; Halsch et al. 2021), but we do not know if peak days are changing at the same rate and how this might impact perceived biodiversity among observers.

First, we ask how peak richness days are changing, employing a moving window sampling approach. We then examine the butterfly assemblages that comprise such days, including the most species-rich day on record, and ask if changes in assemblages are due to changes in phenology, changes in occurrences, or both. Finally, we ask how well species-rich days capture known downward trends in the data and consider how naïve observers in later decades might understand butterfly diversity differently at this site. Our goal is not to describe the causes of decline, which have been discussed elsewhere (Forister et al. 2018; Halsch et al. 2024) but rather to illustrate the consequences of decline for perceptions of biodiversity change.

2 | Methods

2.1 | Butterfly Data

The butterfly data collected at Donner Pass are part of a long-term monitoring program that has recorded butterflies every other week during the adult butterfly season for over 50 years. During each visit, observers walk the same 17.75 km long transect and record the presence of each species observed. The monitoring route was chosen to maximize species and habitat diversity, composed of a mixed conifer forest with an herbaceous understory and a meadow. Data have been collected at Donner Pass since 1973. Until 2018, data were collected by a single observer; since then, two additional observers have monitored this site. Each site visit is typically conducted with a single observer, although a second or third observer is occasionally present. For this analysis, we focus on the most species-rich day of each year or peak richness day, defined as the visit that recorded the highest number of butterfly species within a year. In two instances, two site visits were tied for the peak day of that year; in such cases, both visits were retained. To relate trends in the richness of these days to trends in populations generally, we regenerated a previously used standardized population index, where we calculated the number of days a butterfly was seen divided by the number of days a site was visited. We z-transformed this metric for each species and then took the average value for each year. The resulting metric is an annual site descriptor that describes whether the year was "good" or "bad" at the site relative to other years of monitoring (Halsch et al. 2021).

2.2 | Statistical Analysis

To generate a null expectation for peak days and change in the magnitude of peak days over time, we simulated distributions to represent the highest richness days of each year using a moving window approach, where the probability of seeing a particular species was informed by the probability of seeing that species on the most species-rich days from the 5 preceding years and the 5 following years. The probability that each species would be seen on the peak day was determined by dividing the number of peak days a species was seen in the 10-year moving window by the total number of years in that span. As butterfly observations are not independent events, we accounted for the co-occurrence of species by adjusting the probability of detection based on a covariance matrix (i.e., if two species frequently co-occur, a high probability of seeing one on a simulated day will raise the probability of observing the other). This was done by generating a random multivariate normal distribution using the mvrnorm function in the MASS package (Venables and Ripley 2002), with a mean of zero, standard deviation of one, and a sigma of the species covariance matrix of species in that time window. The multivariate normal distribution was then scaled to a range of 0–1 (for binomial sampling) using the pnorm function to calculate the cumulative density at that point in the multivariate normal distribution. The probabilities of detecting each species were then scaled so that the mean baseline probability of detection for each species was aligned with the detection probability of that species from our data, while conserving the covariance relationships between species. Over many simulations, each species-specific detection probability averages out to the baseline probability of detection for that time window. The co-occurrence matrix of species was calculated separately for each moving window. Once the probability of seeing each species was determined, we sampled from a Bernoulli distribution 10,000 times for each species and totaled the number of positive observations to determine the richness on each peak day.

We calculated two additional species-specific indices to examine the composition of species-rich days. The first was an index of phenology, calculated from a phenological distribution for each species based on the mean and standard deviation of the days of the year on which a species was observed across all site visits. For each peak day a species was observed, we determined the density of the phenological distribution preceding that day of the year using the pnorm function. The index ranges from zero to one, where a value of 0.5 indicates that a particular peak day occurred exactly in the middle of a species' expected flight period. If a butterfly was seen on a peak day that occurred earlier than average (based on that species' historical phenology), it received a value closer to zero. We also generated an index of the historical prevalence of each species by dividing the number of years a species was observed by the total number of years the transect has been monitored. We classified rare species as those seen in less than half of the monitored years. These metrics were first calculated at a species-specific level and then averaged across species observed on each peak richness day, providing a single metric of how phenologically and historically unusual a butterfly assemblage was on a particular day. All analyses were performed in R Core Team (2023).

3 | Results

Simulated distributions of peak days generally contained the observed values of butterfly richness, with only 3 days (1982, 1992, and 2008) classified as highly improbable (Figure 1). Every parameter of these distributions showed reductions over four decades of monitoring at Donner Pass (Figure 1). The annual rate of decline of the median of the distributions was 0.28 species per year, where a typical high species day now has 10 fewer species, about 82% of the expected species richness, relative to the high of 1992 (Figure 1). The richness of high peak days has also shifted, described by the upper tail of the richness distributions, where the most species-rich contemporary days would be considered average or even below average in previous decades (Figure 2). For example, the probability of observing the all-time high of 62 species in 1992 was 0.02. Using the detection parameters for the most recent year in the dataset, this all-time high is never seen, even when sampling from the distribution one million times, the highest generated richness value is 52 (Figure S1).

Species observed on the most species-rich butterfly days of the year tended to be in the latter half of their flight window; specifically, the average observed butterfly is 69% into its expected flight period at the time of the peak richness day (Figure 2A,B). Peak richness days also document two rare species on average; however, there are days on record where the rare species count has been considerably higher (Figure 2A,B). The number of total species seen on a peak richness day was more related to the number of rare species than anomalies in phenology (Figure 2B). That said, the most extreme day in the dataset was caused by anomalies in both rare species and phenology. On that day, nine rare species were observed. At the same time, many species emerged in that year much earlier than their expected phenology, on average only 12% into their expected flight window, the most extreme instances for both of those metrics (Figure 2C). When examining trends across these two metrics over the entire time series, we did not find a change in the phenological composition of butterfly assemblages on peak diversity days. Rather, there was a trend in the frequency with which rare species are observed (Figure 2B), indicating that declines in species-rich days are due to the loss of rare species rather than shifts in phenologies.

Our analysis found that peak day as a metric for biodiversity indeed captured the known trends in the data when summarized at an annual resolution (Figure 3). In fact, the trends of these extreme days are slightly more extreme than previously documented population declines, indicating that reductions in peak richness may be due to losses of rare species that used to be seen more frequently on species-rich days. Equally concerning, the major trends in the data, both the overall reduction of richness and the loss of rare species, would only be detectable to observers

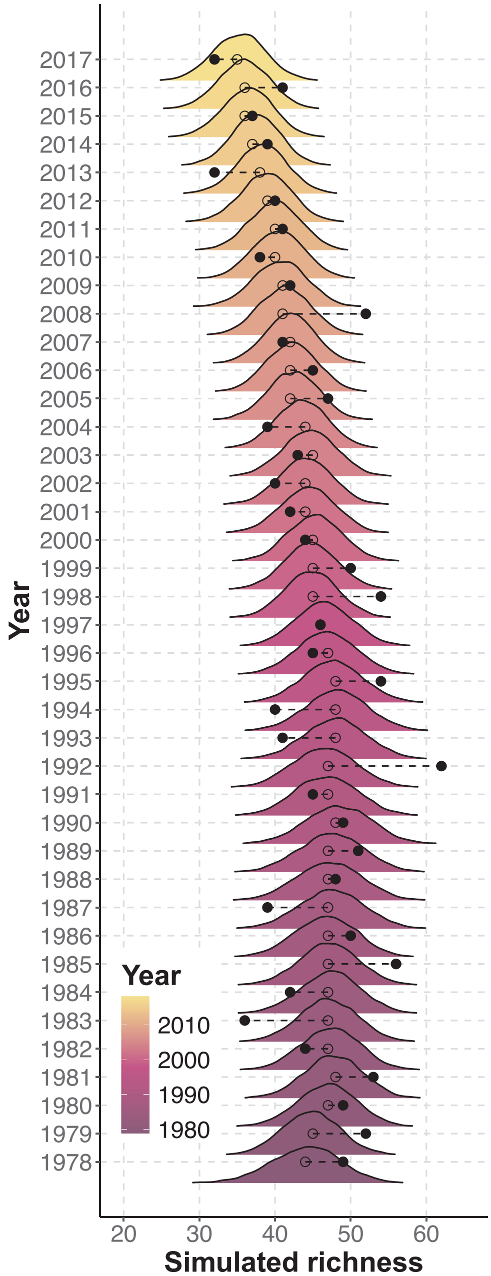

FIGURE 1 | The simulated distribution of species richness of the most species-rich day of the year based on the observed butterfly assemblages on the peak days of the 5 years before and after. Open dots show the median, and closed dots show the observed richness.

who visited Donner Pass prior to the 2010s. Without these data, any visitor to the site would consider the peak day to be a day on which they saw 35–40 species, when this is only 75%–85% of the site's previously recorded richness (Figure 3).

4 | Discussion

Long-term monitoring data are essential for providing insight into the rates and drivers of decline, but also for describing previous states of biodiversity. The Shapiro transect has been an important part of our understanding of butterfly declines in North America (Edwards et al. 2025). Using different metrics

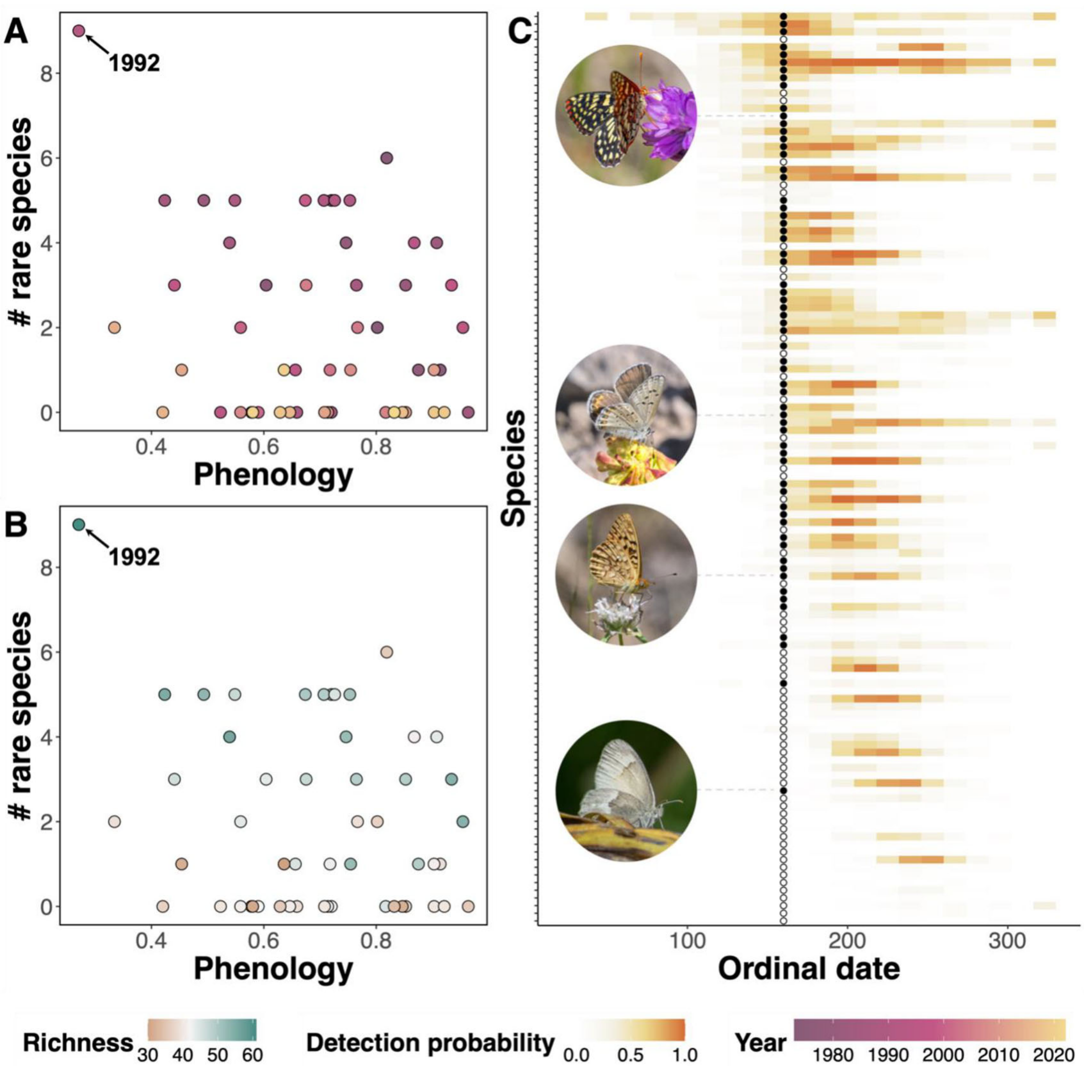

FIGURE 2 | The assemblages of species-rich butterfly days over time. The relationship between the average phenology for the butterfly observed on a species-rich day and the number of rare species observed where points are colored by (A) year or (B) the overall richness of the day. (C) The full observed assemblages on June 8, 1992. The average phenology over the entire butterfly monitoring at this site is shown in orange, where darker shades show a higher probability of a species being detected on that date. Filled circles indicate that a species was observed. Photos show *Euphydryas chalcedona, Plebejus acmon, Speyeria egleis*, and *Anthocharis lanceolata*. *Source:* Photo credit: CAH.

and methodologies, we detect this same signal in some of the most significant events shaping perceptions of biodiversity, peak richness days. These analyses also reveal the species composition of such days, providing insight into how these peak richness days have changed and how baseline butterfly diversity should be viewed.

On a standard peak richness day, an observer will likely encounter common butterflies that characterize the early and middle summer (but will be too early for the later phenology butterflies), while also recording a few rarer species (Figure 2A,B). On June 8, 1992, the best day on record, anomalies in space (rare species) coincided with anomalies in time, where species that fly in different parts of the year emerged simultaneously. Nine rare species were observed, and more unusually, many butterflies flew early, even those whose flight period is typically expected in the latter half of summer (Figure 2C). Although this day stands out for its richness, it is an exception to the pattern we see for other peak days. Generally, better-than-expected peak days are driven by the increased appearance of rare species rather than changes in phenology. This is likely due to shifting demographic input from lower elevation species, which do not have established populations at Donner Pass. Some of these species will be recorded in any given year, but as they are not resident, their presence is more stochastic, and nonresidents form a large portion of our species classified as "rare." The decline of lowland butterflies in California has been well documented (Forister et al. 2010; Edwards et al. 2025; Forister et al. 2016), and the reduction of rare species on peak richness days likely reflects regional dynamics beyond this one site (Pardikes et al. 2017).

Donner Pass is visited between 10 and 20 times annually, from the snow melt in spring to the return of cool and wet conditions in the fall. Over these visits, no day is as memorable as the one when butterfly richness is at its peak, and the erosion of such days could disproportionately reshape ideas of baseline butterfly diversity.

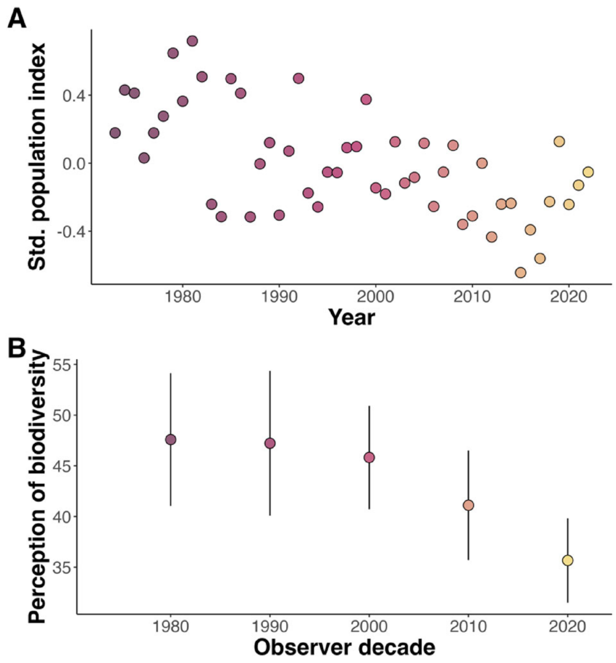

FIGURE 3 | Potential generational amnesia over five decades of monitoring in Donner Pass, CA. (A) The annual decline of butterfly populations from continuous monitoring based on the standardized population index (Halsch et al. 2021). (B) The perceived biodiversity (defined by the most species-rich day of the year) of a naïve observer in five different decades. Values indicate the mean and standard deviation of species richness and show what an observer would consider the peak of butterfly diversity in each decade.

Used in this way, these days are not a metric of population dynamics (although they are related), but rather a metric of how butterfly diversity is perceived. This is not without uncertainty, as we did not directly measure people's perceptions; however, the link between the number of observed species and the perceived diversity of a system is somewhat self-evident and has been observed in previous studies (Schipperijn et al. 2010; Dallimer et al. 2012; Ganzevoort and van den Born 2019). By this metric, contemporary observers at Donner Pass are likely to experience only a fraction of the single-day butterfly diversity that Arthur Shapiro did a few decades ago. In 1992, an observer had a 50% chance of seeing 47 or more butterfly species on the most species-rich day; now, this has dropped to less than a 1% chance. Thus, the expected distribution of peak richness from which contemporary observers are sampling has entirely shifted.

In light of the decline of butterflies and the potential erosion of perceptions of biodiversity, it is important to consider how to establish a baseline. While June 8, 1992, is the best day on record at Donner Pass, we have shown it to be highly improbable, even given the greater numbers of butterflies 30 years ago. Rather than using a single day as the historical baseline, our approach of creating distributions of peak butterfly days incorporates information collected over a decade, providing a more accurate metric of baseline butterfly richness. Although it is not perfect, and some outlier days were not well predicted, the simulated distributions generally contained the observed species-rich days. If the goal were to predict the presence of each species, a more mechanistic approach would be necessary; however, our goal is to understand the assemblages of species as a whole. For this, our method offers a relatively straightforward and interpretable approach for examining how communities have shifted over time.

5 | Conclusion

The American West has experienced reductions in butterfly populations due to land use change, climate change, and pesticide exposure across large areas (Edwards et al. 2025; Forister et al. 2023). We demonstrate that without a historical perspective, the threat of generational amnesia is considerable, as declines are only detectable when compared to a pre-2010s baseline. Of course, we have a record that effectively negates the effect of generational amnesia in this one location; however, it is precisely that record that allowed us to investigate what the effects of amnesia likely are in other places that are popular for recreational naturalists or are the subject of contemporary ecological investigations. Long-term records of insects, especially those started before the year 2000, are rare, underscoring the importance of developing resources to identify and digitize historical data, particularly historical monitoring records. Even a few historical occurrence records from specific locations can be highly informative. They can alert modern observers to the phenomenon of loss when a species is no longer present, providing insight even if the data are insufficient to quantify the extent of loss across the entire fauna. This is particularly important as biodiversity applications, such as iNaturalist, eBird, and eButterfly, expand the number of people participating in species observation. Although they are innovative and valuable sources of contemporary data, these databases may inadvertently set the baseline for many people firmly in an era of biodiversity loss.

Author Contributions

Christopher A. Halsch: conceptualization, methodology, formal analysis, investigation, data curation, visualization, writing – original draft, writing – review and editing, funding acquisition. **Arthur M. Shapiro**: investigation, data curation, writing – review and editing. **Matthew L. Forister**: conceptualization, methodology, investigation, data curation, writing – review and editing. **Eliza M. Grames**: conceptualization, methodology, writing – review and editing.

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Data Availability Statement

The data and code to reproduce all results can be found at https://doi.org/10.6084/m9.figshare.28175522.v1 .

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting Figure: conl13116-sup-0001-SuppMat.docx