

ARTICLE

Animal Ecology

Patterns of richness in a long-term citizen science butterfly dataset from Cuyahoga Valley National Park

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Abstract

Insect populations are experiencing ongoing declines in abundance and diversity, but their dynamics are often complex and trends are difficult to identify. Butterflies are an important, convenient, and useful insect group to monitor. They are a well-recorded group of insects and play important ecological roles as both pollinators and herbivores, and there is a large community of amateur lepidopterists that contribute to citizen science butterfly monitoring programs. In the present study, we analyzed 27 years of citizen science butterfly monitoring data collected across four sites in Cuyahoga Valley National Park, Ohio. We aimed to investigate patterns of species richness and abundance across years and sites and elucidate potential climatic variables that influence the butterfly community. We found similar levels of estimated butterfly species richness at three sites, yet one site had noticeably higher estimated species richness. Abundance fluctuated annually and was relatively consistent across sites. Further, we found that the butterfly communities changed directionally over time across all sites. Additionally, we identified degree days and average daily precipitation as drivers of butterfly community variability. Overall, this work identified patterns of richness and abundance in a unique national park and identified potential climatic drivers of butterfly community variability.

KEYWORDS

biodiversity survey, butterflies, citizen science, community science, insect declines, insect ecology, long-term data, species richness

INTRODUCTION

Insect populations often undergo complex dynamics, and it can be difficult to collect adequate data to explain patterns of fluctuations (Samways et al., 2010; Wilson & Fox, 2021). Because insects mediate many ecological processes, including pollination, herbivory, and nutrient translocation, shifts in insect population processes or

community composition can interrupt or negatively affect these processes (Losey & Vaughan, 2006; Satterfield et al., 2020; Wagner, 2020); thus, elucidating patterns in insect communities is important to maintain ecological function. With ongoing insect declines observed in ecoregions across the world, there is a pressing need to improve monitoring to enable the identification of population trends and inform conservation and management

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decisions (Forister et al., 2018; Hallmann et al., 2017; Potts et al., 2016; Wagner, 2020). However, drawing robust inferences about insect populations is difficult (Bahlai, 2023). For example, insect data may present false baselines and inaccurate snapshots of population trajectory, and implicit researcher bias may promote the detection of spurious trends (Didham et al., 2020). To ameliorate these potential pitfalls and increase understanding of complex insect population dynamics, long-term data and incorporation of citizen science paradigms into data collection can be employed to facilitate more robust investigation of changes in community composition and abundance through time (Didham et al., 2020; Zipkin et al., 2021).

Butterflies are a data-rich insect group to study at longer time scales due to strong public interest and relatively straightforward and standardized survey procedures (Pollard & Yates, 1993). Further, butterflies are ecologically important due to their role as pollinators in the adult stage and herbivores in the larval stage (Rani & Raju, 2016). Evidence of butterfly declines in North America is accumulating (Edwards et al., 2025; Kucherov et al., 2021; Wepprich et al., 2019), and declines in butterflies threaten to disrupt ecosystem services with potentially far-reaching impacts. For example, butterflies are a major food source for many insectivorous birds, and the loss of this energy source may already be contributing to declines in some bird species (Tallamy & Shriver, 2021). Thus, understanding changes in butterfly communities and identifying potential drivers of community shifts has implications for maintenance of biodiversity and ecological services.

In Cuyahoga Valley National Park (CVNP) in northeastern Ohio, USA, a butterfly monitoring program has been in place for nearly 30 years. CVNP is a unique national park due to its proximity to major urban centers and long history of agriculture, mining, and other intensive land uses. Today, much of the park has undergone some degree of ecological restoration or management (NPS, 2013). In the late 1990s, a volunteer-led butterfly monitoring program was established at Terra Vista Natural Study Area in the park, and since then, several sites have been added to the program. This long-term butterfly dataset can allow investigation of community richness and abundance patterns through time and identify community shifts at each site. Previous work investigating butterfly community ecology found highly localized shifts in butterfly communities (Habel et al., 2016; Wepprich et al., 2019), thus identifying patterns at individual sites can provide insight into community shifts and identify potential drivers of shifts. Indeed, given the unique and varied land-use history at each site (see below), it is likely sites have spatially independent noise terms

(Hillary & Bees, 2004), which may induce differential patterns of variation at each site. Further, given the diverse land-use history among sites, investigating the effect of climatic variables on the butterfly community at each site can provide insight into how land-use history interacts with climate to influence community composition (Marta et al., 2021; Millard et al., 2021).

Here, we examine several decades of monitoring data collected from a national park in areas undergoing active restoration and management. Specifically, we ask: how has richness and abundance changed across years at each site and what climatic variables are associated with shifts in the butterfly community? We expect to detect signals of change in the butterfly community; given accumulating evidence of butterfly declines in North America, we expect declines in richness and abundance through time. Further, we predict temperature, and precipitation drivers will be associated with changes in the butterfly community. Investigating site-specific changes in the butterfly community in the park will offer insight into a unique system, inform future conservation action, and inform future monitoring in the park and at large.

METHODS

Site descriptions

Surveys were conducted across four sites within CVNP between 1996 and 2023. Site locations are coded as Terra Vista, Indigo Lake, Pine Hollow, and Coliseum (Figure 1). All sites were generally composed of a mix of grasslands and woodlands, although the proportion of habitat among sites varied (see below for methods to calculate proportion of habitat area per site). Site history varied among locations, but all have a history of intensive land use. The Coliseum site was a sports stadium for 20 years before it was demolished and converted to grassland habitat in 1999. Indigo Lake was a quarry before it was converted to a lake with maintained forest and grassland surrounding it, and Terra Vista was a sand and gravel mining site before acquisition by NPS in 1985 when it was restored into meadow and forested habitat. Pine Hollow was part of a regularly mowed sledding area in the park, situated in the Virginia Kendall Area of CVNP which has a long history of recreational use.

Site habitat

The proportion of habitat types at each site was quantified using ArcGIS. We drew borders around areas of differing habitat at each site using satellite maps on ArcGIS

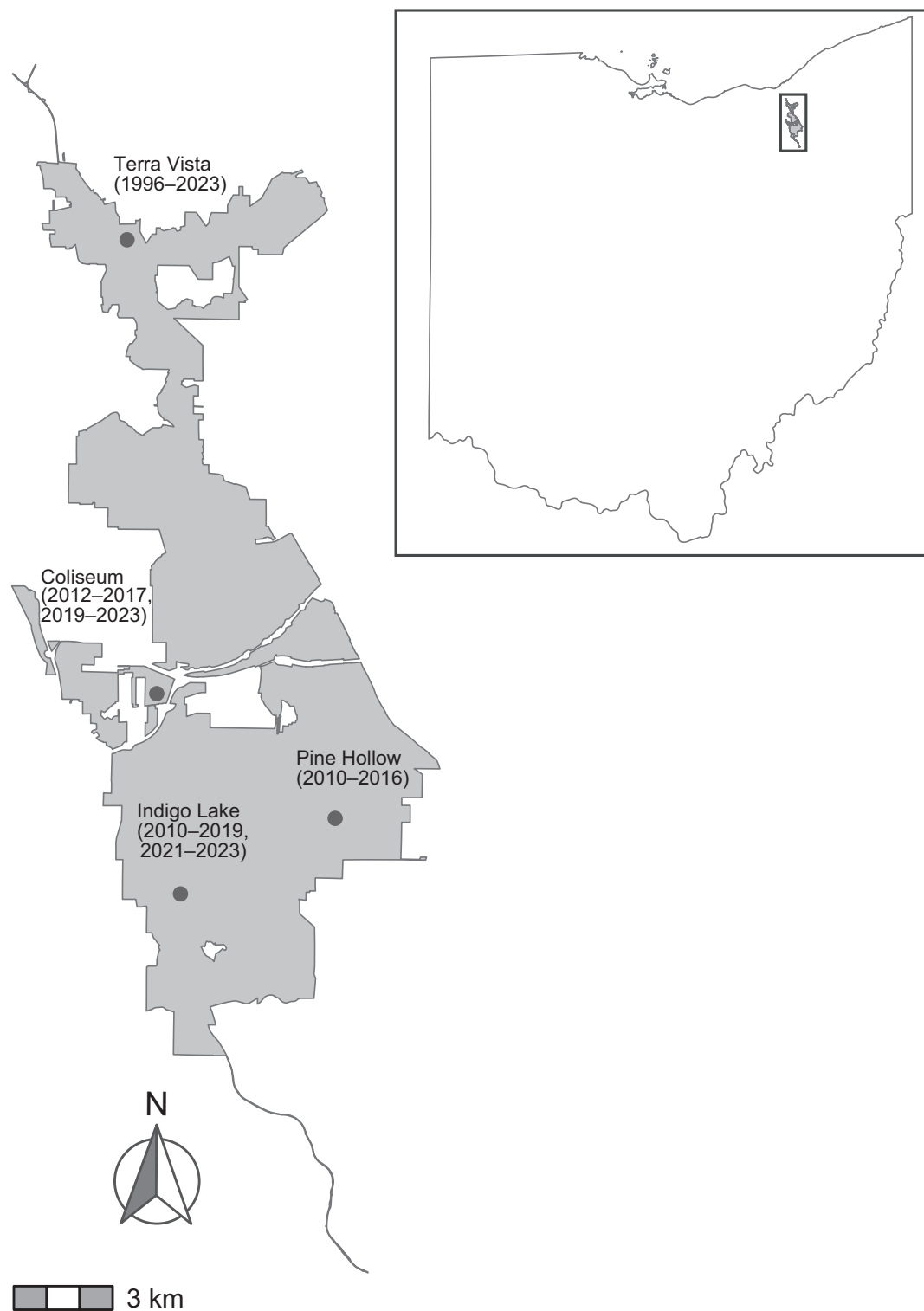


FIGURE 1 Butterfly monitoring sites in Cuyahoga Valley National Park, OH, USA. Years associated with each site label indicate the time period during which surveys occurred at each site.

and calculated the total area of each habitat type within the established boundaries of each site per NPS documentation. Habitat bins were “grassland,” “woodland,”

or “other.” We define “grassland” as open habitats, including meadows, mowed areas, and early successional habitat. In the case of “other,” a brief description of the

habitat in question was noted. The percentage of each habitat was calculated from the area of the habitat type and the total area of the site.

Butterfly surveys

Butterfly surveys were conducted by trained volunteers on a weekly basis from April to October and utilized a modified Pollard walk protocol, wherein observers walk at a steady pace along a transect and record all butterflies observed within a roughly 5-m³ area extending from the observer (Wiedmann, 2020). Transect area varied among sites, so comparisons among sites are limited by unequal sampling area. Thus, this study focuses on within-site trends through time. Terra Vista was surveyed continuously from 1996 to 2023. The other sites were surveyed for shorter and sometimes discontinuous intervals. Indigo Lake was surveyed from 2010 to 2019 and 2021 to 2023, Pine Hollow was surveyed from 2010 to 2016, and Coliseum was surveyed from 2012 to 2017 and 2019 to 2023. When analyzing the data, we removed 2023 from the Coliseum dataset because only one survey was conducted at that site in that year. Transects at each site were divided into sections, and transect sections did not span more than one habitat type (i.e., a single section would not consist of both grassland and woodland). Surveys were only conducted when temperatures were above 15.5°C, wind speed was 30.5–38.6 k/h (19–24 miles/h) or lower on the Beaufort scale, and it was not raining.

Data analysis

Richness patterns

We computed butterfly richness at each site and year of observation. First, we filtered out entries in the dataset that were marked as unknown or unidentified species. We next filtered the dataset to create a matrix with years as rows and species as columns, with each cell containing the total number of observations for that species, at that site, in a given year. We calculated observed richness using the “specnumber” function in the package *vegan* (Oksanen et al., 2024). We calculated rarefied richness at each site across all years by first obtaining the minimum number of observations in a given year and using that number as the subsample size for rarefying the community. We then used the “rarefy” function in *vegan* and constructed a rarefaction curve with the “rarecurve” function (step = 20) (Oksanen et al., 2024).

To provide a further estimate of richness, we calculated the total expected species (TES) per site by fitting a Weibull-logistic model to the observed abundance of each species at a given site (Zou et al., 2023). We used the function “TES” from Zou et al. (2022) to implement this methodology. We calculated TES at each site within each year and then pooled data across all years. To pool the data for TES, we summed the observed abundance across all sample years and used this vector of species abundance as the input data for the “TES” function. When calculating TES for the pooled data, we based inference on the TESb equation using the Weibull model for Terra Vista, Pine Hollow, and Indigo Lake, which is a more conservative estimate and less likely to overestimate species richness, especially when there are singletons or doubletons in the input data. However, for Coliseum, constraints of the data structure due to irregular sampling produced an error in the four-parameter Weibull model, so we instead used the TESa equation using the three-parameter logistic model (Zou et al., 2022, 2023). For the estimates of TES within each year, we used the TESb with a Weibull model for all sites. We used the “plot.tes” function from Zou et al. (2022) to display the accumulation curves at each site.

Abundance patterns

Because most of the sites had intermittent monitoring with large data gaps, we focused our abundance analysis on Terra Vista. We selected the 12 most abundant species overall from Terra Vista to investigate abundance patterns. We calculated the relative abundance of these 12 species from all sites and plotted a time series to show changes in relative abundance over time.

Community composition

To investigate community change at each site, we obtained the total number of observations of each observed species per site in each year. We then subjected this dataset to non-metric multi-dimensional scaling (NMDS) via the “metaMDS” function in *vegan* with the number of dimensions set to 2, and autotransform enabled. The autotransform function transformed the data with a Wisconsin double standardization and then used Bray–Curtis similarities. We used taxonomic family as a treatment group and constructed CIs around the centroid for each family. We also generated plots with survey years as treatment groups and similarly constructed CIs around the centroid for each year grouping to investigate temporal shifts in the observed butterfly community.

Because sampling effort differed between sites, we created seven treatment groups for Terra Vista that each consisted of 4 years of survey data, and for Pine Hollow, Indigo Lake, and Coliseum, we made two treatment groups that each represented half of the survey years.

Environmental variables related to community composition

We downloaded daily weather data from nearby National Oceanic and Atmospheric Administration (NOAA) weather stations (Station IDs: USW00014813, USC00330061, USW00014820; NOAA Climate Data Online, 2024) for all survey years. We imputed missing values in the dataset (0.39% of precipitation observations and 0.63% of temperature observations) via linear interpolation using the “na.approx” function in the R package “zoo” (Zeileis & Grothendieck, 2005). From the maximum and minimum temperature, we calculated degree days in each year using a modified-sine wave function (Allen, 1976). We calculated average degree days over an entire year and over four seasonal quarters to characterize seasonal weather patterns throughout the year (Arnold et al., 2023). The four quarters were January through March, April through June, July through September, and October through December. We also calculated average daily precipitation (in millimeters) over each year.

We used the “ord.fit” function to investigate how degree days and precipitation influenced dissimilarity among sites. Then, using the “env.fit” function, we related environmental variables to the NMDS ordination. Specifically, we fit one model using degree days in the different quarters of the year; for quarters 1–3, we used data from the year that matched the observations, and for quarter 4, we used data from the previous year since we assumed that degree days in the late fall/early winter of the preceding year would influence the abundance of species observed the following year, rather than the late fall early winter of the year of observations influencing the abundance and richness of the butterfly community observed in that year. We fit a second model using

degree days averaged across the entire year and average daily precipitation for each year.

RESULTS

Site habitat and area

Terra Vista was the largest site, followed by Coliseum, Indigo Lake, and Pine Hollow (Table 1). Pine Hollow and Coliseum were >50% grassland habitat, whereas Terra Vista and Indigo Lake were >50% woodland (Table 1). At Terra Vista, woodlands were in a relatively early successional stage, whereas Indigo Lake was a more mature forest. Indigo Lake and Terra Vista had the largest survey areas and were similarly sized, followed by Coliseum, and Pine Hollow had the smallest survey area (Table 1).

Richness patterns

Patterns of richness within each site varied annually (Figure 2, Table 2). We note that sampling effort (i.e., the number of surveys conducted per year) varied through time, which may have impacted the observed patterns of richness, especially for rarefaction (Appendix S1: Table S1). At Terra Vista, observed richness, rarefied richness, and TES are highest around the year 2000 and then decrease but stay relatively consistent for the remainder of the time series (Table 2). Observed richness, rarefied richness, and TES begin high at Pine Hollow and then decrease substantially halfway through the time series before recovering in the last few years. The decrease in richness at Pine Hollow coincides with a year with few surveys (Appendix S1: Table S1); however, in subsequent years, the number of surveys is the same as the number of surveys in the first few years of the time series, but richness remains lower than in the first few years of the time series. Richness at Indigo Lake generally decreased throughout the time series across all measures of richness, and the last 5 years of the time series have consistently lower observed and rarefied richness values relative to the preceding years. Finally, Coliseum

TABLE 1 Summary of habitat and survey area (in square meters) of butterfly monitoring transects in Cuyahoga Valley National Park.

Area	Terra Vista	Indigo Lake	Pine Hollow	Coliseum
Survey	40,980	41,820	20,700	35,460
Total	945,961	444,147	385,455	758,409
Grassland	165,366	59,496	251,645	324,503
Woodland	776,263	348,089	133,810	433,906
Other	4332	36,563	NA	NA

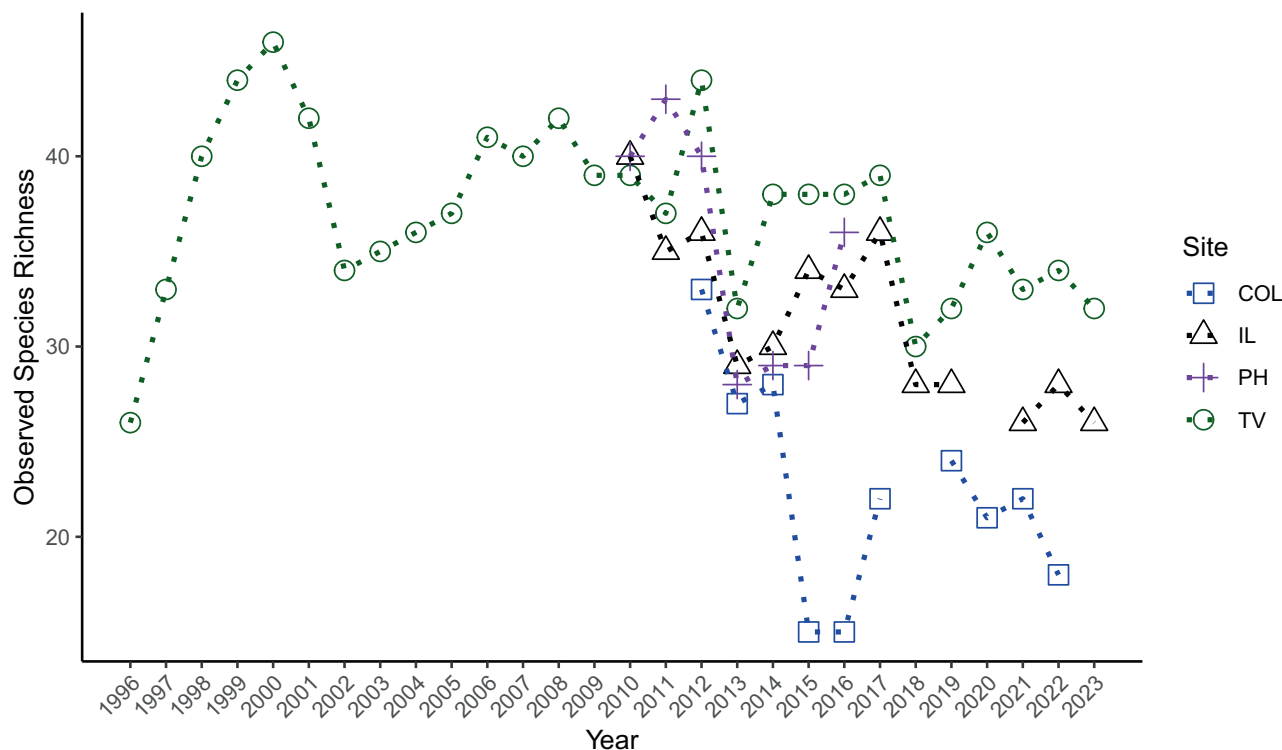


FIGURE 2 Observed butterfly species richness in each survey year at Coliseum (COL), Indigo Lake (IL), Pine Hollow (PH), and Terra Vista (TV) in Cuyahoga Valley National Park.

had the highest richness in the first two years of the time series and reduced but consistent richness for the remainder of the time series. We note that the first two years of sampling at Coliseum had substantially higher survey effort compared to other years; thus, the higher richness in these years is potentially an artifact of sampling effort. Observed richness summed across the entire time series was highest at Terra Vista and lowest at Coliseum, and Indigo Lake and Pine Hollow had the same observed richness (Appendix S1: Table S2). TES summed across the time series followed the same pattern as observed species richness, with the highest in Terra Vista, lowest at Coliseum, and Indigo Lake and Pine Hollow in the middle with similar richness (Figure 3).

Abundance patterns

Each species we plotted showed some cyclicity, with increases and decreases in abundance across years (Figure 4; Appendix S1: Figure S2). For several species, such as *Phyciodes tharos* and *Colias eurytheme*, the increases and decreases in abundance are relatively consistent across sites (Figure 4a,c), but for some species and sites, such as *Megisto cymela* and *Thymelicus lineola*, we see contrasting patterns of cyclical abundance among

sites (Figure 4b,d). Of the top 12 most abundant butterfly species that we plotted, *P. tharos* was the most abundant butterfly, and *Speyeria cybele* was the least abundant.

Community composition

Across sites, Hesperiidae, Nymphalidae, and Lycaenidae account for most of the variation in the observed butterfly community as indicated by their larger ellipses, while Pieridae and Papilionidae generally accounted for less variation, as indicated by their smaller ellipses (Figures 5 and 6). The ellipses corresponding to different years suggest directional community change over time, as indicated by the separation of the ellipses (Figure 7).

Average daily precipitation was significantly associated with community variation at Indigo Lake; both yearly degree days and average daily precipitation contributed to variation at Terra Vista and Coliseum, and neither variable significantly contributed to variation at Pine Hollow (Appendix S1: Table S2). For quarterly degree days, degree days in the last quarter of the previous year (i.e., October–December) significantly contributed to community variation at Indigo Lake; degree days in the third quarter of the year (i.e., July–September) significantly contributed to community variation at

TABLE 2 Observed species richness, rarefied species richness, and total estimated species (TES) from each survey site in each year.

	Species richness			
Year	Observed	Rarefied	TES	TES SD
Terra Vista				
1996	26	26	28.83	0.85
1997	33	28	67.6	53.15
1998	40	31	100.98	57.39
1999	44	34	57.57	7.79
2000	46	38	55.06	7.88
2001	42	39	42.26	0.86
2002	34	31	36.11	1.2
2003	35	32	36.06	0.76
2004	36	34	35.41	1.54
2005	37	32	40.57	4.03
2006	41	33	44.05	3.62
2007	40	33	38.36	1.89
2008	42	35	43.11	2.17
2009	39	34	41.38	1.57
2010	39	34	39.22	0.91
2011	37	34	38.11	1.54
2012	44	36	44.18	2.27
2013	32	30	38.91	2.63
2014	38	33	39.65	3.32
2015	38	35	40.92	3.73
2016	38	35	39.78	1.64
2017	39	36	39.21	1.76
2018	30	30	30.06	0.77
2019	32	32	33.62	1.78
2020	36	35	40.33	2.82
2021	33	31	33.18	1.19
2022	34	32	34.35	0.85
2023	32	31	33.74	0.97
All years	71	NA	128.35	83.76
Pine Hollow				
1996	NA	NA	NA	NA
1997	NA	NA	NA	NA
1998	NA	NA	NA	NA
1999	NA	NA	NA	NA
2000	NA	NA	NA	NA
2001	NA	NA	NA	NA
2002	NA	NA	NA	NA
2003	NA	NA	NA	NA
2004	NA	NA	NA	NA
2005	NA	NA	NA	NA

(Continues)

TABLE 2 (Continued)

Year	Species richness		TES	TES SD
	Observed	Rarefied		
2006	NA	NA	NA	NA
2007	NA	NA	NA	NA
2008	NA	NA	NA	NA
2009	NA	NA	NA	NA
2010	40	23	87.13	47.01
2011	43	27	49.56	2.52
2012	40	32	41.87	2.18
2013	28	28	29.32	1.71
2014	29	23	31.86	3.77
2015	29	23	29.79	1.34
2016	36	28	40.7	2.36
2017	NA	NA	NA	NA
2018	NA	NA	NA	NA
2019	NA	NA	NA	NA
2020	NA	NA	NA	NA
2021	NA	NA	NA	NA
2022	NA	NA	NA	NA
2023	NA	NA	NA	NA
All years	53	NA	60.58	4.66

Indigo Lake

1996	NA	NA	NA	NA
1997	NA	NA	NA	NA
1998	NA	NA	NA	NA
1999	NA	NA	NA	NA
2000	NA	NA	NA	NA
2001	NA	NA	NA	NA
2002	NA	NA	NA	NA
2003	NA	NA	NA	NA
2004	NA	NA	NA	NA
2005	NA	NA	NA	NA
2006	NA	NA	NA	NA
2007	NA	NA	NA	NA
2008	NA	NA	NA	NA
2009	NA	NA	NA	NA
2010	40	30	47.96	3.34
2011	35	31	35.7	0.88
2012	36	33	38.09	1.1
2013	29	25	31.84	2.24
2014	30	29	32.55	0.78
2015	34	31	36.63	2.2
2016	33	30	34.67	1.35

TABLE 2 (Continued)

Year	Species richness		TES	TES SD
	Observed	Rarefied		
2017	36	33	39.7	4.9
2018	28	27	31.24	3.06
2019	28	28	33.9	4.06
2020	NA	NA	NA	NA
2021	26	26	34.47	3.4
2022	28	27	29.99	2.02
2023	26	26	29.61	0.79
All years	53	NA	58.03	13.45
Coliseum				
1996	NA	NA	NA	NA
1997	NA	NA	NA	NA
1998	NA	NA	NA	NA
1999	NA	NA	NA	NA
2000	NA	NA	NA	NA
2001	NA	NA	NA	NA
2002	NA	NA	NA	NA
2003	NA	NA	NA	NA
2004	NA	NA	NA	NA
2005	NA	NA	NA	NA
2006	NA	NA	NA	NA
2007	NA	NA	NA	NA
2008	NA	NA	NA	NA
2009	NA	NA	NA	NA
2010	NA	NA	NA	NA
2011	NA	NA	NA	NA
2012	33	22.57	37.59	1.21
2013	27	17.71	41.33	17.12
2014	28	19.17	33.32	3.58
2015	15	15	17.25	3.16
2016	15	13.59	15.37	0.38
2017	22	19.56	23.36	0.93
2018	NA	NA	NA	NA
2019	24	19.13	25.57	2.21
2020	21	16.10	23.44	2.34
2021	22	17.13	31.49	6.33
2022	18	15.09	19.08	0.19
2023	NA	NA	NA	NA
All years	44	NA	56.59	14.30

Coliseum, and degree days in quarters two and three (i.e., April–June and July–September) affected butterfly communities at Terra Vista (Appendix S1: Table S2).

We found that average degree days and average precipitation acted in effectively opposite directions at each site (Figure 6). The direction of the effect of degree days

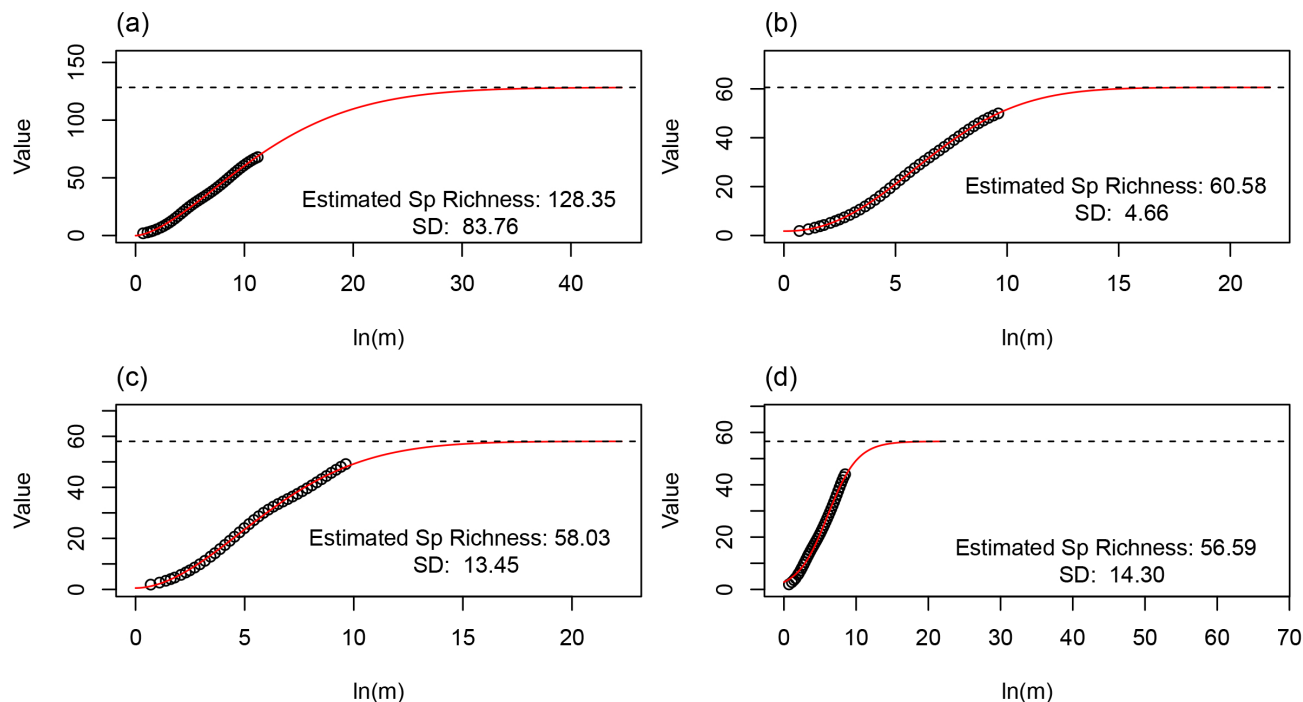


FIGURE 3 Total estimated species (TES) of butterflies at the (a) Terra Vista, (b) Pine Hollow, (c) Indigo Lake, and (d) Coliseum survey sites in Cuyahoga Valley National Park. The x-axis is the natural logarithm of the total sample size, and the y-axis is species richness. Red lines are estimated species accumulation curves, and the dashed horizontal lines represent the asymptote. Estimates were made by fitting a Weibull-logistic model to yearly species abundance data.

in different quarters of the year varied across sites. At Coliseum, the average degree days in different quarters acted effectively in the same direction, whereas at Indigo Lake and Pine Hollow, degree days from January through March behave orthogonally to the other quarters. Finally, at Terra Vista, degree days in January through March and April through June act in the same direction, while degree days from July through September and October through December of the preceding year group together act in a different direction than the other two quarters (Figure 5).

DISCUSSION

The patterns in butterfly richness, abundance, and community composition at each site within CVNP suggest changes in the butterfly community across years and highlight the importance of long-term data to accurately detect trends (Bahlai et al., 2021). The separation of the year-bin ellipses in the NMDS plots at each site suggests a significant turnover in the butterfly community as time progresses: the communities detected at the start of surveys at each site are not the same as the communities detected at the end of surveys. Notably, this pattern was detected at each site, despite differences in area sampled

and sampling effort. This result confirms previous studies that have detected highly localized shifts in the butterfly community through time (Habel et al., 2016; Wepprich et al., 2019). We also detected interannual variation in species abundance. For instance, *M. cymela* displayed pronounced cyclicity. *M. cymela* constituted a third of observations in the Terra Vista dataset in peak years and less than a tenth of observations in trough years (Figure 4b). Some species had notable declines in relative abundance. The relative abundance of *C. eurytheme* has been an order of magnitude below peak levels at Terra Vista since 2015, for example (Figure 4c).

Cyclical changes in the relative abundance of species varied; time series abundance for some species suggested synchrony among sites, while others suggested asynchrony. Species that displayed synchrony in abundance trends, such as *P. tharos* and *C. eurytheme*, are broadly distributed in the Eastern United States and are habitat generalists (VanDyk, 2025), thus connectivity among populations in our study sites is putatively high, which could explain the synchronized increases and decreases in abundance. Species with asynchronous abundance trends either had more specialized habitat requirements or this region of Ohio was on the edge of their distribution. For example, *M. cymela* occurs mostly in brush-filled woods and shrubby areas; their habitat

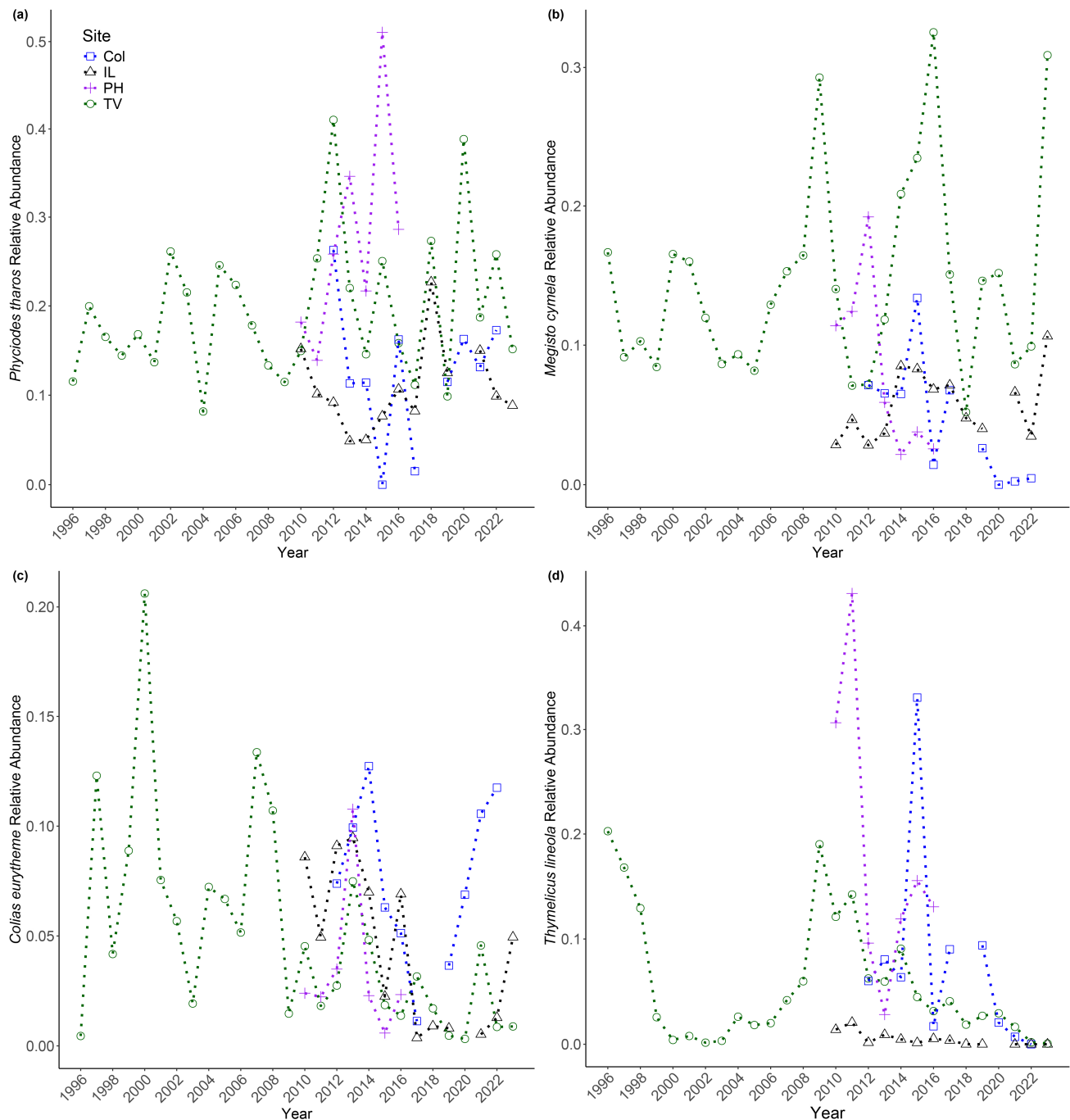


FIGURE 4 Time series of the relative abundance for the four most abundant butterfly species observed at Terra Vista (green line). The same species from Coliseum (blue line), Indigo Lake (gray line), and Pine Hollow (purple line) are plotted as well, but they may not be the most abundant species in their respective dataset.

specificity potentially limits the exchange of individuals between sites. In another example, *T. lineola*'s range in North America is primarily in Canada and higher elevation locations in Appalachia (VanDyk, 2025). Ohio is on the southern edge of its range, so populations may be discontinuous, thus leading to population asynchrony. Previous research on the synchrony of lepidoptera populations has often focused on forest pests, and thus,

future research exploring the synchrony among non-pest species at the community scale may provide novel insights into metapopulation dynamics in lepidoptera (Abbot & Dwyer, 2008; Adamski et al., 2019). Further exploration of synchrony among lepidoptera communities can also elucidate how spatial scale influences cyclicity among populations; we hypothesize that the size of the study area likely influences cyclical dynamics and

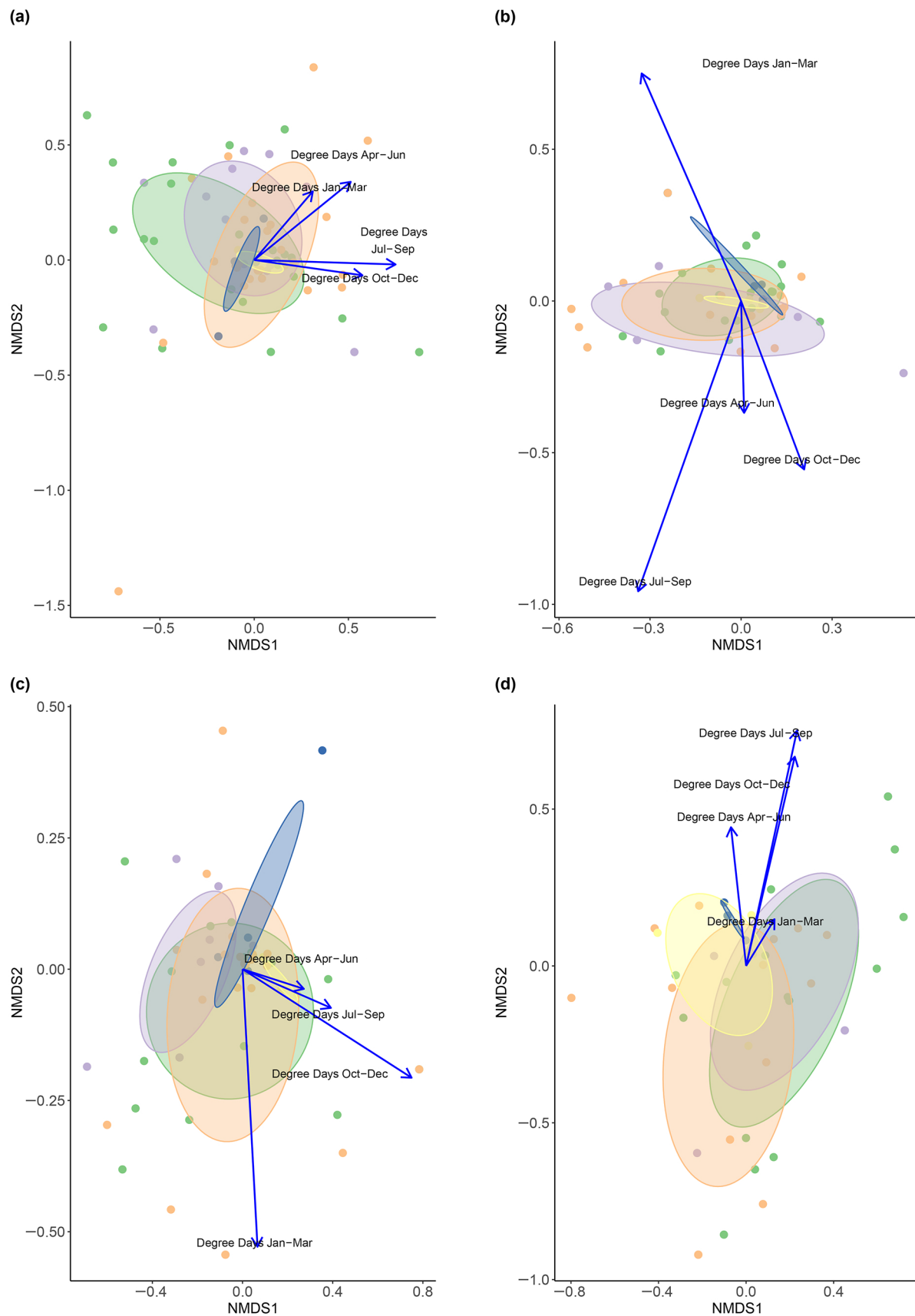


FIGURE 5 Non-metric multi-dimensional scaling plots for (a) Terra Vista, (b) Pine Hollow, (c) Indigo Lake, and (d) Coliseum. Ellipses represent the CI around the centroid of points, with taxonomic family identity as the grouping variable. Quarterly degree days were fit as environmental variables.

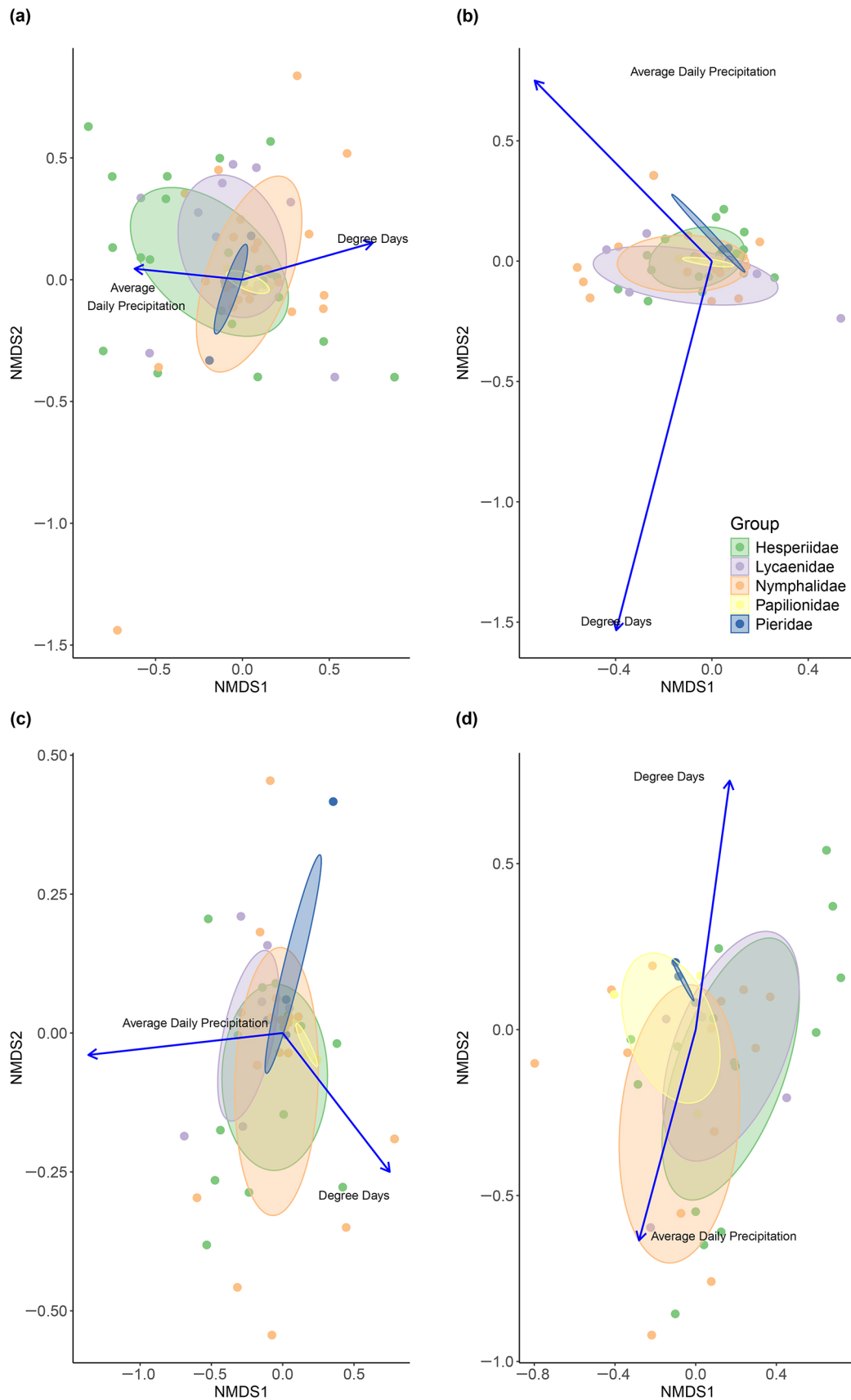


FIGURE 6 Non-metric multi-dimensional scaling plots for (a) Terra Vista, (b) Pine Hollow, (c) Indigo Lake, and (d) Coliseum. Ellipses represent the CI around the centroid of points, with taxonomic family identity as the grouping variable. Average yearly degree days and average daily precipitation (in millimeters) were fit as environmental variables.

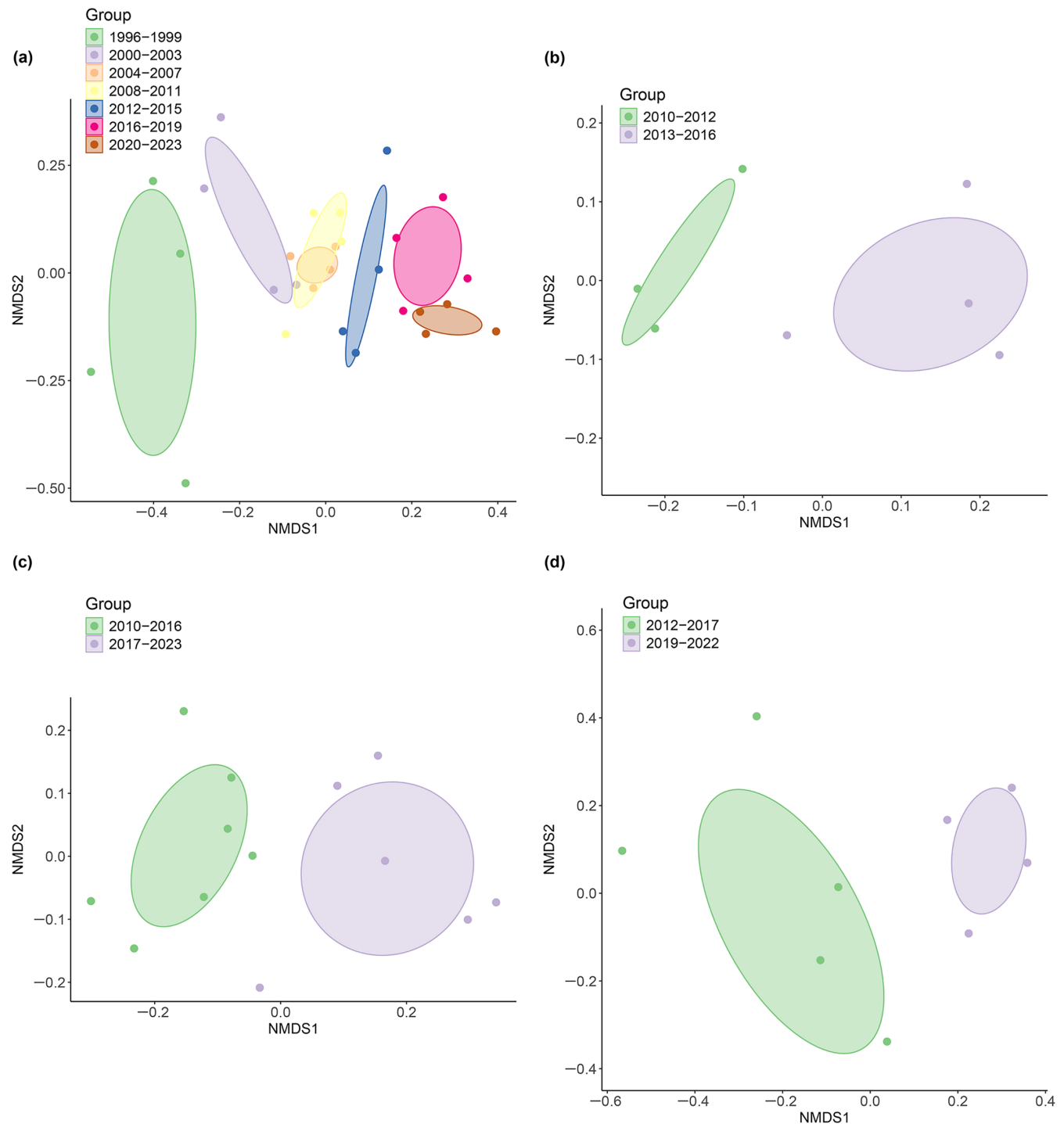


FIGURE 7 Non-metric multi-dimensional scaling plots for (a) Terra Vista, (b) Pine Hollow, (c) Indigo Lake, and (d) Coliseum. Ellipses represent the CI around the centroid of points, with time periods as the group.

synchrony among populations because spatial structure can increase independent noise terms and stochastic dynamics among populations (Abbot & Dwyer, 2008; Hillary & Bees, 2004).

TES was similar at Indigo Lake, Pine Hollow, and Coliseum. TES was substantially higher at Terra Vista, although with a much wider SD, the lower end of which

brings it to around the same level as the estimated species at the other sites. It is likely that Terra Vista does have higher species richness than the other sites, given its higher observed richness and the larger proportion of singletons and doubletons in the dataset, which indicates that more rare species are represented in the Terra Vista dataset. However, some of this observed pattern could

also be explained by the sustained sampling effort at this site. Indeed, sampling effort varied between years and among sites, which likely had an impact on the patterns of richness we detected. Further, Terra Vista was the largest site and had the largest survey area among sites, so given the species–area relationship (Connor & McCoy, 1979) the higher observed richness and TES at Terra Vista is unsurprising. A more in-depth analysis investigating potential spatial drivers of richness among sites was not feasible due to relatively few sites, unequal survey area, and unequal sampling effort among sites. Future research could aim to explicitly elucidate spatial drivers of richness using a combination of purpose-collected data and the long-term data we used here. Future examination of spatial drivers of richness will be possible if these surveys continue consistently across multiple sites with standardized sample area.

Variation in the butterfly community at all sites was driven primarily by three families, which indicates that family-level taxonomic identity is a strong driver of variation within the butterfly community. This trend holds across sites, indicating that the signal in the data driven by family composition overrides the unequal sampling effort and different site histories. The dominance of Nymphalidae, Hesperiidae, and Lycaenidae in our dataset matches other butterfly community studies (Dover et al., 2011; Mukherjee & Hossain, 2024; Pires et al., 2020) that found that these families account for the majority of the abundance and richness in the butterfly community. Biodiversity monitoring and management paradigms are shifting to focus on integrating data at higher taxonomic levels, so this finding can inform future butterfly monitoring and conservation decisions (De Oliveira et al., 2020; Egli et al., 2020; Kallimanis et al., 2012).

Our results support previous work that concluded increasing degree days is a driver of butterfly community shifts in North America (Crossley et al., 2021). Previous studies have found degree days are the best predictor of butterfly phenology and resultant compositional changes through time, even when richness and abundance remain the same (Cayton et al., 2015; Gezon et al., 2018; Lang et al., 2020). Similar to other insect groups, climate change is a major putative driver of butterfly declines (Gebremariam, 2024). Although we cannot directly conclude how degree days influence variability in the butterfly community in the present study given the temporal resolution of sampling and observation-only data, we hypothesize that it is via phenological shifts.

Climate change can restructure butterfly communities because warmer temperatures can alter phenology and development, changes in precipitation can increase water stress and induce phenological mismatch with host plants, and both increased temperature and precipitation

changes can induce mortality for vulnerable life stages (Breed et al., 2013; Forister et al., 2018; Kerner et al., 2023). At three of four sites, degree days in spring, when many butterfly species are emerging, acted orthogonally to the other quarters of the year in the NMDS analysis, which suggests that early spring temperatures induce changes in the butterfly community differently relative to temperature in other seasons, though these were not statistically significant. At Indigo Lake, degree days in October through December of the preceding year influenced community structure, which indicates degree days toward the end of the season, when many butterfly species begin to enter diapause either as eggs or as pupae, may influence community structure in the following year. Our results indicate that seasonal warming may drive butterfly community shifts. Indeed, climate is changing non-uniformly across seasons (Zhao et al., 2018; Zohner & Renner, 2019), and uneven seasonal warming may be impacting aspects of butterfly phenology and community ecology (Hamon et al., 2024). Average degree days and average daily precipitation acted in opposite directions at each site, which indicates that temperature changes drive variability in community composition differently than precipitation changes. More work aimed directly at disentangling how precipitation patterns influence butterfly community variability could be insightful, especially since butterfly eggs and early larval instars are especially susceptible to water stress (Herrando et al., 2019; Klockmann & Fischer, 2017).

No climate variables were found to be significantly associated with community shifts at Pine Hollow. Pine Hollow had the least intensive land-use history of the sites and is also the only site with a larger proportion of grassland area than woodland area. Grassland areas typically provide more floral resources to pollinators, which may confer resilience to unfavorable climate conditions. Future work aimed directly at investigating how climate, habitat, and land-use history interact to influence butterfly phenology and richness patterns could elucidate this point further.

Contemporary site management likely contributed to patterns in the butterfly community as well; however, due to inconsistent or vague record keeping across the survey sites, we could not construct a clear, usable chronology of management actions at each site. For example, we attempted to gather data on how often grassland areas in sites were mowed per year, and although we were able to find a mow plan for some of the survey years, we found records that indicated the mow plan was not followed, but no record of how often the sites were indeed mowed in a given year. Because of this, we were unable to directly examine management action in relation to shifts in the butterfly community, which

would have provided greater context to our analysis. Emerging text-mining techniques to extract information from textual data may help address this issue in the future (Farrell et al., 2022). Despite the potential of text mining to reconstruct management practices from text data, detailed record keeping concerning management action, in both the CVNP butterfly monitoring program and biodiversity monitoring programs as a whole, should be prioritized to facilitate future investigation of management practices. Similarly, survey metadata and data collected on site-level vegetation were inconsistently collected, and when collected, they were not always informative. Collecting metadata on citizen science surveys has been found to improve data quality and utility relative to citizen science surveys that do not collect survey metadata, particularly metadata that allows sampling effort to be quantified (Gigliotti et al., 2023). Thus, we suggest enhanced metadata collection could produce more useful data in future surveys. Further, vegetation data were recorded at various taxonomic levels or used inconsistent common names, and the number of individuals was never recorded, thus complicating the calculation of plant diversity and quantification of floral resources. Detailed surveys of the plant community were beyond the scope of this volunteer-led monitoring effort, but more information on the plant community would certainly provide greater context to the butterfly data. A potential middle ground could be to perform vegetation surveys in the spring, summer, and fall at each site to characterize richness throughout the growing season. Alternatively, using a simplified summary of the vegetation community could still be informative while being easy to collect. For example, flower density (regardless of species identity) (Mahon & Hodge, 2022) or vegetation height (Dvořák et al., 2022) could be useful and straightforward metrics to summarize the vegetation at each site.

CONCLUSIONS

This long-term dataset facilitated a detailed investigation of changes in the butterfly community and abundance through time. These data document consistent shifts in butterfly communities across several locations in a National Park in recent decades. Changing climate patterns may be responsible for observed shifts; however, site-level processes related to management, habitat, and land-use history likely contribute to patterns as well. CVNP is an intensively managed park, and indeed, most of the sites surveyed have undergone some form of restoration from previous intensive human use. The challenges with characterizing the influence of management practices highlight the need for detailed record-keeping

to facilitate accurate, contextualized, and detailed assessments of biodiversity, particularly for guiding restoration management. This study demonstrates the sensitivity of the butterfly community to changes in their environment, and the directional shifts we observed indicate that the community observed today is different from the communities observed when surveys began at each site. We echo the conclusions of Edwards et al. (2025) and suggest that despite observed changes in the butterfly community, conservation and recovery of species are still feasible. Indeed, the signals of synchrony and asynchrony of abundance trends among sites that we detected suggest that metapopulation dynamics may be at play for some species we examined (Matter, 2013), which presents tangible actions for conservation and population persistence (Anderson et al., 2015). For example, increasing floral resources and larval habitat in the park would benefit many species by increasing habitat area. Further, enhancing spatial connectivity among sites and, if required, physically moving individuals between sites may increase the viability of populations, especially for species that have experienced sustained decline in abundance through time. Continued monitoring of these sites and periodic reanalysis of the data as monitoring continues will provide continued insight into population and community dynamics, especially in relation to environmental variables and changing management practices.

AUTHOR CONTRIBUTIONS

Mariammar Gutierrez Ramirez wrote the grant proposal that funded this work. Thomas P. Franzem, Christie A. Bahlai, Mariamar Gutierrez Ramirez, and Leo Kuck contributed to the data analysis plan. Jerome Wiedmann curated the dataset and ensured data quality across the life of the monitoring program in the park. Leo Kuck prepared the datasets for the analysis presented here and collated relevant environmental variables. Thomas P. Franzem conducted data analysis with input from Christie A. Bahlai and generated Figures 2–7. Leo Kuck made Figure 1 and prepared the information in Table 1. Thomas P. Franzem and Leo Kuck wrote the initial manuscript draft. All authors edited the manuscript, read and approved the manuscript prior to submission, and were involved in revisions through the peer-review process.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Franzem et al., 2025) are available from Zenodo: <https://doi.org/10.5281/zenodo.14865798>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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