

Negative relationships between species richness and evenness render common diversity indices inadequate for assessing long-term trends in butterfly diversity

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Abstract Species richness and evenness, the two principle components of species diversity, are frequently used to describe variation in species assemblages in space and time. Compound indices, including variations of both the Shannon–Wiener index and Simpson’s index, are assumed to intelligibly integrate species richness and evenness into all-encompassing measures. However, the efficacy of compound indices is disputed by the possibility of inverse relationships between species richness and evenness. Past studies have assessed relationships between various diversity measures across survey locations for a variety of taxa, often finding species richness and evenness to be inversely related. Butterflies are one of the most intensively monitored taxa worldwide, but have been largely neglected in such studies. Long-term butterfly monitoring programs provide a unique opportunity for analyzing how trends in species diversity relate to habitat and environmental conditions. However, analyzing trends in butterfly diversity first requires an assessment of the applicability of common diversity measures to butterfly assemblages. To accomplish this, we quantified relationships between butterfly diversity measures estimated from 10 years of butterfly population data collected in the North Saskatchewan River Valley in Edmonton, Alberta, Canada. Species richness and evenness were inversely related within the butterfly assemblage. We conclude that species evenness may be used in conjunction with richness to deepen our understandings of assemblage organization, but combining these two components within compound indices does not produce measures that consistently align with our intuitive sense of species diversity.

Keywords Butterfly monitoring · Species diversity · Abundance data · Effective number of species · Shannon–Wiener index · Simpson’s index

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Introduction

Due to their charismatic nature and popularity among naturalists, butterflies are among the most intensively monitored taxonomic groups worldwide (Thomas 2005; Nowicki et al. 2014). Consequently, butterfly diversity has been invoked as an indicator of biological diversity and environmental health (Fleishman and Murphy 2009; Schmucki et al. 2015). Independent of their positive societal reputes, many ecological traits make butterflies promising ecological indicators. Because of their short life cycles relative to other popular indicator taxa, butterfly populations respond rapidly to environmental stimuli, making them sensitive surrogates for trends in habitat and environmental conditions (van Swaay and Warren 1999; Nowicki et al. 2008). Additionally, many butterflies complete their life cycles within small patches of habitat, meaning their movements and distributions can be used to map habitat conditions at relatively fine scales (van Swaay et al. 2006). Supporting this a priori indicative potential, butterfly diversity correlates with the diversity of many terrestrial, herbivorous insect groups (Thomas 2005). Together, such groups comprise a large proportion of terrestrial biological diversity (Nowicki et al. 2008). These traits, coupled with high detectability, make butterflies excellent subjects for long-term diversity monitoring projects. Indeed, Thomas (2005, p. 340) suggests that butterflies “are often the most—or only—practical insect group to study across the world.” The question therefore arises: how should the diversity of butterfly assemblages be assessed?

Ecologists have long struggled to find a simple index that is commensurate with the common notion of biological diversity, a.k.a. “biodiversity” (Humphries et al. 1995). The terms “species diversity” and “biodiversity” are often used interchangeably, although genetic (allelic) and landscape (ecosystem) diversity also fit within broad definitions of biodiversity (Magurran 2013). Species diversity is most often parsed into two principle components; (i) species richness, a count of the total number of species, and (ii) species evenness, a measure of how evenly sampled individuals are distributed among species (Hurlbert 1971; Magurran 2013). If data on the relative abundances of species are available, compound indices accounting for both species richness and evenness, most commonly (but not always; see Jost 2006) giving less weight to rare species, may be calculated. The most common and widely used of these indices are variations of the Shannon–Wiener index and Simpson’s index (Hill 1973; Izsák and Papp 2000). It has been suggested, however, that not all compound indices are true indices of diversity, but are entropies, reflecting distinct properties of species assemblages relating to diversity (Jost 2006).

Rooted in information theory, the Shannon–Wiener index is an entropy, measuring uncertainty in the outcome of a diversity sampling process. It has also been shown that most other nonparametric compound indices, including Simpson’s index, are generalized entropies (Tóthmérész 1995; Ricotta 2003; Keylock 2005). Entropies measure properties of species assemblage data, but are not themselves true diversities (Jost 2006). Furthermore, these entropies are nonlinear, complicating their interpretations. Transformations of entropies to Hill numbers, indicating the “effective number of species,” result in units akin to species richness, allowing for more intuitive, linear comparisons of species diversity (Table 1). The effective number of species represents the species richness of a theoretical assemblage, equivalent in diversity to a sampled assemblage (yielding the same value for the root entropy), but with a perfectly even species abundance distribution (Hill 1973; Jost 2006; Chao et al. 2014). The most common of these transformations is Simpson’s reciprocal index, calculated as the inverse of Simpson’s index. Jost (2006) recommends

Table 1 Conversion of common indices to Hill numbers (true diversities), where p_i represents the proportion of individuals within an assemblage belonging to species i

Index	Formula	Transformation to Hill numbers (true diversities)	Transformed index name
Species richness	$S = \sum_{i=1}^S p_i^0$	$H_0 = S$	Species richness (S)
Shannon–Wiener index	$H' = - \sum_{i=1}^S p_i \ln p_i$	$H_1 = \exp H'$	Exponential of Shannon–Wiener index ($\exp H'$)
Simpson’s index	$\gamma = \sum_{i=1}^S p_i^2$	$H_2 = \frac{1}{\gamma} = D$	Simpson’s reciprocal index (D)

exponentiating the Shannon–Wiener index to give an effective number of species; however, comparisons of untransformed Shannon–Wiener index values are still common.

Contrasting with their conventional appeal as all-encompassing species diversity measures, both entropies and their transformations have been criticized for their potential to mask variation among the various components of diversity, obscuring the results of ecological studies (Hurlbert 1971; Purvis and Hector 2000; Bock et al. 2007). For instance, species richness and evenness can counteract each other within compound indices if they are negatively correlated (Buzas and Hayek 1996), obscuring spatial or temporal gradients in species diversity. This potential for error within indices, coupled with conflicting behaviour between indices, has led some authors to conclude that compound indices are largely meaningless (Hurlbert 1971). Thus, species richness is frequently cited as the most reliable and straightforward measure of species diversity, and remains the central means for identifying biodiversity hotspots and monitoring trends in biodiversity worldwide (Andelman and Willig 2003; Wilsey et al. 2005; Magurran 2013).

When using species richness as a single measure of species diversity, it is traditionally assumed that (i) species richness is positively correlated with evenness, and (ii) species richness accounts for much of the spatial and temporal variance in diversity (Wilsey et al. 2005). These assumptions suggest that relationships between species richness and evenness are consistent between species assemblages, and that the two components represent different interpretations of a coherent ecological property known as “diversity.”

Empirical studies have tested the assumption that species richness and evenness are positively correlated, and whether inconsistencies in relationships between the two components can compromise the efficacy of compound indices. In partitioning the Shannon–Wiener index into species richness and evenness, Buzas and Hayek (1996) found that species richness and evenness affect the Shannon–Weiner index in a counteracting manner when negatively related. Stirling and Wilsey (2001) compared empirical relationships between species richness, species evenness, and the Shannon–Wiener index to null relationships generated from Caswell’s neutral model (simulation of log-normal and log-series species abundance distributions; Caswell 1976) and found that relationships were generally weak and inconsistent across taxa. Through spatial comparisons of plant diversity, Ma (2005) found no consistent patterns between species richness and evenness, with the two components having different responses to edaphic factors. Wilsey et al. (2005) found that species richness and evenness were positively correlated within invertebrate communities, weakly positively correlated within vertebrate communities, and negatively correlated within plant communities. Bock et al. (2007) found neutral to moderately negative correlations between species richness and evenness within angiosperm, grasshopper, butterfly, bird, and rodent communities in a savanna landscape. In that study, butterfly diversity was

assessed on four occasions in four different survey plots. No significant negative correlation between butterfly species richness and evenness was observed; however, the small sample size in this study questions the statistical power to resolve relationships. To our knowledge, all past studies addressing relationships between diversity measures did so across multiple survey locations, effectively addressing relationships between diversity indices across assemblages that may be influenced by different biophysical factors. In conservation biology, assessing temporal variability of diversity indices for single localities and species assemblages is just as important.

Long-term, standardized biodiversity monitoring programs are essential for assessing the conservation status of species and ecosystems (Schmucki et al. 2015), as well as for measuring the impacts of environmental change on biodiversity (van Swaay et al. 2011). Butterfly diversity monitoring programs, beginning with the establishment of the United Kingdom Butterfly Monitoring Scheme (UKBMS) in 1976, have appeared in a growing number of countries over the last two decades (Schmeller et al. 2009; Schmucki et al. 2015). Corresponding long-term population datasets are likewise expanding. Long-term population datasets are especially relevant for butterflies, among other invertebrate taxa, as they frequently exhibit inter-annual population fluctuations and shifts in phenology that may indicate changes in habitat and environmental conditions (Roy et al. 2001; Saarinen et al. 2003; Westwood and Blair 2010; Schmucki et al. 2015). Butterfly monitoring programs generally place emphasis on the collection of density and abundance data, which can be used to generate species diversity indices (Stephens et al. 2015). Therefore, assessing the viability of species richness, species evenness, and compound indices as measures of butterfly diversity is paramount.

Expanding on the works of Bock et al. (2007), we implemented a higher sampling frequency and longer study duration to assess variability in butterfly species diversity indices through time. Specifically, we examined ten years of butterfly population data from surveys completed over a 16 year period within the largest protected urban green space in North America, the North Saskatchewan River Valley in Edmonton, Alberta, Canada. The objectives of this study were to (i) assess how different indices of butterfly species diversity correlate through time, and (ii) measure the relative variability of diversity indices to assess which indices sufficiently capture temporal variation in species diversity of butterfly assemblages. We hypothesized that butterfly assemblages have a propensity towards unevenness as species' abundances increase under more favourable environmental conditions. To test this hypothesis, butterfly abundance and measures of diversity were correlated with annual precipitation and mean growing season temperature, as these environmental factors have been shown to positively affect butterfly abundances (Pollard 1988; Roy et al. 2001).

Materials and methods

Study area

Butterfly surveys were completed within the North Saskatchewan River Valley in Edmonton, Alberta, Canada, a municipally protected green space. The specific location of this ongoing study is a south-facing slope along the north bank of the North Saskatchewan River, from Government House Park to the mouths of Ramsay and McKinnon Ravines. The survey location has historically been maintained as a natural recreation area, and is set

in a matrix of mixed forest comprised primarily of balsam poplar (*Populus balsamifera*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*). Grassy areas line the transect route, as well as numerous willows (*Salix* spp.), alders (*Alnus* spp.), and caragana (*Caragana arborescens*). Approximately 60% of the grassy areas along the transect route are mowed regularly, with remaining sections left unkempt. Unkempt grassy areas border the mowed areas along the entire transect route. Nectar resources were generally concentrated within unkempt areas. However, mowed areas did not exceed more than 100 m in breadth, meaning nectar resources were not dramatically fragmented.

Survey methods

A modified form of fixed-route transects, or “Pollard walks,” was employed to sample the butterfly assemblage. This method was first conceptualized by Ernest Pollard in the early 1970s, and has since been implemented around the world in a wide array of butterfly monitoring schemes (Pollard 1977; Pellet et al. 2012). Butterfly surveys approximately 1–1.5 h in duration and following a single transect route were completed between May 1st and August 31st in 10 different years over a 16-year period (1999, 2000, 2002, 2007, 2009, 2010, 2011, 2012, 2013, and 2014). Surveys with low butterfly activity relative to other surveys within a two week window were eliminated. From the remaining data, eight transect counts were randomly selected from four four-week blocks within each year (two surveys selected per block). Starting at the GPS coordinates 53°32.336'N, 113°32.432'W, c. 629 m elevation, the transect route extends roughly 1350 m westward along the base of the south-facing hill slope, to the mouths of Ramsay and McKinnon Ravines, and about half way up a cleared grassy hillside to the stairs leading up to St. George’s Crescent, before doubling back 1050 m eastward, running parallel to the North Saskatchewan River. Total length of the transect route was approximately 2400 m. Surveys started between 12:00 and 15:45, subject to the condition that butterfly activity was apparent. Surveys were only completed in sunny conditions (less than 40% cloud cover) if temperatures were between 13 and 17 °C. At temperatures over 17 °C, surveys were completed regardless of cloud cover, but only if butterflies were obviously active. Transect counts were not completed in high wind conditions, or during any form of precipitation. Only butterflies occurring to the north of the transect route while traveling west were recorded. Similarly, only butterflies occurring to the south of the transect route while doubling back and travelling east were recorded. This method limits the possibility of “double counts,” where individuals are recorded twice in a single survey. However, when observing the first individual of any species during a survey, there exists no possibility of a double count, thus individuals belonging to “new species” were recorded irrelevant of their orientation relative to the set transect route.

Diversity analyses

Eight variables related to species diversity were estimated for each survey year, including: butterfly abundance (N), species richness (S), Simpson’s reciprocal index (D), the Shannon–Wiener index (H'), the exponential of the Shannon–Wiener index ($\exp H'$), Pielou’s evenness (J), species evenness (D/S), and proportion of rare species (*Rarity*). Butterfly abundance was calculated in each survey year as the sum of individuals observed across all eight surveys. Species richness was the total number of species observed in each survey year. Simpson’s reciprocal index was calculated as $D = 1 / \sum_{i=1}^s p_i^2$, where p_i represents the proportion of total butterfly abundance belonging to species i . The Shannon–Wiener

index was calculated as $H' = \sum_{i=1}^S p_i \ln p_i$. The exponential Shannon–Wiener index was calculated as $\exp H'$. Pielou's evenness was calculated as $J' = H'/\ln S$. Species evenness was calculated as D/S . Rarity was calculated in each year as the proportion of species that had relative abundances less than $1/S$ (Camargo 1992). Coefficients of variation (CV) and pairwise product-moment correlations were used to infer which measures best captured variation in species diversity and how the different measures fluctuate through time within a single assemblage, respectively. Diversity variables were correlated with annual precipitation and mean growing season temperature (April through August; calculated from daily highs) of both the same and the previous year, as these environmental factors have been shown to positively affect butterfly abundances and diversity (Pollard 1988; Roy et al. 2001). Historical weather data was obtained through Environment Canada (<http://climate.weather.gc.ca/>).

Results

A total of 37 butterfly species were recorded over the 10 survey years. Table 2 summarizes estimates for eight variables relating to species diversity: butterfly abundance (N), species richness (S), Simpson's reciprocal index (D), the Shannon–Wiener index (H'), the exponential of the Shannon–Wiener index ($\exp H'$), Pielou's evenness (J'), species evenness (D/S), and proportion of rare species (*Rarity*). Butterfly abundance ranged from 285 to 1270 individuals, and species richness ranged from 16 to 30 species. Coefficients of variation (CV) reveal that, of the three measures of species diversity most commonly reported—species richness, Simpson's reciprocal index, and the Shannon–Weiner index (Hill 1973)—species richness was the most variable (sensitive) through time (CV = 21.6), with Simpson's reciprocal index only slightly less variable (CV = 20.1). The untransformed Shannon–Wiener index proved to be the least variable among common diversity indices (CV = 10.8); however, exponentiating the Shannon–Wiener index appeared to improve

Table 2 Butterfly abundance (N), species richness (S), Simpson's reciprocal index (D), the Shannon–Wiener index (H'), the exponential of the Shannon–Wiener index ($\exp H'$), Pielou's evenness (J'), species evenness (D/S), and proportion of rare species (*Rarity*) calculated for 10 years of butterfly surveys completed within the North Saskatchewan River Valley in Edmonton, Alberta, Canada. Coefficient of variation (CV) is given for each metric

Year	N	S	D	H'	$\exp H'$	J'	D/S	<i>Rarity</i>
1999	436	20	3.79	1.91	6.72	0.64	0.19	0.80
2000	419	18	3.60	1.68	5.34	0.58	0.20	0.72
2002	361	23	5.48	2.17	8.77	0.69	0.24	0.78
2007	434	19	4.04	1.79	5.98	0.61	0.21	0.78
2009	367	20	3.77	1.75	5.75	0.58	0.19	0.8
2010	318	17	3.70	1.76	5.81	0.62	0.22	0.82
2011	285	16	4.20	1.77	5.87	0.64	0.26	0.75
2012	970	28	3.43	1.61	4.99	0.48	0.12	0.85
2013	1270	30	2.84	1.50	4.47	0.44	0.09	0.90
2014	840	23	2.79	1.58	4.85	0.50	0.12	0.82
CV	58.8	21.6	20.1	10.8	20.7	13.7	29.7	6.3

discriminating power (exponential of the Shannon–Wiener index; $CV = 20.7$). Species evenness, as measured by D/S , proved to be the most variable index of all ($CV = 29.7$), likely resulting from the negative correlation between the index's two constituent parts: Simpson's reciprocal index and species richness. Of all population variables, butterfly abundance was the most variable, with a coefficient of variation of 58.8.

Pairwise product-moment correlations reveal that species richness was positively correlated with butterfly abundance ($P < 0.001$) and of proportion rare species ($P < 0.01$), but was negatively correlated with Pielou's evenness ($P < 0.05$) and species evenness (D/S ; $P < 0.01$; Fig. 1; Table 3). Species richness correlated more strongly with untransformed butterfly abundances ($r = 0.91$) than log-transformed butterfly abundances ($r = 0.90$). No significant correlations were observed between species richness and Simpson's reciprocal index ($P > 0.05$), the Shannon–Wiener index ($P > 0.05$), or the exponential of the Shannon–Wiener index ($P > 0.05$), although correlation coefficients between species richness and the compound indices were consistently negative. Butterfly abundance was positively correlated with proportion of rare species ($P < 0.01$), and was negatively correlated with all diversity indices accounting for species evenness (Simpson's reciprocal index [$P < 0.05$], the Shannon–Wiener index [$P < 0.05$], Pielou's evenness [$P < 0.001$], and species evenness [D/S ; $P < 0.001$]), save the exponential of the Shannon–Wiener index, with which it was still negatively related ($P < 0.1$). Both measures of evenness were positively correlated with all three compound indices (Simpson's reciprocal index, the Shannon–Wiener index, and the exponential of the Shannon–Wiener index).

Relationships between diversity measures and environmental conditions (annual precipitation and mean growing season temperature) of the same year (Table 4) were consistently stronger than relationships between diversity measures and environmental conditions of the previous year. Butterfly abundance (N), species richness (S), and proportion of rare species (*Rarity*) were positively related to annual precipitation and mean growing season temperature of the same year. Contrastingly, indices accounting for evenness (D , H' , $\exp H'$) and measuring evenness explicitly (J' , D/S) were negatively related to annual precipitation and mean growing season temperature of the same year.

Discussion

Species richness, butterfly abundance, and proportion of rare species were all positively correlated within our long-term butterfly population dataset. All three measures were also positively related to annual precipitation and to mean growing season temperature. These findings agree with other studies suggesting that butterfly populations respond quickly to favourable environmental conditions (i.e., higher precipitation and warmer temperatures; Pollard 1988; Roy et al. 2001). It seems likely that, in years of higher precipitation and warmer temperatures, increases in species richness are driven by increases in the abundances, and thus detection, of rare species. Notably, conditions for butterflies improved in 2012, a year in which numerous irruptive species also made appearances, and with conditions also favourable the following year, 2013 produced the highest butterfly abundance and species richness values. By 2014, conditions were returning to less favourable measures.

In contrast, increases in butterfly abundance and species richness were associated with decreases in the two measures of species evenness (J' and D/S). These relationships can be

Fig. 1 Scatter plots of **a** Butterfly abundance (N) and proportion of rare species (*Rarity*) as they relate to species richness; **b** Simpson's reciprocal index (D), the Shannon–Wiener index (H'), and the exponential of the Shannon–Wiener index ($\exp H'$) as they relate to species richness; and **c** Pielou's evenness (J') and species evenness (D/S) as they relate to species richness. All eight variables are in units of S.D. r = pairwise product-moment correlation coefficient

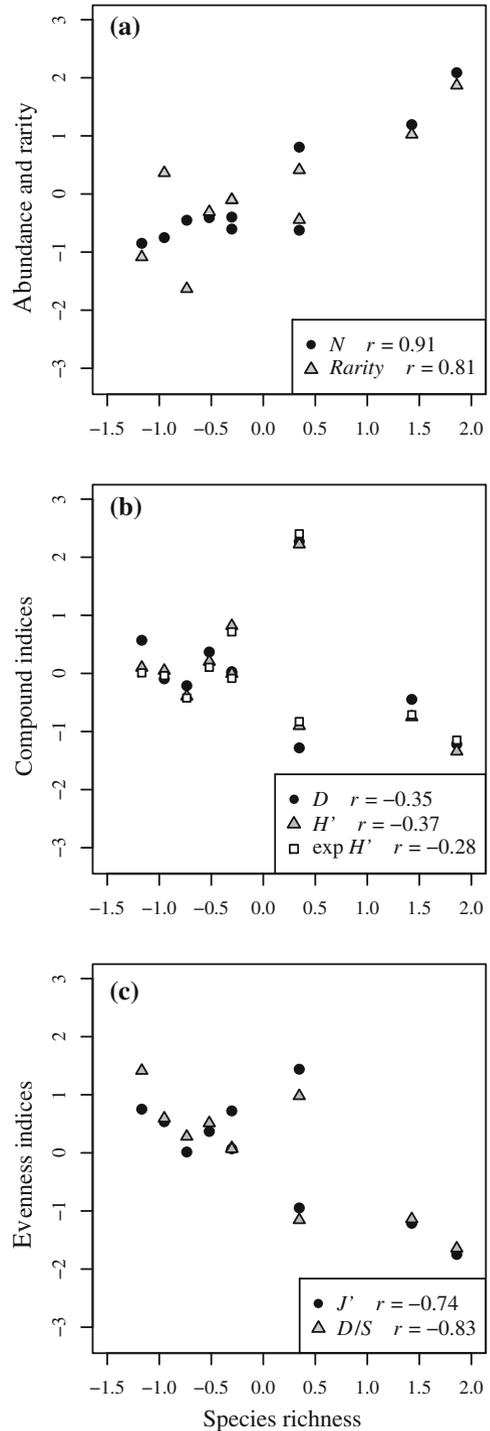


Table 3 Pairwise product-moment correlation coefficients for butterfly abundance (*N*) and seven indices related to species diversity—species richness (*S*), Simpson’s reciprocal index (*D*), the Shannon–Wiener index (*H'*), the exponential of the Shannon–Wiener index (*exp H'*), Pielou’s evenness (*J'*), species evenness (*D/S*), and proportion of rare species (*Rarity*)—derived from 10 years of butterfly population data

	<i>N</i>	<i>S</i>	<i>D</i>	<i>H'</i>	<i>Exp H'</i>	<i>J'</i>	<i>D/S</i>
<i>S</i>	0.91***						
<i>D</i>	−0.67*	−0.35					
<i>H'</i>	−0.69*	−0.37	0.94***				
<i>exp H'</i>	−0.61	−0.28	0.93***	0.99***			
<i>J'</i>	−0.92***	−0.74*	0.85**	0.90***	0.85**		
<i>D/S</i>	−0.93***	−0.83**	0.79**	0.72*	0.67*	0.93***	
<i>Rarity</i>	0.82**	0.81**	−0.52	−0.47	−0.41	−0.71*	−0.79**

Significance is denoted by * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4 Pairwise product-moment correlation coefficients for eight variables related to butterfly diversity and annual precipitation (mm) and mean growing season temperature (°C; April–August; based on daily highs) of the same year for Edmonton, Alberta, Canada

	<i>N</i>	<i>S</i>	<i>D</i>	<i>H'</i>	<i>Exp H'</i>	<i>J</i>	<i>D/S</i>	<i>Rarity</i>
Precipitation	0.52	0.25	−0.65*	−0.60	−0.58	−0.51	−0.45	0.34
Temperature	0.45	0.28	−0.48	−0.50	−0.52	−0.48	−0.43	0.42

Significance is denoted by * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

explained in terms of either: (i) increases in the abundances (and thus detection) of rare species, which decreases evenness; or (ii) disproportional increases in abundance within common species (Pollard et al. 1995), which also decreases evenness. Our results support both possibilities, as the proportion of rare species was negatively correlated with both measures of evenness, and rapid population growth within common species was observed in years with favourable environmental conditions (in this study; *Thymelicus lineola*, *Glaucopsyche lygdamus*, and *Pieris rapae*). Our measure of rarity was not independent of the abundances of common species and thus separating the effects of these two factors on evenness was not possible.

Population increases in common species are expected to depress species evenness when relative magnitudes of population increase are unequal among species within assemblages (sensu Gosselin 2006). It is therefore predictable that butterfly assemblages may inherently become “less even” under favorable environmental conditions. Our results support this hypothesis. This relationship may indicate (but does not demonstrate) interspecific competition within assemblages, where rapid increases in the populations of common species moderate population increases in other species, effectively depressing species evenness (Stirling and Wilsey 2001; Mulder et al. 2004; Bock et al. 2007). Interspecific competition has been shown to decrease species evenness within plant assemblages (Mulder et al. 2004), but to our knowledge, this relationship remains to be empirically tested within butterfly assemblages. Considering butterfly species vary in both host and nectar plant species (Hawkins and Porter 2003; Kitahara et al. 2008), niche overlap and interspecific

competition are not expected to be the primary determinants of abundance distributions. More likely, negative relationships between butterfly abundance and measures of species evenness may indicate differences in reproductive potential across species coupled with interspecific variation in environmental preferences. These hypotheses warrant further study.

Most interestingly, species richness in our study was not correlated with Simpson's reciprocal index, the Shannon–Weiner index, or the exponential of the Shannon–Wiener index. Both measures of species evenness, however, were positively correlated with the three compound indices. These results suggest that the compound indices weigh the evenness component of diversity more heavily than the richness component. This obscures the importance of species richness, the measure that accords best with our intuitive sense of biodiversity (Ma 2005; Magurran 2013). Indeed, coefficients of variation suggest that species richness captured more variability than any of the three compound indices, although Simpson's reciprocal index and the exponential of the Shannon–Wiener index proved to be almost as variable. The untransformed Shannon–Weiner index had the lowest coefficient of variation among species richness, measures of species evenness, and the three compound indices, suggesting that it has the greatest potential to mask temporal variability in species diversity.

Besides the possibility of negative correlations between constituent parts, the Shannon–Wiener index has been criticized for its potential to “compress” data due to the log-transformation of species proportion values, effectively weakening the discriminating power of the index (Magurran 2013). To compensate for this data compression, the Shannon–Wiener index may be exponentiated (Jost 2006), yielding an effective number of species for an assemblage. Within our butterfly population dataset, exponentiating the Shannon–Wiener index effectively improved discriminating power while maintaining approximate relationships with other diversity measures. However, both untransformed and exponentiated Shannon–Wiener index values were weakly negatively related to species richness, suggesting the two indices are not consistent with our intuitive sense of diversity. Despite this incongruence, the Shannon–Wiener index does serve as an entropy, effectively measuring a distinct property of species assemblage data.

Using logarithms with a base of two in the Shannon–Wiener index results in the average minimum number of yes/no questions required to determine the species identity of a sampled individual (Jost 2006). A more even distribution of individuals among species will require more dichotomous questions, on average, to determine individuals' species identities. This indicates higher uncertainty within abundance distributions, and yields higher Shannon–Wiener index values. Additionally, as Simpson's index represents the probability that two species randomly selected from an assemblage will be of the same species, the inverse of this probability (Simpson's reciprocal index) is positively related to the uncertainty of individuals' species identities. These relationships effectively explain why compound indices were strongly related to species evenness in our butterfly assemblage, with increases in evenness corresponding with increases in uncertainty in the identities of sampled individuals. Compound indices and species evenness therefore represent similar interpretations of abundance distributions. These results, coupled with weak, negative relationships to richness, suggest that compound indices do not integrate species richness and species evenness into all-encompassing measures that align well with the traditional biodiversity concept. While entropies and their respective transformations are mathematically related to species richness (Gosselin 2006; Jost 2006), their empirical relationships with richness have been shown to be largely inconsistent (e.g., Stirling and Wilsey 2001; Wilsey et al. 2005; Bock et al. 2007), and, as our study confers, often negative.

Distinctions between richness, evenness, and entropies (including their transformations to Hill numbers) are necessary because the three approaches to measuring diversity convey different information on distinct, but related, properties of assemblage organization. By analogy, Jost (2006, p. 363) states that, “the radius of a sphere is an index of its volume but is not itself the volume, and using the radius in place of the volume in engineering equations will give dangerously misleading results. This is what biologists have done with diversity indices.” However, this too may be misleading. Relationships between radii and volumes are consistent across spheres of all sizes, and a sphere’s radius serves as a proxy for other properties relating to size (e.g., diameter, circumference, surface area, and volume). Although species evenness, species richness, and compound indices all measure different aspects of single species assemblages, the broad extension of the sphere metaphor to measures of assemblage diversity is unadvised. Unlike the properties of a sphere, relationships between measures of species diversity are unpredictable, varying across space (Ma 2005), between taxa (Stirling and Wilsey 2001; Wilsey et al. 2005; Bock et al. 2007), and, as our study shows, through time. One measure of species diversity cannot adequately proxy another; thus, single measures cannot be used to assess all properties of an assemblage’s diversity in isolation. Despite this point, however, species richness is thought to be more central to the concept of diversity than other measures (Ma 2005; Jost 2006; Magurran 2013), and does, on its own, provide meaningful information on species assemblages.

In conclusion, when analyzing long-term butterfly population datasets, species evenness may be used in conjunction with richness to deepen our understandings of changes in butterfly diversity through time; however, combining these two components within compound indices does not produce measures that consistently align with our intuitive sense of biodiversity. Compound indices measure different, but not independent, properties of species assemblages. Entropies, including Simpson’s index the Shannon–Wiener index, measure uncertainty, not diversity, which is a property of data, not species assemblages. Entropies may convey meaningful information about butterfly assemblage data if used in conjunction with more intelligible measures, such as richness, and the transformations of entropies into Hill numbers result in values that are easier to interpret. Species richness is the most viable measure of butterfly species diversity. However, other diversity indices accounting for abundance distributions can provide additional information, effectively deepening our understandings of the enigmatic ecological property that is diversity.

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