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Inter-annual monitoring improves diversity estimation of tropical butterfly assemblages

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Abstract

Monitoring programs for diverse tropical butterfly assemblages are scarce, and temporal diversity patterns in these assemblages are poorly understood. We adopted an additive partitioning approach to determine how temporal butterfly species richness was structured at the levels of days, months, and years in five tropical/subtropical sites across three continents covering up to 9 years of monitoring. We found that observed butterfly richness was not uniformly distributed across temporal extents. Butterfly species composition differed across months and years, potentially accounting for the fact that temporal butterfly species richness contributed a high proportion to total species richness. We further examined how species richness of common and uncommon species (> and <0.5% of total abundance, respectively) were structured across temporal extents. The results showed that the common species relative contribution to total species richness was higher at lower-temporal levels, whereas uncommon species contributed more at higher-temporal resolutions. This suggests that long-term sampling will be more effective in capturing patterns of rare species and the total species pool while lower-temporal level sampling (e.g., daily or weekly) may be more useful in examining common species demographic patterns. We therefore encourage careful consideration of temporal replication at different extents in developing butterfly monitoring schemes. Long-term monitoring is essential for improvement in the resolution of species estimation and diversity patterns for tropical ecosystems.

Abstract in Chinese is available with online material.

KEYWORDS

additive partitioning, biodiversity monitoring, temporal variation, tropical butterfly

1 | INTRODUCTION

Species composition and diversity structure vary across time and space (Rosenzweig, 1995). As the tropics harbor a high proportion of global biodiversity (Gaston, 2000) and about 90% of all butterfly species, evaluating diversity patterns for tropical butterflies is critical (Bonebrake, Ponisio, Boggs & Ehrlich, 2010). Understanding

diversity patterns broadly is especially urgent given that long-term anthropogenic impacts are likely driving many butterfly and moth species toward extinction (Basset et al., 2015; Bonebrake & Cooper, 2014; Bonebrake et al., 2016; Brook, Sodhi & Ng, 2003; Habel et al., 2016; Thomas, 2005) through population declines (Conrad, Woiwod, Parsons, Fox & Warren, 2004; Pelini et al., 2009; Swengel, Schlicht, Olsen & Swengel, 2011), assemblage turnover

(Brown & Freitas, 2000; Habel et al., 2016; Koh, 2008), and species range shifts (Chen et al., 2009; Parmesan et al., 1999; Thomas, 2005).

Systematic long-term butterfly and moth monitoring programmes have been successfully conducted in Europe and have shown considerable conservation value for assessing biodiversity changes (Brereton, van Swaay & van Strien, 2009; Merckx & Slade, 2014; Pollard & Yates, 1994; van Swaay, Nowicki, Settele & van Strien, 2008). A few long-term butterfly studies have been conducted in the Neotropics (DeVries & Walla, 2001; Grøtan, Lande, Chacon & DeVries, 2014; Iserhard, Brown & Freitas, 2013; Iserhard, Romanowski, Richter & Mendonça, 2017) and in Africa (Valtonen et al., 2013), which have consistently suggested that short-term sampling could largely underestimate tropical butterfly species diversity. Previous studies have shown that butterfly diversity can vary within a day (Herrera, 1990; Young, 2008), between seasons (Bailey, Hines, Nichols & MacKenzie, 2007; Grøtan, Lande, Engen, Sæther & DeVries, 2012; MacKenzie, 2006; Ribeiro, Prado, Brown & Freitas, 2010), and among years (DeVries & Walla, 2001; Grøtan et al., 2014; Valtonen et al., 2013; Wiklund & Friberg, 2009). A major challenge in examining biodiversity changes across temporal scales is the lack of consistently sampled and long-term biodiversity monitoring data. From a global monitoring perspective, Essential Biodiversity Variables have been proposed such as species, population, community composition, genetic composition, and ecosystem services, which should be repeatedly measured for the same taxa and at the same locations (Haase et al., 2018; Kissling et al., 2018). Similarly, the ForestGEO programme conducts a standardized, long-term tropical butterfly biodiversity monitoring protocol, which provides highly comparable data for examining diversity patterns (Anderson-Teixeira et al., 2015; Basset et al., 2011, 2012).

Local species richness can be determined by local environmental factors and regional species richness (Ricklefs, 1987; White & Hurlbert, 2009). Tropical butterfly diversity in particular is well-known to be affected by local environmental variation (Basset et al., 2012; Bonebrake et al., 2010). On the other hand, it can be influenced by regional community dynamics and evolutionary history (Lawes, Eeley & Piper, 2000; Rundlöf, Bengtsson & Smith, 2008), such that local butterfly species richness can be driven by colonization and extinction (Cornell & Lawton, 1992; Harrison & Cornell, 2008). Observed species communities are usually composed of a few common species and many rare species (Chao et al., 2014; Gering, Crist & Veech, 2003; Novotný & Basset, 2000), which are usually better explained by ecological processes such as community assembly (Tsang & Bonebrake, 2017; White & Hurlbert, 2009) rather than sampling effects (i.e., sampling intensity, White, 2004). Relative to rare species, common species are more abundant and are usually better adapted to local scale environmental variation (e.g., temperature and humidity) and thus have a much lower probability of local extinction in addition to a higher likelihood of being captured at smaller sampling scales (White & Hurlbert, 2009). In contrast, larger spatial or temporal

sampling scales are needed for sampling rare species, which are driven by regional species richness pools (White & Hurlbert, 2009). As conservation and management efforts are generally more concerned with rare or uncommon species rather than common species (Lawler, White, Sifneos & Master, 2003), higher-temporal level sampling such as inter-annual replication may therefore be essential for improving the evaluation of butterfly diversity patterns for tropical ecosystems.

To evaluate the importance of tropical butterfly monitoring across temporal extents, we analyzed tropical butterfly monitoring data collected over two to nine consecutive year periods in five tropical/subtropical forest sites under standardized monitoring protocols (Anderson-Teixeira et al., 2015; Basset et al., 2011, 2012). Using these data, (a) we quantified and examined local diversity components (i.e., α and β) at different temporal extents by using an additive partitioning approach to decompose total sampled diversity (i.e., γ; Crist, Veech, Gering & Summerville, 2003; Gering et al., 2003; Lande, 1996; Veech, Summerville, Crist & Gering, 2002; Whittaker, 1960). We additionally tested whether α and β butterfly temporal richness were obtained by a random distribution of individuals among samples using null model simulations. We also (b) examined the importance of common and uncommon species in driving diversity patterns over time. Finally, (c) we evaluated whether temporally dependent environmental factors such as temperature and relative humidity across time scales affected species composition.

2 | METHODS

2.1 | Study sites

We studied butterfly diversity in five forest sites distributed across three biogeographic regions: Barro Colorado Island (BCI) in Panama as Neotropical; Wanang (WAN) in Papua New Guinea as Australasian; Khao Chong (KHC) in Thailand, Dinghushan (DHS) in Southern China, and a nearby site (~250 km), Tai Po Kau (TPK) in Hong Kong as Oriental (Table 1). All sites are under the long-term forest observation network initiated by ForestGEO (Anderson-Teixeira et al., 2015). TPK is a secondary (~70 years) forest while all other forest sites are old growth primary forest (Table 1).

2.2 | Butterfly sampling

We conducted Pollard walks (Pollard, 1977) and followed the modified protocol described in Basset et al. (2011, 2012) for butterfly sampling. We developed five to ten 350–500 m transects for each forest site within or near the ForestGEO forest plots (Table 1). For BCI, KHC, and WAN, we developed ten transects, with a minimum distance between transects of 200 m. For DHS and TPK, we established five 350 m transects to maximize plot coverage of the 20-hectare forest plots. For each transect survey, trained and experienced observers walked at a slow and constant pace for about 30 min and

TABLE 1 Sampling design of the butterfly transects as well as geographic and climatic features of Barro Colorado Island (BCI) in Panama; Khao Chong (KHC) in Thailand, Wanang (WAN) in Papua New Guinea, Dinghushan (DHS) in Southern China, and Tai Po Kau (TPK), in Hong Kong. The climatic information is extracted from Anderson-Teixeira et al. (2015)

	Barro Colorado Island (BCI)	Khao Chong (KHC)	Wanang (WAN)	Dinghushan (DHS)	Tai Po Kau (TPK)
Coordinates	9°9′N, 79°51′W	7°32′N, 99°47′E	5°15′N, 145°16′E	23°10′N, 112°30′E	22°25′N, 114°10′E
Biogeographic region	Neotropic	Oriental	Australian	Oriental	Oriental
Vegetation type	Semi-deciduous lowland moist forest	Mixed evergreen hill forest	Lowland seasonal evergreen forest	Monsoon evergreen broad-leaved forest	Monsoon evergreen broad-leaved forest
Disturbance/management background	Island was isolated from mainland since 1910–1914 by the rising of Lake Gatum	No recent major disturbance	No recent major disturbance	No recent major disturbance	Massively destructed during the 1950s, the forest is generally 70 years natural growth since then.
Elevation (m)	120–160	90–180	120–330	255–336	230–470
Sampling period	Throughout the year	Throughout the year	Throughout the year	May–Oct	May–Oct
Sampling year	2009–2017	2011–2016	2014–2016	2015–2016	2015–2016
Sampling effort no of transect walk	1080	720	360	160	160
No of samples in partitioning days/month/year	108/36/9	72/24/6	36/12/3	32/8/2	32/8/2
Butterfly transect number/length	10/500 m	10/400 m	10/500 m	5/350 m	5/350 m
Annual average rainfall (mm)	2,551	2,611	3,500	1,985	2,399
Annual average daily air temperature (°C)	27.1	27.1	26	20.9	23.3

recorded the number of individuals of each butterfly species observed at a horizontal distance of 5 m from the trail and at a vertical height of 7 m. We netted and further examined those butterflies which could not be identified immediately in the field. Most of these individuals were then released following examination, and only in a few exceptional cases were specimens kept. We recorded butterflies during non-rainy days between 08:00 hr and 14:00 hr for two to nine consecutive years between 2009 and 2017 (Table 1). For each year, we collected data on three to 4 days for each of the four sampling months. We conducted the sampling throughout the year for BCI, WAN, and KHC. Because we aimed to optimize the effectiveness of assessing total species pools, we conducted the sampling in the subtropical sites of DHS and TPK during the wet "summer" season between May and Oct because all species captured during the winter period were nested within the summer period. We conducted a pilot study with 24 transect walks in DHS and TPK during November 2014 to March 2015 and observed that butterfly activity was very low (both abundance & richness <15% compared to summer), and consisted mostly of common satyrines (*Mycalesis* spp., Nymphalidae). We followed Wahlberg et al. (2005, 2009) for taxonomic classifications, and we identified butterfly species according to families: Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, and Riodinidae. For each transect walk, we recorded temperature (in Celsius) and relative humidity (in percentage) when sampling had begun.

2.3 | Data analysis

Additive partitioning of diversity evaluates diversity patterns in two ways. First, it quantifies how local diversities among defined partitions (temporal levels for our study) contribute relatively to the diversity sum (Lande, 1996; Whittaker, 1960). The protocol is based on the definition of regional or total diversity, γ, which is the sum of local diversity within samples, α, and local diversities among samples, β. Therefore, $\gamma = \alpha + \beta$ (Whittaker, 1960). The hierarchal sampling level of $i = 1, 2, 3, \ldots m$ was then applied to the local diversity component, where m was the highest sampling level. Thus, the equation can be expressed as: $\alpha_{i+1} = \alpha_i + \beta_i$, with the highest sampling level of diversity α_m $(=\gamma)$ expressed as $\alpha_1 + \beta_1 + \beta_2 + \ldots + \beta_m$. Hence,

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i$$

Second, Crist et al. (2003) developed a statistical framework for testing whether locally observed diversities (α, β) differ from an expected distribution, generated by null models and randomized partitions. The null model can be developed by either individual- or sample-based randomizations. Individual-based randomization generates a null model by shuffling individuals among defined partitioned levels. In contrast, sample-based randomization allocates lower-level samples among higher-level samples randomly.

We implemented the individual-based diversity partition analytical protocol described in Veech et al. (2002) and Crist et al. (2003) for each site and used species richness as the diversity unit. For each forest plot, we pooled the butterfly sample data among transects at the day level to reduce spatial variation (DeVries & Walla, 2001) and calculated mean temperature and relative humidity. We partitioned the data according to the hierarchical temporal level of day, month, and year (i = 1, 2, 3, respectively). We randomized the process 1,000 times to obtain the null distributions of diversity (species richness in this case). Significant differences were determined by whether the observed value was larger or smaller than the expected value obtained by the randomization process (Crist et al., 2003). Gering et al. (2003) used additive diversity partitioning to show that species at different abundance classes had different diversity patterns across sampling scales. We used the threshold defined by Gering et al. (2003) to classify species with abundances larger than 0.5% of the total community abundance as common species and the rest as uncommon species. We further analyzed the data set for year 2015–2016 with the same approach to determine whether different temporal extents of sampling affected total species diversity patterns as sampling efforts differed across sites. We used the R function "adipart" from the *vegan* Package to implement the partitioning analysis for common, uncommon, and total butterfly species for each site (Oksanen et al., 2007).

Rarefaction evaluates sampled diversity, and extrapolation evaluates estimated species diversity by standardizing sampling effort without losing information of species' relative abundances (Chao et al., 2014; Colwell et al., 2012; Gotelli & Colwell, 2001). We constructed individual-based rarefaction and extrapolation curves to assess the adequacy of sampling efficiency of butterfly assemblages among sites. We used the R package *iNEXT* (Hsieh, Ma & Chao, 2016) to rarefy the data and to construct the curves.

We tested the effects of temporally dependent factors on butterfly composition for each site. Temperature and humidity are considered important factors that affect butterfly diversity (Basset et al., 2012; Bonebrake et al., 2010). We therefore pooled the butterfly species data among transects for each site at the day level and tested whether butterfly composition was affected by temperature, relative humidity, as well as monthly and yearly sampling. We used the permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001), with the model of "month %in% year + year + temp + relative humidity." We used the Bray–Curtis dissimilarity as resemblance measures and permuted 500 times. As different temporal and spatial extents sampled across sites might have different results, we additionally applied the PERMANOVA by using subset data sets of (a) the year 2015–2016 across sites; and (b) standardized transect numbers of five for BCI, WAN, and KHC (the other two sites have five transects only) by 50 randomizations (with 500 iterations) and reported the median pseudo F-statistics, R-squared values, and p-values. We used the R package *vegan* to conduct the analyses (Oksanen et al., 2007).

3 | RESULTS

In total, we recorded 851 species and 29,985 individuals across the five sites for this study. Uncommon species made up 56% to 94% of the total species richness, yet only less than 26% of the total individuals recorded for all sites.

Barro Colorado Island had the highest number of species recorded (289), followed by KHC and WAN (Figure 1). The rarefaction and extrapolation analyses estimated that about 90% of butterfly species had been recorded from the estimated regional butterfly species pool in the site of WAN, and the other four sites had records for between 60% and 70% of the estimated regional species pools. The total species richness curves would likely reach an asymptote if about 2,000 butterfly individuals were recorded for the subtropical sites of TPK and DHS, while tropical sites of BCI, KHC, and WAN would require approximately five times more individuals recorded (Figure 1).

The additive partitioning analysis showed that observed butterfly richness was not randomly distributed across temporal extents (Table 2; Figure 2). Generally, observed species richness at each temporal level had significantly different results from expected species richness. Butterfly richness among years (β_3) weighed up to 66.7% in contributing to γ and was the most weighted temporal level in capturing the species pools. The relative contribution of richness among months (β_2) to γ was 19.1% to 40.2%. Among and within the day level (β_1 and α respectively), there was a generally lower proportion in structuring γ. Partitioning analysis using the lower temporal extent data set (year 2015–2016) showed that β_2 contributed the highest proportion to γ (34.23%–40.82%) rather than β_3 (14.2%–33.1%; Table S1). The relative contribution of species richness at lower-temporal levels to γ was higher for the common species pool (α and β_1 contributed 51.2%–94%). In contrast, uncommon species showed greater contributions at higher-temporal levels (β_2 and β_3 contributed 67.5%–89.8%; Table 2; Figure 2).

The PERMANOVA indicated that butterfly species composition was significantly affected by all tested factors in all sites, including temperature, relative humidity, month nested within year, and year (Table 3). The effect of monthly sampling (nested within year) contributed the highest variation (28%–54%) in butterfly species composition. Yearly sampling explained 11% to 23% of the variation in species composition, while temperature and relative humidity together contributed <12%. When compared to the lower temporal extent data set analysis (year 2015–2016), the variation of species composition explained by yearly sampling was lower. In contrast, the environmental variables of temperature and relative humidity showed the opposite trend (Table S2). Using the site of BCI as an example, yearly sampling explained 20% of species composition variation when the 9-year data set was used (year 2008–2016) in contrast to 2% for the 2-year (year 2015–2016) data set. The proportion of variation in species composition explained by temperature increased from 1.3% to 21% when the lower temporal extent data set (year 2015–2016) was used in the analysis. The proportion of variation explained by relative humidity increased from 4.7% to 14%. However, different temporal extents did not affect the overall patterns or significance of factors obtained from the PERMONOVA results (Table S3).

4 | DISCUSSION

In a biodiversity monitoring context, species captured in a sample represent a "snapshot" of the regional species pool, and temporal diversity is considered to be determined by several scale-dependent ecological, physical, and geographic forces (Adler et al., 2005; Korhonen, Soininen & Hillebrand, 2010; White & Hurlbert, 2009; White et al., 2006). For example, temporal species turnover at seasonal and inter-annual levels are mainly affected by ecological processes such as species phenology, primary productivity, and temperature (White et al., 2006). Butterfly richness was not randomly distributed across temporal levels, supporting the hypothesis that the effects of day, month, and year structured the species

richness and composition of tropical butterflies. Previous studies have consistently shown inter-annual variation as a significant factor for structuring butterfly diversity that could be caused by biannual cycles, host plant availability, and global climatic events such as El Niño (DeVries & Walla, 2001; Grøtan et al., 2014; Valtonen et al., 2013; Wiklund & Friberg, 2009). While most diversity sampling or monitoring designs appropriately emphasize the importance of seasons (Bailey et al., 2007; Grøtan et al., 2012; MacKenzie, 2006), we highlight the importance of intra-annual replication in improving diversity estimation.

Like most communities, uncommon species dominated observed patterns (Chao et al., 2014; Gering et al., 2003; Novotný & Basset, 2000), which could be explained by ecological processes
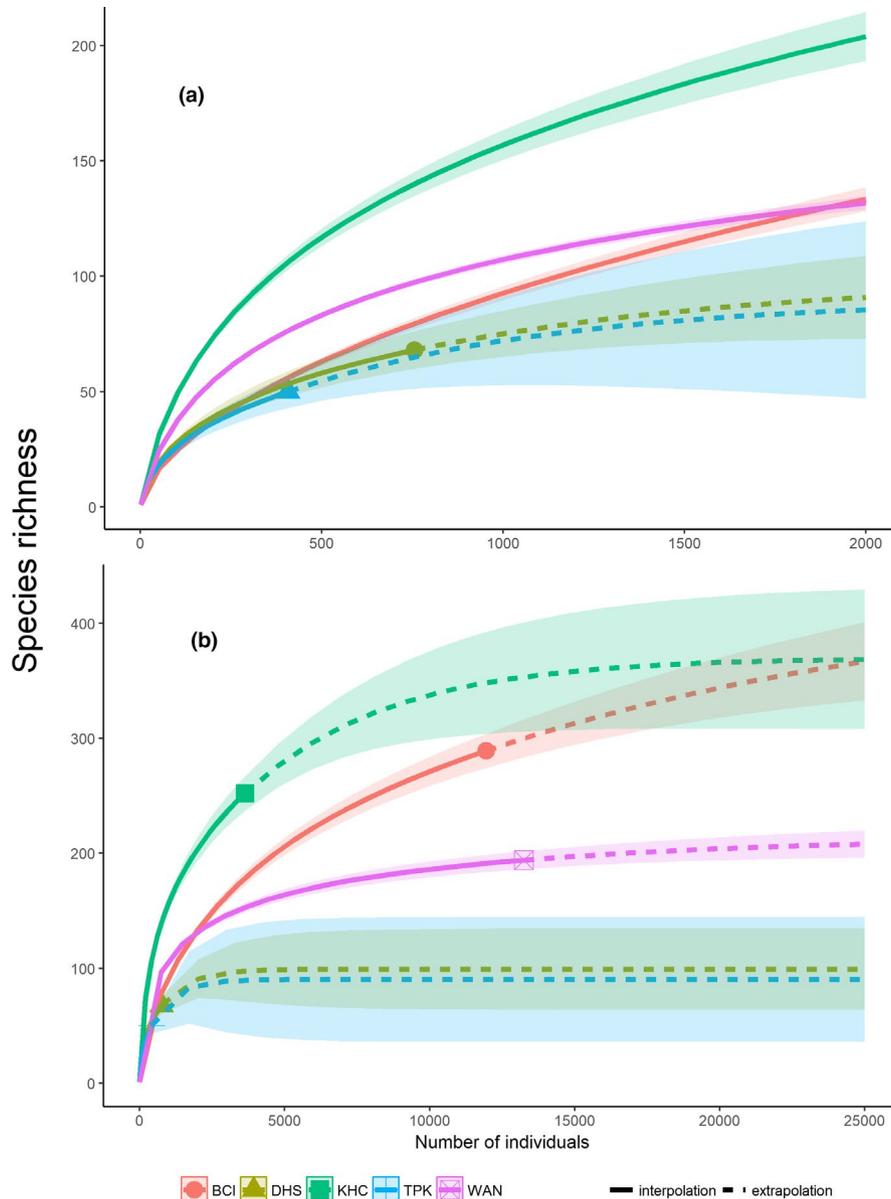

FIGURE 1 Butterfly species richness at 2,000 (a) and 25,000 (b) of individuals recorded, respectively. Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves of the butterfly communities covering 2 to 6 years of sampling in Barro Colorado Island (BCI), Khao Chong (KHC), Wanang (WAN), Dinghushan (DHS), and Tai Po Kau (TPK). Shaded area indicates the standard error, and broken lines indicate extrapolated species richness rarefied 1,000 times

TABLE 2 Additive partitioning of butterfly temporal species richness of all butterfly species, common species, and uncommon species recorded in Barro Colorado Island (BCI), Khao Chong (KHC), Wanang (WAN), Dinghushan (DHS), and Tai Po Kau (TPK)

		BCI			KHC			WAN			DHS			TPK		
		Observed	(%)	Expected	Observed	(%)	Expected	Observed	(%)	Expected	Observed	(%)	Expected	Observed	(%)	Expected
All species		11,947 individuals			3,634 individuals			13,241 individuals			756 individuals			407 individuals		
α	Within days	**20.51**	7.1	25.17	**26.03**	10.3	30.11	**56.14**	29.2	71.29	**9.22**	13.6	11.65	**6.66**	13.3	7.57
β1	Among days	**20.57**	7.1	23.26	**26.47**	10.5	31.33	**27.94**	14.6	37.11	**12.03**	17.7	14.25	**8.21**	16.4	10.15
β2	Among months	55.14	19.1	57.48	62.83	24.9	65.3	60.25	31.4	50.11	24.25	35.7	25.91	20.12	40.2	18.73
β3	Among years	192.78	66.7	183.09	136.67	54.2	125.26	47.67	24.8	33.5	22.50	33.1	16.19	15	30.0	13.55
γ	Total	289			252			192			68			50		
Common species		10,383 individuals			2,711 individuals			11,266 individuals			690 individuals			373 individuals		
α	Within days	**9.57**	59.8	12.05	**15.68**	43.6	18.03	**29.22**	83.5	32.78	**7.49**	28.8	9.71	**5.69**	25.9	6.47
β1	Among days	**3.76**	23.5	2.88	**9.61**	26.7	10.84	**3.69**	10.5	2.14	**7.02**	27.0	8.12	**5.56**	25.3	7.1
β2	Among months	**2.44**	15.3	1.03	**8.71**	24.2	6.84	**2.08**	5.9	0.085	8.00	30.8	7.67	**9.25**	42.0	7.24
β3	Among years	**0.22**	1.38	0.03	2	5.6	0.29	0	0.0	0	**3.50**	13.5	0.5	1.5	6.8	1.21
γ	Total	16			36			35			26			22		
Uncommon species		1,574 individuals			923 individuals			1,975 individuals			66 individuals			34 individuals		
α	Within days	**11.04**	4	12.95	**10.35**	4.8	11.92	**26.92**	17.1	37.54	2.33	5.5	2.39	**1.63**	5.8	1.78
β1	Among days	**16.71**	6.1	19.73	**16.86**	7.8	20.02	**24.25**	15.4	33.59	**4.41**	10.5	5.39	**1.99**	7.1	2.36
β2	Among months	**52.69**	19.3	57.2	**54.13**	25.1	58.56	**58.17**	37.1	51.3	**16.25**	38.7	18.38	10.88	38.9	11.28
β3	Among years	**192.56**	70.5	183.1	**134.67**	62.3	125.51	**47.67**	30.4	34.57	**19.00**	45.2	15.84	13.5	48.2	12.58
γ	Total	273			216			157			42			28		

Note: Bold values indicate observed butterfly diversities significantly different from expected at a significance level of 0.05.

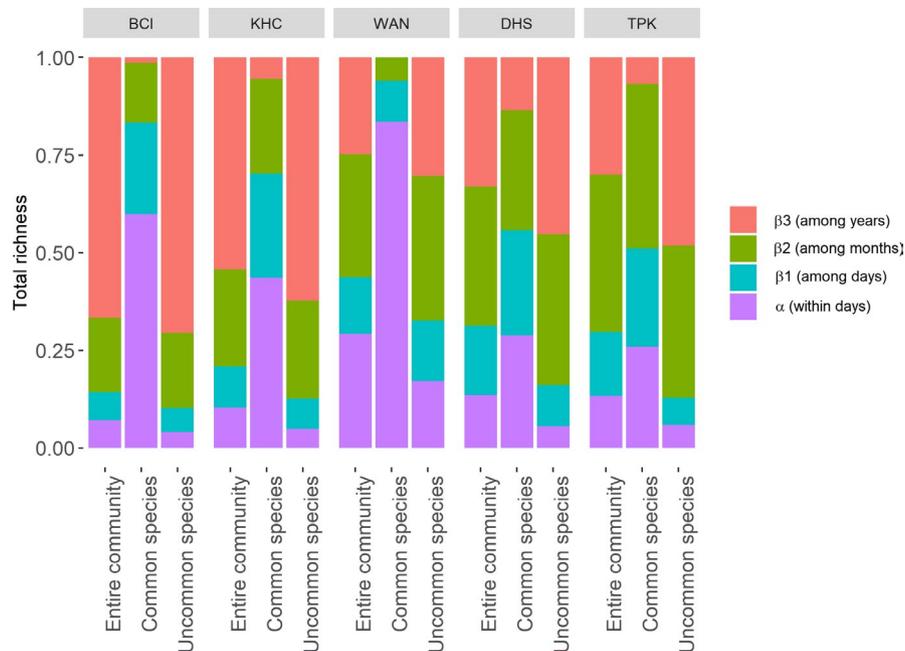**FIGURE 2** The relative contribution of observed α and β at different temporal scales to total butterfly richness for the entire assemblage, common species, and uncommon species. The butterflies were recorded in Barro Colorado Island (BCI), Khao Chong (KHC), Wanang (WAN), Dinghushan (DHS), and Tai Po Kau (TPK)

and sampling effects. We acknowledge that higher sampling intensities may lead to higher proportions of uncommon species that are driven by sampling effects (Magurran, 2007; McGill, 2003). Nevertheless, we showed that common and uncommon species are sensitive to sampling at different temporal levels which would not likely be the case if sampling effects were the primary drivers of observed community patterns (White, 2004). In particular, the results are consistent with similar studies that show higher-temporal level sampling more effectively records uncommon species contributed by regional enrichment (White & Hurlbert, 2009; White et al., 2006).

Previous studies have identified temperature and humidity as important environmental factors which influence butterfly activities and resource availability (Basset et al., 2011; Bonebrake et al., 2016; DeVries, Walla & Greeney, 1999; Grøtan et al., 2012; Pollard, 1988; Ribeiro et al., 2010). However, our results show that these environmental variables explained relatively little variation in tropical butterfly composition for large temporal extents (Table 3, Table S2). This might be explained by other factors being more important at monthly or yearly levels, such as annual life cycles, complex environmental variation, or species interactions (Basset et al., 2012; Grøtan et al., 2012; Ribeiro et al., 2010; Wolda, 1978). In addition, observed species richness and composition patterns are determined by the proportions of common and rare species. Uncommon or rare species may be assembled through randomization processes that are driven by regional enrichment rather than local environments which are restricted to local conditions (Tsang & Bonebrake, 2017; White & Hurlbert, 2009). This could also explain why environmental variables were less important at

higher-temporal levels as uncommon species composed a higher proportion of total species richness compared with lower-temporal levels.

Standardized, long-term and large-scale monitoring approaches provide highly comparable data well-suited for understanding complex ecological patterns (Anderson-Teixeira et al., 2015; Haase et al., 2018). Anthropogenic impacts increasingly threaten tropical biodiversity, while *in situ* disturbance, such as habitat destruction, is considered a primary driver of species extinction (Dirzo & Raven, 2003; Pimm & Raven, 2000). For example, habitat loss has caused catastrophic tropical butterfly extinction in a highly modified tropical landscape in Singapore, where 30% of butterfly species have gone extinct within 100 years of landscape development (Brook et al., 2003; Koh, Sodhi & Brook, 2004). However, a study conducted in Panama reported that 6% of the tropical butterfly species were considered locally extinct in 60 years (Basset et al., 2015) even though there was little or no local disturbance. In temperate regions, climate change is considered to have strongly affected butterfly populations (Pelini et al., 2009; Swengel et al., 2011) and species range shifts (Parmesan et al., 1999); however, it is unknown whether such patterns also occur in the tropics. Given the complexity of global change effects on butterfly diversity, long-term and high-resolution data in the tropics are critical in documenting such impacts as well as potentially managing them.

While studies focusing on temporal patterns receive much less attention compared with spatial studies (Vaughn & Young, 2010; White et al., 2006), we highlight here the importance in considering temporal replication at different extents in developing biodiversity assessments and butterfly monitoring schemes. Though the

TABLE 3 Results of PERMANOVA analyses of the effects of month within year, year, temperature, and relative humidity on butterfly species composition at each study site

	BCI				KHC				WAN				DHS				TPK			
	df	F	R²	p	df	F	R²	p	df	F	R²	p	df	F	R²	p	df	F	R²	p
Month:year	27	2.32	0.35	**0.002**	18	1.33	0.28	**0.002**	9	4.84	0.54	**0.002**	6	5.39	0.39	**0.002**	6	2.11	0.28	**0.002**
Year	8	4.5	0.2	**0.002**	5	2.32	0.14	**0.002**	2	4.54	0.11	**0.002**	1	19.1	0.23	**0.002**	1	5.27	0.12	**0.002**
Temperature	1	2.24	0.013	**0.028**	1	1.03	0.01	ns	1	2.52	0.03	**0.012**	1	3.73	0.05	**0.002**	1	2.26	0.05	**0.014**
Relative humidity	1	8.42	0.047	**0.002**	1	2.54	0.03	**0.002**	1	4.3	0.053	**0.012**	1	6.13	0.07	**0.002**	1	2.45	0.05	**0.002**
Residuals	70		0.39		46		0.54		22		0.27		15		0.26		22		0.49	
Total	101				71				35				22				31			

Bold values indicate significance at 0.05.

importance of seasonal variation in tropical butterflies has received considerable attention, using multiple long-term data sets, this study quantifies and emphasizes the need for examining long-term variation in these species' diverse assemblages for accurate characterization of diversity patterns.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j35fq7r (Luk, Basset, Kongnoo, Hau & Bonebrake, 2019).

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