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A comparison between time-constrained counts and line transects as methods to estimate butterfly diversity and monitor populations in tropical habitats

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Abstract

1. Long-term species monitoring programmes have revealed catastrophic declines in insect populations and disruption of biological communities that are contributing to biodiversity loss. Such discoveries have been possible because of standardised methods, such as line transects, of counting butterflies and other insects. However, line transects are not feasible in many tropical and mountainous habitats, so alternative methods must be explored.
2. To tackle this issue, we devised time-constrained (30-min) counts and compared butterfly diversity estimated through timed counts and line transects in three tropical habitats in India (evergreen forest, dry deciduous forest and an urban woodland). We tested the relative performance of the two methods in sampling species richness and abundance, as well as numbers of rare, endemic and specialist butterflies.
3. We observed greater overall species richness, and more species of habitat specialists and endemics per sample in time-constrained counts in the evergreen forest, but not in the other two habitats. Thus, time-constrained counts were relatively more efficient in detecting species in the species-rich evergreen habitat. Apart from this difference, the two sampling methods captured similar levels of species richness and other measures of diversity.
4. Our study thus shows that time-constrained counts are a suitable if not a superior alternative to line transects to conduct butterfly diversity surveys and population monitoring in complex tropical landscapes. Due to methodological flexibility and simplicity, time-constrained counts may be particularly useful to study the impacts of climate change, habitat fragmentation and land use practices on butterfly, Odonata and other insect populations in populous and tech-ready tropical countries using citizen science frameworks.

KEYWORDS
biodiversity inventories, butterfly conservation, butterfly monitoring, citizen science, population sampling methods

INTRODUCTION

Survey and monitoring of insects are fundamental to their conservation (Brown, 1997; Clark & Samways, 1996; Kim, 1993; Leather et al., 2008; Rohr et al., 2007). Spatial distribution maps obtained through ecological surveys can inform conservation planning and layout of reserves by identifying biogeographic units and areas of high species diversity, endemism or rarity (Kremen et al., 1993).

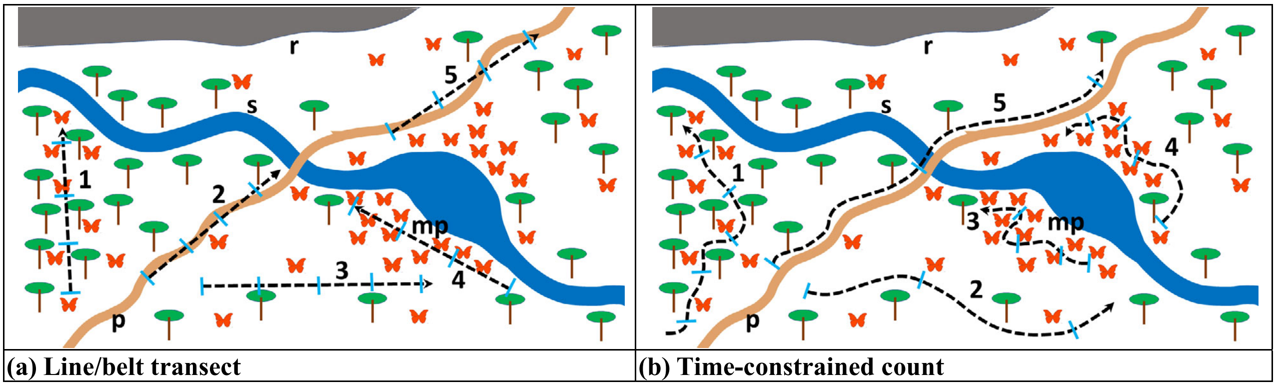
The baseline data can also be used to set up monitoring programmes and assess the impact of anthropogenic disturbance on insect populations. This is especially relevant in tropical areas, where the diversity of insects is extremely high but resources are scarce to undertake detailed studies of individual species (Braschler et al., 2010; Lewis & Basset, 2007). Butterflies are a good target taxon for characterising species diversity and monitoring populations for ecology and conservation, because their taxonomy is relatively well known, they are conspicuous and relatively easy to identify in the field compared with many other insect groups and they feature prominently in the public as well as conservation policy domains (Basset et al., 2013; Thomas, 2005).

Long-term butterfly monitoring programmes have been remarkably successful in the United Kingdom, Europe and the United States (Brereton et al., 2011; Schmeller et al., 2009; Thomas, 2005; van Swaay et al., 2008). Their objective is to assess regional- and national-level trends in the abundance of butterfly species (van Swaay et al., 2008). All such programmes employ spatially explicit transects—popularly known in butterfly monitoring schemes as 'Pollard walks'—in which recorders walk the transects at a uniform pace, counting all butterfly individuals observed within a certain width along the transect line (Pollard & Yates, 1994). The transects are predefined, that is, fixed a priori, and revisited every sampling session. The transect method is popular because it is simple to implement in open, relatively flat habitats with few butterfly species and low population densities, and is easily replicable and repeatable once the line transects have been identified by experienced butterfly watchers. The protocol allows rapid collection of data on the relative abundance of butterflies using a fixed effort. Long-term population monitoring using this method has yielded valuable insights into the population and community dynamics of temperate butterflies, including changes in community structure and diversity, and the recent alarming population declines due to climate change, habitat fragmentation and habitat alterations from land use practices (Botham et al., 2015; Devictor et al., 2012; Fourcade et al., 2021; Mills et al., 2017; Roy & Sparks, 2000; Van Dyck et al., 2009; van Strien et al., 2019; Warren et al., 2021). Monitoring schemes of comparable magnitude are lacking in tropical countries and habitats, even though the tropics harbour a much larger proportion of butterfly diversity (Bonebrake et al., 2010).

The difficulty is that line transects and related statistical models for data analysis were originally devised to count large mammals and other game animals, as well as to estimate their population densities in simpler habitats. These methods have inherent limitations in monitoring insects in more complex habitats (Spitzer et al., 1993; Zhang et al., 2018). For example, line transects require the transect line to be more or less straight and cover the predefined distance at a more or less uniform pace, which are nearly impossible to achieve in hilly tropical regions with dense vegetation and winding streams in difficult terrain. For practical reasons, the conditions of a straight line and uniform pace may be relaxed to some extent in the case of Pollard walks, which is easily achieved in open habitats with a small pool of easily identified butterfly species such as in the United Kingdom and Europe. These accommodations may be relatively unproblematic in terms of data collection and data quality in these simpler, species-poor habitats. However, accommodating violations of these assumptions poses a considerable problem in dense evergreen forests and difficult mountain terrain with very diverse butterfly faunas. The amount of curvature over which one has to sample butterflies may violate conditions of the straight line to impermissible levels, and it is sometimes not feasible to cover the length of the transect in the prescribed time when very high butterfly diversity may be encountered in a small patch (e.g., thousands of individuals of over a hundred species). Since butterflies and certain other insects are often highly clustered, for example, at puddling sites, the requirement of uniform pace is easily violated (a surveyor may stop and take counts, then continue, but not linger in an area for the majority of the predefined timeline). Besides, the fixed-transect method has been criticised for poor detectability of cryptic, rare or sedentary species (Henry et al., 2015; Kadlec et al., 2012). Certain tropical butterfly genera are difficult to identify on the wing or may be easily missed while walking transects, especially in shaded areas (Caldas & Robbins, 2003; Walpole & Sheldon, 1999). However, line transects have been conducted at certain sites in tropical rainforests as part of previously established permanent vegetation-monitoring plots in slightly more comfortable terrain (Basset et al., 2013).

There is a pressing need to develop appropriate protocols for sampling and monitoring of tropical butterflies. The pace of habitat destruction in the tropics is alarming, and at the same time, interest in butterfly species discovery, diversity documentation and conservation is on the rise. Individual researchers and institutions in the tropics may have adequate financial resources or manpower to conduct biodiversity assessments at small to medium spatio-temporal scales. However, citizen science—in conjunction with mobile apps, networking technologies and web platforms—is emerging as an important new movement in large-scale data generation for biodiversity research. Well-coordinated citizen science programmes using appropriate methods can provide large datasets of high quality that can contribute to conservation research and planning. Line transects, due to their design requirements and reliance on intensive preparations, may not be amenable to be taken up at large scales in complex landscapes and/or by large groups. Alternative methods need to: (a) combine rigour with efficiency, (b) be relatively simple and cost-effective, and (c) be flexible enough to be implementable in a variety of terrains and habitat types so that the protocols may be scaled up to regional and national levels. Initiatives such as day- or week-long national butterfly surveys, butterfly races, and so forth, have found alternatives that engage the general public, but they often lack uniform effort and rigour that are critical for the data to be comparable in scientific analysis.

Time-constrained counts (henceforth, 'timed counts') is an alternative visual-count method for conducting butterfly surveys and population monitoring (Beneš et al., 2003; Kadlec et al., 2012; Kral-O'Brien et al., 2021; Naik et al., 2022a, 2022b; Santorufo et al., 2021; Taron & Ries, 2015). In timed counts, effort is standardised by time rather than by length/area as done in line or belt transects. It involves walking a wandering path rather than a fixed, more or less straight line, thoroughly searching an area in the stipulated time, with the goal of counting all species and individuals observed (Figure 1). This is accomplished by visiting resource patches—puddling sites, nectar plants, canopy gaps, roosting sites, specific host plants, and so forth, that are frequented by a diversity of butterfly species—and recording every individual of every species that is encountered. Unlike line transects, the survey path need not be fixed a priori, so it can be adapted to conduct rapid surveys at new or even well-established field sites. Timed counts also offer flexibility to navigate difficult terrain because a uniform pace and linear paths are not required, but they can still record the spatial and temporal distribution of butterflies or their resources in a standardised and comparable format. Timed counts may be especially advantageous in complex, dynamic landscapes, and even in smaller habitat fragments (Kadlec et al., 2012; Santorufo et al., 2021; Scalercio et al., 2007; Taron & Ries, 2015). Similar to line transects, timed counts assume that: (a) detectability is certain on the path, (b) counts are exact, (c) variation in the number of individuals counted at different sites or in different seasons truly reflect differences in their population sizes, and (d) butterflies are detected at their initial location (Glennie et al., 2015; Taron & Ries, 2015). Other assumptions and violations of line transects should also apply, for



(c)

Attributes	Line/belt transect	Time-constrained count
Length/area	Fixed	Variable
Duration	Usually fixed	Fixed
Width	Usually fixed, so observations outside are excluded	May be fixed or unlimited, as per requirements and species biology (e.g., to include large canopy species)
Route	Fixed a priori; revisited as needed	Variable; adaptable to local conditions, but may be standardised for repeated sampling
Pace	Uniform	Variable according to encounter rates
Assumption	All the animals in the transect are detected and counted. Counts are proportional to population size.	All the animals in the count period are detected and counted. Counts are proportional to population size.
Sampling	Stratified, random	Could be stratified and random, but also easily adaptable to unfamiliar areas, or for opportunistic sampling by actively searching for butterflies
What is measured?	Presence-absence, relative abundance, population density	Presence-absence, relative abundance, and population density if the area sampled is logged in the records

FIGURE 1 Schematic of a landscape, visualising two count methods for conducting butterfly surveys: (a) line/belt transect, and (b) time-constrained count ('timed count'). Transects are usually straight lines (although this condition is relaxed in the case of Pollard walks) laid near paths (p) and other landscape features, requiring the surveyor to walk at a uniform pace, during which organisms are sampled in a fixed area during a fixed time span. In contrast, the goal of timed counts is to actively search an area for butterflies ( ), often sampling different microhabitats, such as vegetation, rocky outcrops (r), stream-sides (s) and mud-puddling spots (mp), while keeping a fixed length of time as a unit of sampling but not the area. In a timed count, a surveyor would spend more time in a patch where butterfly density is higher, whereas in a line transect, the surveyor would normally be expected to maintain pace irrespective of butterfly density. As a result, the transect length and duration of sampling in line transects remain the same irrespective of butterfly density, whereas the physical length/area covered in a timed count may be negatively correlated with butterfly density. A comparison of the attributes of line transects and timed counts is given below (c).

example, (a) individual organisms are not going back and forth on sampling paths; therefore, they are likely to be counted only once; and (b) species with certain biological characteristics such as crepuscular activity patterns and excellent camouflage are under-represented. It may be possible to apply some of the statistical methods and models originally developed for data generated through line transects to those generated through timed counts, especially if the area is predefined and exhaustively surveyed or if the length/area covered under a timed count is estimated. However, this needs to be specifically tested, and perhaps new statistical models and methods need to be developed for the timed count method as the method becomes more popular with both research scientists and citizen scientists, and large-scale data become available.

Our study was motivated by a need to develop and test standardised methods for conducting butterfly surveys in tropical areas such as India, with complex landscapes and high butterfly diversity. While India is home to four globally recognised biodiversity hotspots and over 1400 butterfly species, large-scale data on the population dynamics of butterflies through seasons and space are scarce, even as anthropogenic pressures on butterfly habitats are mounting. This situation is widespread in other tropical countries as well. At the same time, with the rise in the popularity of social media and citizen science initiatives, there is renewed interest in natural history, and an opportunity to engage enthusiastic naturalists to obtain large-scale data on butterfly diversity using standardised protocols. Towards this end, we compared two methods for butterfly surveys (line transects and timed counts) in three habitats: (1) an evergreen forest, (2) a dry deciduous forest, and (3) an urban woodland, in southern India. We evaluated the relative performance of these methods to record the number of species and individuals as well as the numbers of rare, endemic or specialist species.

MATERIALS AND METHODS

Survey methods

We conducted butterfly surveys in three habitats (evergreen forest, dry deciduous forest and urban woodland) (Figure 2). All three study sites were located in Karnataka state of southern India (Figure 2). The evergreen forest site (Brahmagiri Wildlife Sanctuary, 181.8 km^2, altitude 100–1600 m) is hilly with evergreen and semi-evergreen forests at low and mid-elevations, and grasslands and montane forest patches at higher altitudes. It is a protected area located in the Western Ghats biodiversity hotspot. The dry deciduous forest site (Savandurga State Reserve Forest, 26.6 km^2, altitude 750–900 m) is located on the Dakhan (=Deccan) plateau. The urban woodland (Doresanipalya Forest Research Campus, 0.4 km^2, altitude ~900 m), a forest reserve in the midst of the metropolitan city of Bengaluru, has a mix of native and exotic trees and mixed understorey, criss-crossed by paths used by citizens for morning walks.

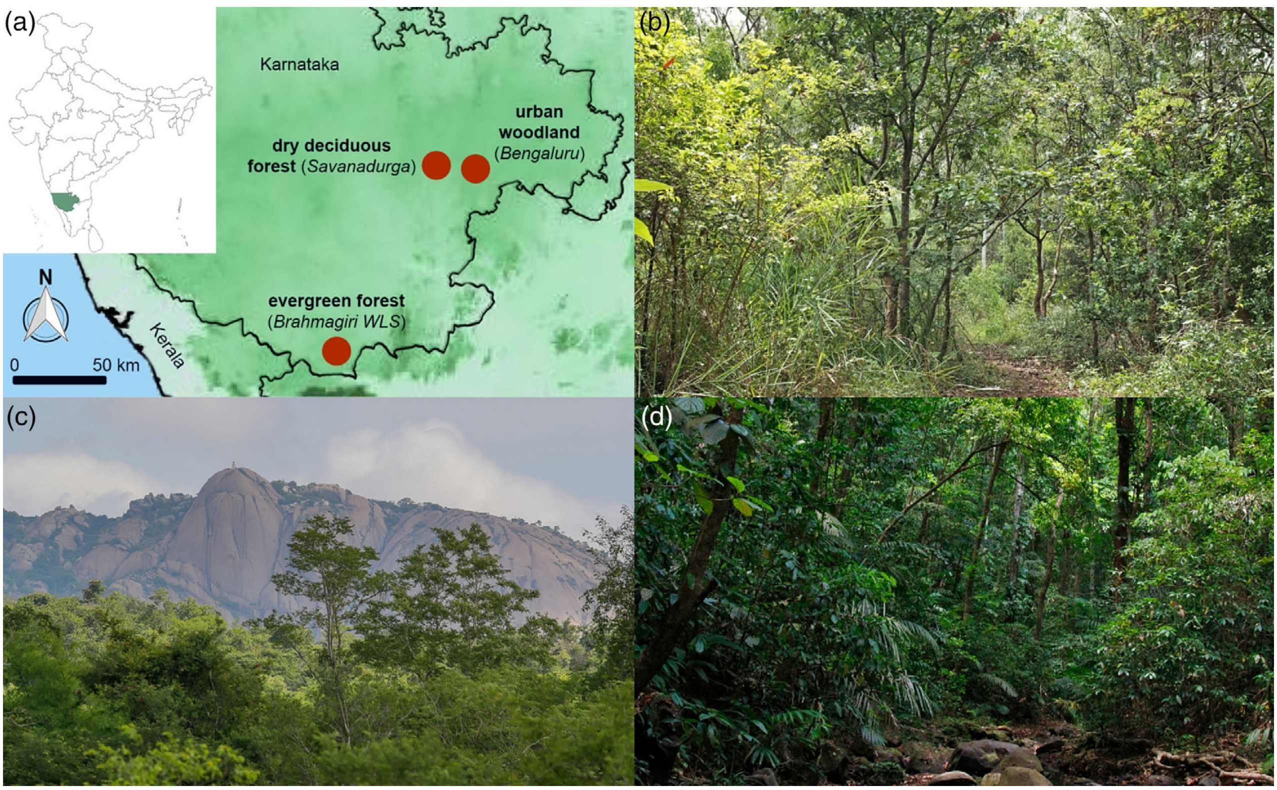


FIGURE 2 Butterfly habitats sampled in this study: (a) Locations of the three study sites, (b) Urban woodland in the Doresanipalya Forest Research Campus, Bengaluru, (c) Dry deciduous forest at Savanadurga, and (d) Evergreen forest in the Brahmagiri Wildlife Sanctuary, Kodagu.

The three sampling locations have been extensively surveyed for butterfly diversity over the past 11 years by a collaboration of professional and citizen scientists (Kunte et al., 2023; Kunte & Ravikanthachari, 2020). Building on this robust experience, we wanted to compare the relative performance of the two survey methods in recording species and individuals in representative habitat patches within the three sites. Accordingly, we demarcated survey areas of nearly 19- and 10-km stretches of roads and forest paths at the evergreen and dry deciduous forest sites, respectively. The urban woodland was small and fully accessible and most of it was covered with both the survey methods. At each of the study sites, we surveyed butterflies using two methods for comparison: (a) line transects (500 m in length, more or less in a straight line, 10 m in width, 10 m in height, covered in 10 mins), and (b) timed counts (length not fixed, covered in 30 min) (Figure 1). We decided on the duration of 30 min for timed counts based on: (a) the sizes of habitat patches (all of which were large enough to conduct many 30-min counts per day); (b) number of sampling replicates that we could do per day (6–12 counts) based on the amount of time spent in the field, seasonal climatic parameters, and butterfly activity, and also repetitions as a total effort over the entire duration of the study; and (c) our knowledge of the general diversity and encounter rates of butterflies based on our long-term field experience in these habitat patches. In our experience, the duration of 30 mins works well for sampling butterflies and odonates in many habitats and habitat patches in India, and this count duration has been used for the past 15 years of sampling (Kunte et al., 2012; Naik et al., 2022a, 2022b; Sondhi & Kunte, 2016). The 30-min counts are also used now as a standard method for data collection under the Indian Butterfly Monitoring Scheme (iBMS, https://ibms-network.in), and are integrated into its mobile data app and Microsoft Excel template for data collection (https://ibms-network.in/resources-for-monitoring).

A single surveyor (NR) with 10 years of experience in surveying butterflies at these locations walked the line transects at a steady pace, noting down all the individuals of each species observed. We used GPS (Garmin eTrex Vista HCX) to record the locations of line transects, which were laid near forest trails (Figures 1 and 2). In the 30-min timed counts, the surveyor (NR) walked a wandering path depending on the accessibility of terrain, adjusting the pace to the encounter rates of butterflies or their resources, often lingering around host plants, forest streams or canopy gaps that are frequented by butterflies (Figure 1). To equalise the effort between the two methods, we walked three 10-min line transects immediately before or after every 30-min timed count. We alternated between the two methods in each sampling session and in each habitat patch so that habitat variability or differences in time of day did not affect the results of a single method.

The potential for double counting of individual butterflies is a confounding factor that is common to all visual-count methods. To minimise double counting, we avoided spending an unnecessary amount of time in the same spot. If we had to stay in one patch for some time (e.g., at a puddling spot or a nectar plant with swarms of butterflies feeding on it), then we noted the minimum number of individuals seen at a single moment or the number of individuals that could be distinguished based on their specific colouration, size, sex or pattern of wing wear. In large congregations, we took approximate, rounded-off estimates of the number of individuals of every species since a precise count was not possible.

TABLE 1 Total monthly sampling effort per habitat and method (timed counts = 30 min each; line transect = 500 m, 10 min each).

	Timed counts Total (forest paths, puddling spots)	Line transects
Evergreen forest		
February	7 (3, 4)	21
March	9 (4, 5)	24
April	8 (4, 4)	24
May	8 (4, 4)	24
Dry deciduous forest		
February	7	21
March	7	21
April	6	18
May	6	18
Urban woodland		
March	6	18
April	6	18
May	6	18

Note: Three line transects were walked before or after each 30-min timed count to standardise timed effort). Evergreen and dry deciduous forests were sampled monthly between February and May, while the urban woodland was sampled from March to May.

We carried out surveys between 0900 and 1300 h on clear, sunny days. We visited the sampling locations for 2–3 days each month and repeated the sampling four times at each location from February to May 2018 (sampling effort shown in Table 1). The species recorded, their habitat-wise occurrence and conservation scores are given in Table S1.

Statistical analysis

In order to test the relative performance of the two methods, we compared: (a) overall species richness; (b) number of species and individuals of butterflies observed per transect or count; (c) number of species and individuals of rare, endemic and specialist species per transect or count; and (d) conservation scores of species observed in transects and counts in each of the three habitats.

Species richness

We used rarefaction curves to compare the overall number of species observed via timed counts versus line transects in each

TABLE 2 Total number of species, unique species (observed only in that habitat or method), habitat specialists, endemics and rare species observed via line transects and timed counts at the evergreen forest, dry deciduous forest and urban woodland sites.

	Total no. of species	Unique species	Habitat specialists	Endemics	Rare species
Evergreen forest	140 (2722)	69 (881)	71 (1297)	11 (57)	25 (110)
Line transects	109 (1080)	19 (23)	49 (517)	7 (22)	15 (48)
Timed counts	121 (1642)	38 (85)	62 (780)	11 (35)	19 (62)
Forest paths	99 (677)	9 (11)	35 (307)	4 (11)	6 (17)
Puddling spots	112 (965)	22 (45)	55 (473)	10 (24)	17 (45)
Dry deciduous forest	106 (2428)	21 (101)	16 (155)	0 (0)	4 (7)
Line transects	87 (1198)	13 (27)	10 (72)	0 (0)	4 (5)
Timed counts	87 (1230)	13 (34)	12 (83)	0 (0)	2 (2)
Urban woodland	69 (806)	4 (5)	10 (54)	0 (0)	0 (0)
Line transects	51 (404)	12 (18)	4 (24)	0 (0)	0 (0)
Timed counts	57 (402)	18 (19)	10 (30)	0 (0)	0 (0)

Note: Counts taken at puddling spots are also shown for the evergreen site. Number of individuals recorded are shown in parentheses after the species numbers.

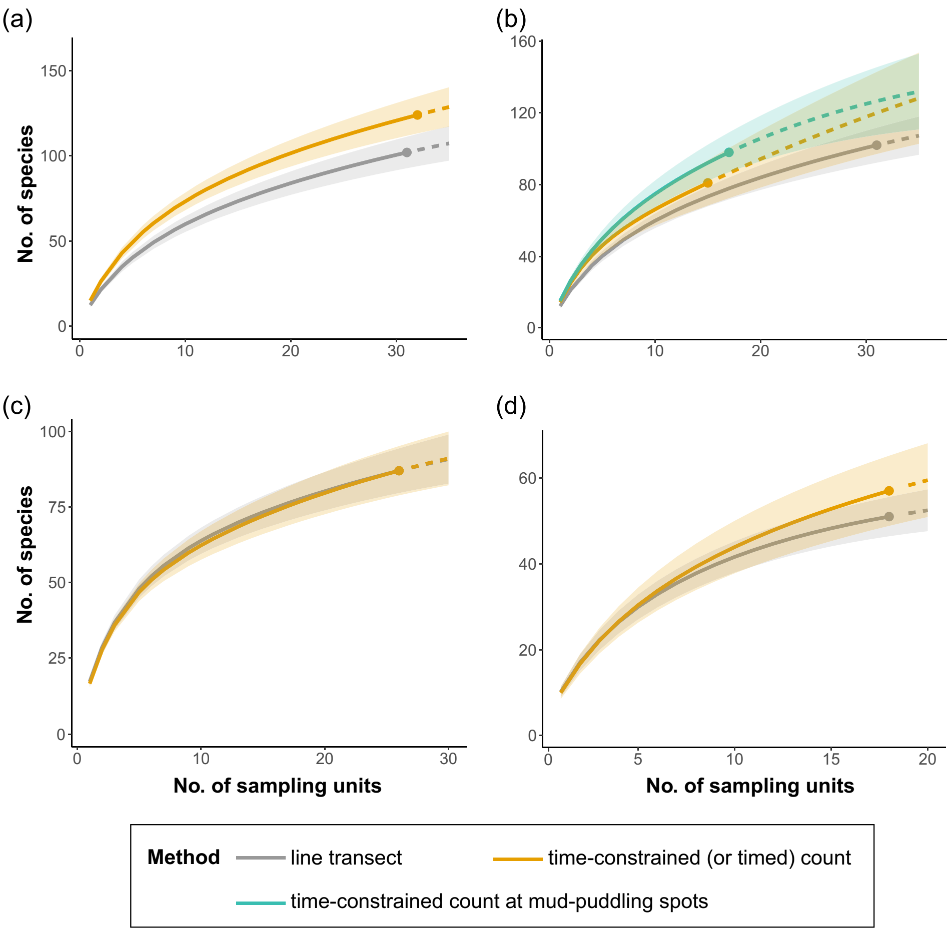


FIGURE 3 Species diversity estimated from sample-based rarefaction curves with 95% confidence intervals, comparing species richness observed in line transects and timed counts in: (a) evergreen forest, (b) puddling spots in evergreen forest, (c) dry deciduous forest and (d) urban woodland. Continuous lines = interpolation; stippled lines = extrapolation.

habitat. Sample-size-based rarefaction curves with bootstrapped confidence intervals can be used to quantify and compare species richness observed between samples (Chao et al., 2014). We pooled the data from the three 10-min line transects walked immediately before or after each timed count, and used 30 min as a uniform sampling unit to compare the results of the two sampling methods.

TABLE 3 Estimated regression coefficients, standard errors, *z*-values and *p*-values for generalised linear models of number of species and individuals observed per sample by the two methods, namely, line transects and timed counts in three habitats, with month of survey as a covariate.

		Species per sample				Individuals per sample			
		Coefficient	SE	*z*-value	*p*	Coefficient	SE	*z*-value	*p*
Evergreen forest		(Negative binomial)				(Negative binomial)			
	Intercept	−0.51	0.09	−5.71	<0.001	0.87	0.15	5.92	<0.001
	Timed counts	0.08	0.08	0.94	0.35	0.24	0.12	1.91	0.06
	March	0.05	0.11	0.45	0.65	−0.24	0.19	−1.26	0.21
	April	−0.47	0.11	−4.13	<0.001	−1.07	0.18	−6.04	<0.001
	May	−0.56	0.11	−4.94	<0.001	−1.26	0.17	−7.24	<0.001
Dry deciduous forest		(Poisson)				(Negative binomial)			
	Intercept	2.58	0.08	31.82	<0.001	3.4	0.1	32.51	<0.001
	Timed counts	−0.04	0.07	−0.58	0.57	0.02	0.09	0.21	0.84
	March	0.26	0.11	2.46	0.01	0.42	0.14	3	<0.001
	April	0.31	0.09	3.32	<0.001	0.65	0.12	5.22	<0.001
	May	0.43	0.1	4.33	<0.001	0.54	0.13	4.01	<0.001
Urban woodland		(Negative binomial)				(Negative binomial)			
	Intercept	2.26	0.12	18.67	<0.001	3.16	0.17	18.64	<0.001
	Timed counts	−0.02	0.12	−0.18	0.86	0.01	0.17	0.06	0.96
	April	−0.06	0.15	−0.42	0.68	−0.32	0.21	−1.54	0.13
	May	0.23	0.14	1.58	0.11	0.12	0.21	0.57	0.57

Note: Intercept represents line transects in February for evergreen and dry deciduous forest and March for urban woodland.

We computed rarefaction curves for the combined data from the 4 months of the survey for each method. We used iNext package (Hsieh et al., 2016) in R 3.4.2 (R Development Core Team, 2017) to compute rarefaction curves with 95% confidence intervals.

Number of species and individuals per sample

We used generalised linear models (GLMs) to compare the number of species and the number of individuals of butterflies recorded per sample (i.e., per 30 min of line transect or timed count) by the two methods (METHOD: *timed counts* vs. *line transect*) in each of the three habitats, with survey month as a co-explanatory variable.

Habitat specialists, rare and endemic species per sample

For further analysis, we classified butterfly species encountered at the three study sites on the basis of endemism (Western Ghats endemics), rarity (rare or uncommon in the Western Ghats) and habitat specialisation (habitat preference for the endangered evergreen, semi-evergreen, riparian moist deciduous forests, and montane forests and grasslands) (Kunte, 2008). We ran regression models on the number of species, and number of individuals of habitat specialists, endemics and rare species per sample, similar to the above GLMs with METHOD and MONTH as explanatory variables. As the response variables were counts (of either individuals or species), we used Poisson regression models with log-link function and negative binomial in case of overdispersion. As the dataset of endemics and rare species had many transects/counts with zero observations, we ran zero-inflated Poisson (ZIP) models using the pscl package in R. The ZIP model has two parts: a Poisson count model and a logit model for predicting excess zeros. It is thus appropriate to model count data that have an excess of zero counts.

Conservation score

We assigned a conservation score to each species based on their distribution, habitat preference and population status, as calculated by Kunte (2008). We used a non-parametric, two-sample Wilcoxon signed-rank test to compare conservation scores of species observed in line transects and timed counts in each of the three habitats.

RESULTS

Number of individuals, species, habitat specialists, endemics and rare species observed during the survey are summarised in Table 2.

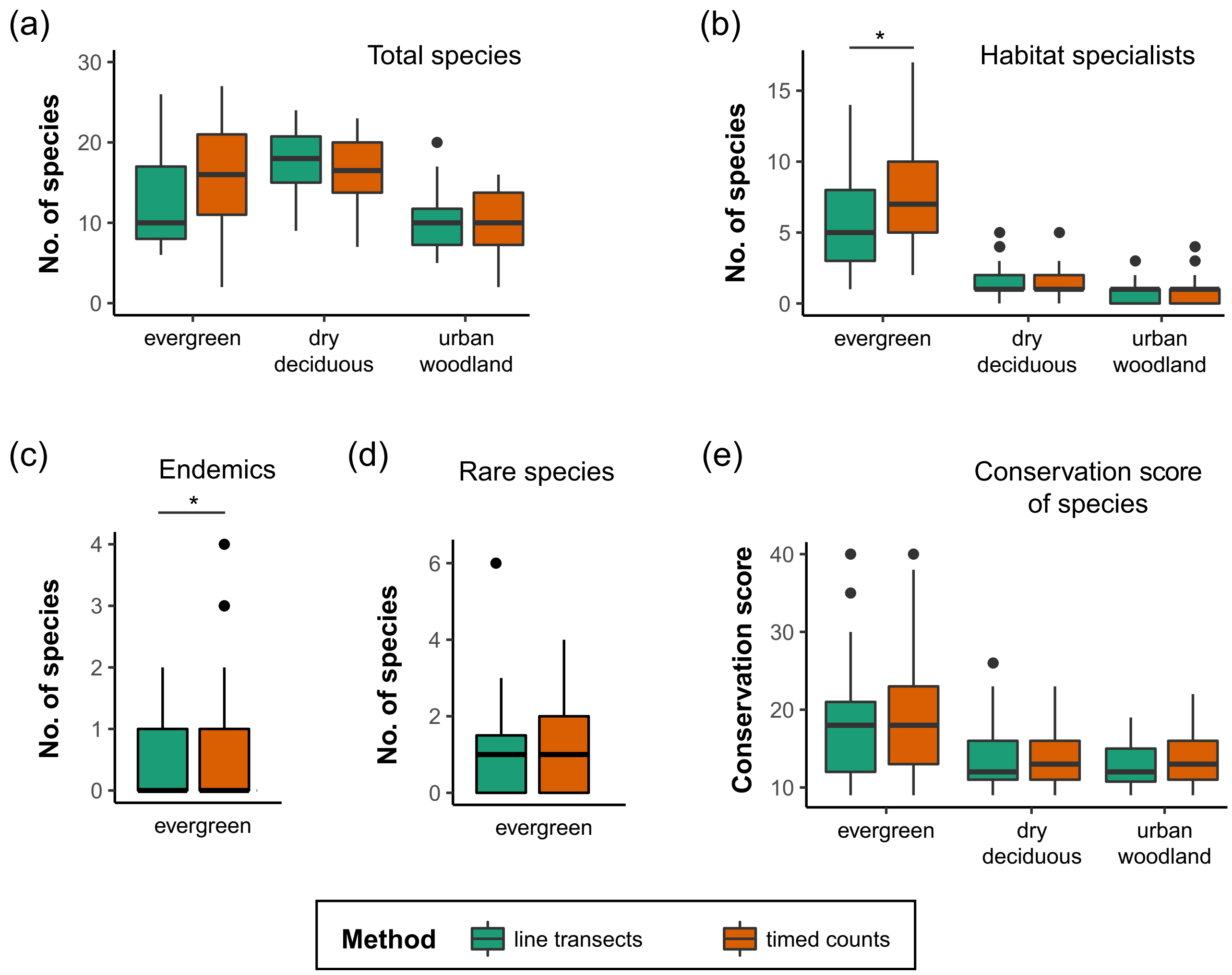


FIGURE 4 Box plots showing (a) total number of species, (b) habitat specialists, (c) endemics, (d) rare species per sample and (e) conservation scores of species observed via line transects and timed counts in evergreen forest, dry deciduous forest and urban woodland. Statistically significant differences are indicated (*).

Species richness

We observed greater species richness in timed counts as compared with line transects at the evergreen forest site ($n = 31$, no. of species: timed counts = 122, 95% CI = 111.3–133.5; line transect = 102, 95% CI = 93.8–110.2) (Figure 3a). This could be partly due to greater number of species observed in the timed counts at puddling spots as compared with timed counts and line transects along partly shaded forest paths ($n = 15$, no. of species: timed counts at mud-puddling spots = 92, 95% CI = 83.1–101.3; timed counts along forest paths = 81, 95% CI = 71.6–90.4; line transects = 73, 95% CI = 66.6–80.3) (Figure 3b). We did not observe any difference in species richness between timed counts and line transects in the other two habitats, viz. dry deciduous forest ($n = 26$, no. of species: timed counts = 87, 95% CI = 79.3–94.7; line transects = 87, 95% CI = 79.4–94.7) and urban woodland ($n = 18$, no. of species: timed counts = 57, 95% CI = 49.4–64.6; line transects = 51, 95% CI = 46.2–55.8) (Figure 3c,d).

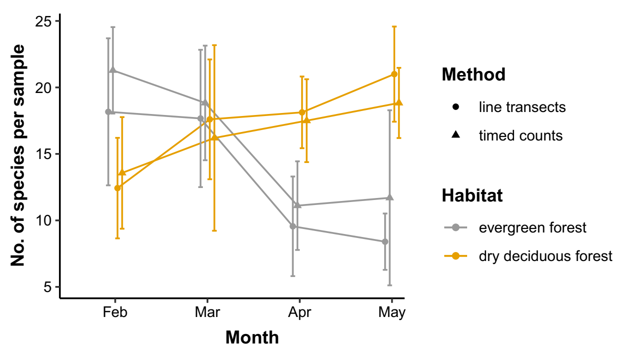


FIGURE 5 Monthly variation in number of species observed per sample in line transects and timed counts in the evergreen and dry deciduous forests.

Number of species and individuals per sample

Numbers of species and individuals observed per sample were similar between timed counts and line transects in all three habitats (Table 3,

TABLE 4 Estimated regression coefficients, standard errors, *z*-values and *p*-values for generalised linear models of number of species and individuals of habitat specialists observed per sample by the two methods, namely, line transects and timed counts in the three habitats (EV, evergreen forest; DDF, dry deciduous forest; UW, urban woodland), with month of survey as a covariate.

		Species per sample				Individuals per sample			
		Coefficient	SE	*z*-value	*p*	Coefficient	SE	*z*-value	*p*
Habitat specialists									
Evergreen forest		(Negative binomial)				(Negative binomial)			
	Intercept	2.02	0.14	14.85	<0.001	3.32	0.21	16.15	<0.001
	Timed counts	0.27	0.12	2.31	0.02	0.35	0.17	2.02	0.04
	March	−0.01	0.17	−0.05	0.96	−0.13	0.26	−0.51	0.61
	April	−0.51	0.17	−3.05	<0.001	−0.95	0.25	−3.86	<0.001
	May	−0.39	0.16	−2.45	0.01	−0.87	0.24	−3.65	<0.001
Dry deciduous forest		(Poisson)				(Negative binomial)			
	Intercept	−0.06	0.3	−0.21	0.83	−0.09	0.33	−0.26	0.79
	Timed counts	−0.02	0.22	−0.11	0.91	0.16	0.23	0.7	0.49
	March	0.66	0.36	1.82	0.07	1.14	0.39	2.92	<0.001
	April	0.7	0.33	2.12	0.03	1.49	0.35	4.24	<0.001
	May	0.77	0.34	2.23	0.03	1.18	0.38	3.15	<0.001
Urban woodland		(Poisson)				(Negative binomial)			
	Intercept	−0.56	0.44	−1.26	0.21	−0.27	0.45	−0.6	0.55
	Timed counts	0.22	0.37	0.6	0.55	0.14	0.39	0.36	0.72
	April	0.12	0.49	0.24	0.81	0.09	0.51	0.18	0.86
	May	0.81	0.42	1.91	0.06	1.19	0.47	2.66	<0.001
Rare species									
Evergreen forest		Count model coefficients (Poisson)				Count model coefficients (Poisson)			
	Intercept	0.83	0.29	2.82	<0.001	1.35	0.21	6.43	<0.001
	Timed counts	−0.02	0.3	−0.07	0.94	−0.12	0.21	−0.57	0.57
	March	−0.03	0.33	−0.1	0.92	0.07	0.25	0.29	0.77
	April	−0.43	0.47	−0.92	0.36	−0.32	0.29	−1.09	0.27
	May	−1.42	0.38	−3.74	<0.001	−1.29	0.46	−2.8	<0.001
		ZIP model coefficients (binomial)				ZIP model coefficients (binomial)			
	Intercept	−1.18	1.15	−1.02	0.3	−0.9	0.8	−1.13	0.26
	Timed counts	−1.31	1.39	−0.95	0.34	−0.87	0.79	−1.11	0.27
	March	0.31	1.44	0.22	0.83	0.15	1.02	0.15	0.88
	April	1.37	1.44	0.95	0.34	1.41	0.91	1.54	0.12
	May	−9.71	212.62	−0.05	0.96	0.22	1.65	0.13	0.9
Endemic species									
Evergreen forest		Count model coefficients (Poisson)				Count model coefficients (Poisson)			
	Intercept	−0.56	0.46	−1.22	0.22	0.75	0.35	2.14	0.03
	Timed counts	0.83	0.41	2.02	0.04	0.27	0.36	0.75	0.46
	March	−0.62	0.7	−0.89	0.37	0.07	0.48	0.15	0.88
	April	−0.31	0.59	−0.52	0.6	−0.58	0.5	−1.15	0.25
	May	−0.14	0.55	−0.25	0.8	−0.54	0.46	−1.19	0.23
		ZIP model coefficients (binomial)				ZIP model coefficients (binomial)			
	Intercept	−10.66	251.79	−0.04	0.97	0.51	0.72	0.71	0.48
	Timed counts	11.09	251.79	0.04	0.97	−0.35	0.7	−0.5	0.62
	March	−5.58	92.62	−0.06	0.95	0.23	0.9	0.26	0.8
	April	−1.38	1.92	−0.72	0.47	−0.43	0.95	−0.45	0.65
	May	−2.47	2.99	−0.83	0.41	−1.02	1.01	−1.01	0.31

Note: The same analysis was repeated for rare and endemic species at the evergreen forest site using zero-inflated Poisson (ZIP) regression. Intercept represents line transects in February for evergreen and dry deciduous forests and March for urban woodland.

Figure 4a). There was a significant monthly variation in the number of species and individuals per sample in the evergreen and dry deciduous forest (Figure 5, Table 3).

Habitat specialists, rare and endemic species per sample

We observed 31% more species (IRR = 1.31, 95% CI = [1.04, 1.66], $p = 0.02$) and 42% more individuals (IRR = 1.42, 95% CI = [1.02, 1.98], $p = 0.04$) of habitat specialists per sample via timed counts as compared with line transects in the evergreen forest, while no difference was observed in other habitats (Table 4, Figure 4b). For rare and endemic species, because the overall abundance in the dry deciduous forest and urban woodland was extremely low (rare species: dry deciduous forest = 7, urban woodland = 0; endemic species: dry deciduous forest = 0, urban woodland = 0; Table 2), we conducted further analysis of these species only for the evergreen forest. Among the samples where endemic species were present, we observed 129% more species (IRR = 2.29, 95% CI = [1.03, 5.12], $p = 0.04$) of endemics per sample (but no significant difference in number of individuals) in timed counts as compared with line transects. No significant difference was found in the case of rare species (Table 4, Figure 4c,d).

Conservation score

We observed no difference in conservation scores of species encountered by the two methods in any of the three habitats (Figure 4e). Evergreen forest had a greater number and abundance of species with a high conservation score as compared with dry deciduous forest (Wilcoxon rank sum test: $W = 7880$, $p < 0.01$) and urban woodland (Wilcoxon rank sum test: $W = 5532.5$, $p < 0.01$), as revealed by both the survey methods (Figure 4).

DISCUSSION

Long-term butterfly monitoring programmes have generated valuable data on population dynamics and conservation status of butterflies (Warren et al., 2021). Most of these studies have been in temperate zones. This article was motivated by the need to develop inexpensive and easily implemented methods for monitoring butterflies in tropical and mountainous areas.

We compared two visual-count survey methods, namely, line transects and timed counts, in three different habitats: (1) evergreen forest, (2) dry deciduous forest and (3) urban woodland. We observed similar species richness via timed counts and line transects in the urban woodland and dry deciduous forest. However, we observed greater overall species richness via timed counts in the evergreen forest. We also observed greater number of species and individuals of habitat specialists and greater number of species of endemics per sample in timed counts as compared with line transects in the evergreen forest. These results are analogous to other studies at different scales and habitats (Kadlec et al., 2012; Kral-O'Brien et al., 2021).

Species richness is a widely used index in ecology and conservation, but surprisingly difficult to measure accurately (Gotelli & Colwell, 2001). Raw species counts underestimate species richness due to many species remaining undetected. Moreover, detectability varies between species and observers and over space, time and habitats (Isaac et al., 2011; Kéry & Plattner, 2007; Nowicki et al., 2008; Pellet et al., 2012). Timed counts may improve the detectability of species by enabling the surveyor to search a habitat more thoroughly at a pace adapted for local habitat conditions or to species being sampled or targeted, and spending more time where butterflies may be concentrated. This may be especially true for rare, cryptic or specialist species, and those that are difficult to identify in flight. Our study detected a higher number of habitat specialist and endemic species per sample in timed counts in the more complex evergreen forest habitat. This was partly due to the inclusion of puddling spots in the timed counts, which sampled overall greater numbers of species, habitat specialists, endemics and rare species as compared with line transects (Table 2). Puddling spots attract concentrations of many species because they are a crucial resource for butterflies, including species that may be easily missed in line transects, such as smaller sized, fast-flying or largely canopy species that will visit puddling spots for extended periods. On the other hand, the results of timed counts versus line transects were similar in less structurally complex habitats (dry deciduous forest and urban woodland) where the possibility of missing canopy species is smaller, and there are fewer species for which close inspection for identification was necessary. Thus, taking a non-linear path, paying particular attention to butterfly resources such as nectar/host plants, wet soil, tree sap, and rotting fruit, crabs or fish may indeed improve species detection and lead to better estimates of species richness in complex, species-rich habitats. In the future, it will also be useful to compare variation in the number of individuals of a species, species richness and community composition, and so forth, as estimated across sampling units of line transects and timed counts in a paired design similar to the one we used. Such a comparison will help understand the relative merits and limitations of both the methods in sampling butterfly populations and communities, especially when repeatability and reliability are important in complex habitats with diverse butterfly faunas.

Given that timed counts are efficient in detecting species and simpler to conduct in complex terrain, this method is particularly suitable for occupancy surveys and mapping of butterfly diversity at large scales. Because the survey path need not be fixed in timed counts, recorders may vary their search efficiency and attention paid to particular resources. Observer bias, which is common to all visual sampling methods, can be minimised by training surveyors prior to conducting the surveys, and by noting down GPS tracks of surveys. Although observer experience may positively influence species identification and efficiency of sampling in any method, experience can be especially leveraged to improve sampling efficiency in timed counts. This improvement stems from more experienced observers being able to use their better judgement of allocating differential amount of time to sampling critical locations such as patches of larval host or nectar plants, puddling spots and sunny patches in shaded habitats. Such leveraging of experience is possible in timed counts, but it violates the assumptions of line transects and therefore limits its widespread use. This flexibility also makes the use of timed counts suitable and attractive for projects involving citizen scientists. For more systematic long-term monitoring or formal scientific studies, we recommend that the habitat patch for each count be predefined (in advance or based on first visit) and properly geo-referenced. For such scientific studies, weather parameters, habitat parameters (light, relative humidity, etc.), vegetation condition and other ecological data may also be recorded more rigorously during timed counts. With these additional measures, time-constrained surveys may be conducted in any place within the broader field site.

It should be noted that both line/belt transects and timed counts represent a relative measure of butterfly activity rather than true abundance. These methods cannot be used to estimate population sizes without further validation using methods such as capture–mark–recapture. While line/belt transects standardise effort by length/area of the transect, timed counts do so by time expended. Thus, many of the methodological factors that influence counts of butterflies in line transects (including Pollard walks, discussed in Basset et al., 2013) are equally applicable to timed counts. For example, environmental factors such as ambient temperature, wind velocity and elevation may need to be either controlled for during survey efforts (van Swaay et al., 2008) or measured and accounted for during statistical analysis (Basset et al., 2013). Seasonal variation can also considerably affect butterfly numbers. We found significant seasonal variation in butterfly abundance at our study sites. Thus, depending on the goals of the study, the number of surveys per year will need to be optimised for adequate representation of seasonal variation (Basset et al., 2013). Similarly, for large areas, sampling locations must be representative of all the habitats in the area (Basset et al., 2013). For mapping and monitoring studies at local and/or large spatial scales, protocols for timed counts can be rigorously formalised, so that the counts are replicable and comparable across space and time. These may include setting up tracks with GPS locations/delineation of sampled patches, time of day, sampling frequency, fixed group of surveyors, and so forth, agreed to by a research team for long-term monitoring. The strictness of the methodological criteria for monitoring should depend on the scope of the monitoring programme (Lindenmayer & Likens, 2010), such as whether it is conducted at local or regional scales (Chiarucci et al., 2011; Scheiner et al., 2011), and whether professional or citizen scientists are involved in a formalised, centrally coordinated project. In general, more question-driven and goal-oriented monitoring programmes would require stricter design criteria. In any case, the timed count method can be formalised and standardised just as well as line transects and other sampling methods for a given project.

Timed counts appear to be more useful in tropical and mountainous terrain as discussed above, but may also be useful in many situations where the entire transect width is difficult to see, for instance, in dense shrublands where shrubs block part of the view. They may also be used in conjunction with bait-trapping, capture–mark–recapture and other methods to estimate population sizes, community composition and species diversity (Taron & Ries, 2015). Indeed, bait traps have traditionally been used commonly for butterfly surveys in tropical regions, for example, to evaluate the effects of natural disturbance such as tree-fall gaps (Hill et al., 2001; Pardonnet et al., 2013), vertical stratification of butterfly communities (Fermon et al., 2003; Molleman et al., 2006), forest fragmentation (Uehara-Prado et al., 2007) and intensification within agroecosystems (Mas & Dietsch, 2003). However, bait-trapping is suitable to survey a narrow range of subfamilies and genera within one family (Nymphalidae). This method is not suitable to sample larger butterfly communities, and this method can also not scale up over large areas. Hence, bait-trapping is complementary to visual census methods (Jakubikova & Kadlec, 2015; Kral et al., 2018; Sparrow et al., 1994), and we promote its broader use in conjunction with timed counts.

Based on our findings as well as those of other recent studies (Kadlec et al., 2012; Kral-O'Brien et al., 2021), we conclude that timed counts are a viable and perhaps even a superior alternative to line transects for conducting butterfly surveys and monitoring butterfly populations/communities in tropical and mountainous habitats. Although timed counts and line transects (including Pollard walks) may appear similar in species-poor landscapes in the United Kingdom and parts of northern Europe, the methodological contrast between these two sampling methods should not remain underappreciated. Transects use space as the primary unit of sampling, whereas timed counts use time as the primary unit. This contrast has considerable implications for utility in complex or biodiverse landscapes, the statistical models and analysis pipelines required, and their power of inference. Statistical methods to analyse data generated through timed counts are not yet as well developed as those for transects, or they have limited statistical models available for the study of population dynamics and community diversity. However, many of the existing statistical methods may be easily adapted. Considering the difficulty of conducting line transects in tropical and mountainous regions where butterfly occurrence is highly uneven and species diversity very high, it will serve the scientific and conservation communities to urgently develop additional statistical methods to analyse data generated through timed counts. This may prove to be especially important at a time when large amounts of data are being generated through citizen science projects. It is easy to train people to conduct timed counts, and the counts are simple to implement. Smartphones, mobile apps and citizen science platforms can greatly facilitate these steps. In fact, timed counts are fast becoming a standard and preferred method of butterfly sampling, being integrated into mobile data apps as well as Microsoft Excel templates for data collection of the European Butterfly Monitoring Scheme (eBMS, https://butterfly-monitoring.net), eButterfly (https://www.e-butterfly.org) and the Indian Butterfly Monitoring Scheme (iBMS; https://ibms-network.in). Our work shows that switching to timed counts has many advantages without losing the coverage of butterfly diversity and quality of data irrespective of whether simple or complex habitats are sampled. Hence, the timed count method has great promise in sampling butterfly diversity in mountainous and/or tropical biodiversity hotspots such as southern Europe and the Mediterranean, Western Ghats and Himalaya. Indeed, technology-primed biodiverse countries such as India, China, Thailand and Brazil, which have historically been under-sampled and under-represented in biodiversity monitoring efforts, may be able to take advantage of this sampling method as well as of numerous apps and citizen science platforms to rapidly generate large datasets on the impacts of habitat change, climate change and conservation management practices on native butterfly diversity and population persistence.

AUTHOR CONTRIBUTIONS

Suman Attiwilli: Data curation (lead); formal analysis (lead); investigation (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **Nitin Ravikanthachari:** Data curation (supporting); investigation (equal). **Krushnamegh Kunte:** Conceptualization (lead); funding acquisition (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); visualization (supporting); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The original butterfly count data are available upon request.

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SUPPORTING INFORMATION

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

Table S1. List of species observed in the study, indicating the habitat where they were observed and their habitat specialisation, rarity, endemism and conservation score (based on Kunte, 2008). Species names follow Kunte et al. (2023).

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