Title: A comparison between time-constrained counts and line transects as methods to estimate

butterfly diversity in tropical habitats

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Abstract: Long-term monitoring programmes have revealed catastrophic population declines that are

contributing to biodiversity loss. These discoveries and the underlying programmes have been

possible because of standardised methods of counting butterflies. Butterflies have been monitored

using modified line transects, known in butterfly monitoring schemes as Pollard walks. However, line

transects are not feasible in many tropical and mountainous habitats. To tackle this problem, we

devised time-constrained (30-min) counts and compared butterfly diversity as estimated through this

method with that estimated through line transects (500 m, 10 min) in three tropical habitats in India

(evergreen forest, dry deciduous forest and an urban woodland). We tested the efficacy of the two

methods to sample species richness and abundance, as well as numbers of rare, endemic and specialist

butterflies. We observed greater species richness, and more species of habitat specialists and endemics

per sample in time-constrained counts when compared with line transects in evergreen forest, but not

in the other two habitats. Thus, time-constrained counts were more efficient at detecting species than

line transects 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. Time-constrained

counts may thus be viewed as a feasible alternative to line transects to carry out butterfly surveys in

tropical and mountainous landscapes. This method is particularly suited for biodiversity assessments

and mapping involving citizen science initiatives, which has considerable potential in populous and

tech-ready countries such as India.

Keywords: butterfly monitoring, long-term monitoring, biodiversity inventories, citizen science

INTRODUCTION

Survey and monitoring of insects is fundamental to their conservation (Kim 1993; Clark and Samways 1996; Brown 1997; Rohr et al. 2007; Leather et al. 2008). 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 diversity of insects is extremely high but resources are scarce to undertake detailed studies of individual species (Braschler at al. 2010, Lewis and Basset 2007). Butterflies are a good target taxon for recording and monitoring because their taxonomy is relatively well-known, and they are conspicuous and relatively easy to identify in the field as compared to other insects (Thomas 2005; Basset et al. 2013).

Long-term butterfly monitoring programmes have been remarkably successful in Europe (Thomas 2005; van Swaay et al. 2008; Schmeller et al. 2009; Brereton et al. 2011). Their objective is to assess regional and national-level trends in abundance of butterfly species (van Swaay et al. 2008). All such programmes employ spatially and temporally explicit transects—popularly known in butterfly monitoring literature 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 and Yates 1994). The transects are predefined, i.e., fixed a priori, and revisited every sampling session. Pollard walks are popular because they are simple to conduct in open, relatively flat habitats with fewer butterfly species and lower population densities, and are easily replicable once the line transects have been identified by experienced butterfly-watchers. The protocol allows rapid collection of data on relative abundances of butterflies using a fixed effort. Long-term population monitoring using this method has yielded valuable insights into population dynamics of European butterflies, including the recent alarming declines due to climate change and habitat alterations (Roy and Sparks 2000; Devictor et al. 2012). Monitoring schemes of comparable magnitude are lacking in the tropics, 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 methods for data analysis were originally devised to count large mammals and other conspicuous organisms 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, which is nearly impossible to do in hilly tropical regions with dense vegetation, sometimes with difficult terrain. Moreover, line transects require recorders to cover the transect length at a uniform pace. Since butterflies and certain other insects are often highly clustered, e.g., at puddling sites in hundreds or thousands, the requirement of uniform pace is easily violated. Such highly clustered occurrence is also not easy to account for in the analysis of line transect data. Besides, the

fixed-transect method has been criticized for poor detectability of cryptic, rare or sedentary species

(Kadlec et al. 2012; Henry et al. 2015). Certain tropical butterfly genera are difficult to identify on the

wing or may be easily missed while walking transects, especially in shaded areas (Walpole and

Sheldon 1999; Caldas and Robbins 2003). However, Pollard walks 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, with their

design requirements and reliance on costly 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, etc., 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 a scientific analysis.

Time-constrained counts is an alternative method to line transects for conducting butterfly

surveys and population monitoring (Beneš et al. 2003; Kadlec et al. 2012; Kral-O'Brien et al. 2021).

In time-constrained counts, effort is standardised by time rather than by length of the transect and area

under the belt transect. 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 maximizing the number of

species and individuals observed (Fig. 1). This is accomplished by visiting resource patches—

puddling sites, canopy gaps, roosting sites, etc., that are frequented by a diversity of butterfly

species—and recording every individual and every species that is encountered. Unlike line transects,

the survey path need not be fixed a priori, so it offers more flexibility for rapid surveys at new or even

well-established field sites. Time-constrained counts also offer flexibility to navigate difficult terrain

because a uniform pace and linear paths are not required, but they can still record spatial and temporal

distribution of butterflies or their resources. Time-constrained counts may be especially advantageous

in complex, dynamic landscapes. Similar to line transects, time-constrained 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). Other assumptions and

violations of line transects should also apply, e.g., (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 models originally developed for data

generated through line transects to those generated through time-constrained counts. However, this

needs to be specifically tested, and perhaps new statistical models and methods need to be developed

for the time-constrained 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 its complex landscapes and high butterfly

diversity. While India is home to four globally recognized biodiversity hotspots and over 1,400

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 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 time-

constrained counts) in three habitats: (1) an evergreen forest, (2) a dry deciduous forest, and (3) an

urban woodland, in southern India. We evaluated the efficacy of these methods to record the number

of species and individuals as well as numbers of rare, endemic or specialist species.

METHODS

Survey methods: We conducted butterfly surveys (six families: Papilionidae, Pieridae, Nymphalidae,

Riodinidae, Lycaenidae and Hesperiidae) in three habitats (evergreen forest, dry deciduous forest,

urban woodland) (Fig. S1). All three study sites were located in Karnataka state of southern India

(Fig. S1). The evergreen forest site (Brahmagiri Wildlife Sanctuary, 181.8 km^2, altitude 100-1,600 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 Campus, 0.4 km^2, altitude ~ 900 m), a reserved forest 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.

The three sampling locations have been extensively surveyed for butterfly diversity over the

past 11 years, with their butterfly faunas enumerated by a collaborative of professional and citizen

scientists (Kunte and Ravikanthachari 2020; Kunte et al. 2021). Building on this robust experience,

we wanted to compare the efficacy of the two survey methods in recording species and individuals in

representative habitat patches within the three sites. Accordingly, we demarcated survey areas along

19 km 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) time-constrained counts (length not fixed, covered in 30 mins)

(Fig. 1). A single surveyor (NR) with 10 years of experience of watching and sampling butterflies at

these locations, walked the line transect at a steady pace, noting down all the individuals of each

species observed. We used GPS (Garmin eTrex Vista HCX) to record the location of the line

transects, which were laid near forest trails (Fig 1). In the 30-min time-constrained 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 (Fig. 1). To equalize the effort between the

two methods, we walked three 10-min line transects immediately before or after every 30-min time-

constrained count. We alternated between the two methods in each sampling session and in each

habitat patch so that habitat variability did not affect results of a single method.

We carried out surveys between 0900 and 1300 hrs 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 (Table 1). The total sampling effort for line transects and time-

constrained counts for each habitat is shown in Table 1. Sampling datasets will be made available on

Dryad upon provisional acceptance of the paper.

Statistical analysis: We used rarefaction to compare the overall number of species observed via time-

constrained counts vs. line transects. We used iNext package (Hsieh et al. 2016) in R 3.4.2 (R core

team 2017) to compute rarefaction curves with 95% confidence intervals. The 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 the time-constrained counts, and used 30 min as a

uniform sampling effort to compare results of the two sampling methods. We computed rarefaction

curves for the combined data from the four months of the survey. We used generalized linear models

(GLMs) to compare number of species and number of individuals of butterflies recorded per sample

(i.e., per 30 mins of line transect or time-constrained count) by the two methods (METHOD: *time-*

constrained counts vs. *line transect*) in each of the three habitats, with survey month as a co-

explanatory variable. 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), and assigned

conservation value to each species as calculated by Kunte (2008). We ran regression models on the
number of habitat specialists, endemics and rare species per sample similar to above with METHOD
and MONTH as explanatory variables. Since both 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 (Table 3-4). Since the dataset of endemics and rare species had
excess of zero observations, we ran zero-inflated poisson (ZIP) models using the pscl package in R.
The zero-inflated poisson 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. We used
non-parametric, two-sample Wilcoxon signed-rank test to compare conservation values of species
observed in pairs of sampling methods in each of the three habitats.
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RESULTS
Number of individuals, species, habitat specialists, endemics and rare species observed during
the survey are summarized in Tables 2.
Species richness: Species richness was similar in time-constrained counts and line transects in two
habitats: urban woodland (time-constrained counts = 57 species, lower confidence limit (LCL) = 49.4,
upper confidence limit (UCL) = 64.6; line transects = 51 species, LCL = 46.2, UCL = 55.8), and dry
deciduous forest (time-constrained counts = 87 species, LCL = 79.3, UCL = 94.7; line transects = 87
species, LCL = 79.4, UCL = 94.7) (Fig. 2a-b). Species richness was higher in time-constrained counts
as compared to line transects at the evergreen forest site (time-constrained counts = 122 species, LCL
= 111.3, UCL = 133.5; line transect = 102 species, LCL = 93.8, UCL = 110.2) (Fig. 2c). This could be
partly due to higher number of species observed in the time-constrained counts at mud-puddling spots
and small openings along forest paths as compared to time-constrained counts and line transects along
shaded forest paths (time-constrained counts at mud-puddling spots and forest openings = 92 species,
LCL = 83.1, UCL = 101.3; time-constrained counts along forest paths = 81 species, LCL = 71.6, UCL
= 90.4; line transects = 73 species, LCL = 66.6, UCL = 80.3) (Fig. 2d).
Numbers of species and individuals per sample: Numbers of species and individuals per sample
were similar between time-constrained counts and line transects in all three habitats (Table 3, Fig. 3).
However, there was significant monthly variation in species and abundance per sample in the
evergreen (species: $\chi^2(3)$=32.73, p<0.00; abundance: $\chi^2(3)$=49.71, p<0.00; Fig. 4; Table 3) and dry
deciduous forests (species: $\chi^2(3)$ = 20.57, p<0.00; abundance: $\chi^2(3)$ = 22.76, p<0.00; Fig.4; Table 3).
While the species per sample reduced from Feb–May in the evergreen forest, it increased during the
same period in the dry deciduous forest habitat (Fig. 4; Table 3).
Habitat specialists, rare and endemic species: Numbers of species and individuals of habitat
specialists observed *per sample* were higher in time-constrained counts only in the evergreen forest
(no. of species: Est_{timed}=0.27±0.12, z=2.31, p=0.02; no. of individuals: Est_{timed}=0.35±0.17, z=2.02,
p=0.04) (Table 4, Fig. 3). For rare and endemic species, since 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 for these species only for the evergreen forest. A greater number of endemic species

(but not their abundance) per sample was observed in time-constrained counts as compared to line

transects (Poisson count model coefficients for no. of endemic species: Est_{timed}=0.83±0.41, z=2.02,

p=0.04), while no difference was found for rare species (Table 4, Fig. 3).

Conservation value: We observed no difference in conservation values of species encountered by the

two methods in any of the three habitats (Fig. 3). However, evergreen forest had a greater number and

abundance of species with a high conservation value as compared to dry deciduous forest (Wilcoxon

rank sum test: W=7880, p<0.00) and urban woodland (Wilcoxon rank sum test: W=5532.5, p<0.00),

as revealed by both the survey methods (Fig. 3).

DISCUSSION

231   Long-term butterfly monitoring programmes have generated valuable data on population

232   dynamics and conservation status of butterflies (Warren et al. 2021). Most of these studies have been

233   in temperate countries in Europe. This paper was motivated by the need to develop inexpensive and

234   easily implemented methods for monitoring butterflies in tropical and mountainous areas.

235   We compared two visual-count survey methods, namely, line transects and time-constrained

counts, in three different habitats: (1) evergreen forest, (2) dry deciduous forest, and (3) urban

woodland. We observed similar species richness via time-constrained counts and line transects in the

urban woodland and dry deciduous forest. However, we observed greater species richness via time-

constrained counts in the evergreen forest. We also observed greater number of species and

abundance of habitat specialists, and greater number of species of habitat specialists and endemics *per*

sample, in time-constrained counts as compared to line transects in evergreen forest. These results are

parallel to those from other studies at different scales and habitats (Kadlec et al. 2012; Kral-O'Brien et

al. 2021).

244   Species richness is a widely used index in ecology and conservation, but surprisingly difficult

to measure accurately (Gotelli and 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 (Kéry and Plattner 2007; Nowicki et al. 2008; Isaac et al.

2011; Pellet et al. 2012). Time-constrained counts may improve 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, 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 higher number of habitat specialist and endemic species per sample in time-

constrained counts in the more complex evergreen forest habitat. This was partly due to inclusion of

puddling spots in the surveys, which sampled overall greater numbers of species, habitat specialists,

endemics and rare species as compared to line transects (Table 2). Puddling spots attract

concentrations of many species since 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. On

the other hand, the results of time-constrained counts vs. 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 that can be identified only with close inspection. 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.

Traditionally, bait traps have been used commonly for butterfly surveys in tropical regions,

e.g., to evaluate 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 and

Dietsch 2003). However, bait-trapping is suitable to surveying 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 such as transect counts (Sparrow et al. 1994; Jakubikova and

Kadlec 2015; Kral et al. 2018). Given that time-constrained counts are more efficient at detecting

species and simpler to conduct in complex terrain, this method is particularly suited for studies

requiring occupancy surveys and for mapping butterfly diversity at large scales. Since the survey path

need not be fixed in time-constrained counts, recorders may vary in their search efficiency and

attention paid to particular resources. Observer bias can be minimized by training surveyors prior to

conducting the surveys, and by noting down GPS tracks of surveys. For ecological studies at smaller

spatial scales, given better detectability via time-constrained counts as compared to line transects even

at relatively small study plots (Kadlec et al. 2012), a grid-based, area-proportionate scheme of time-

constrained counts by a team of well-trained recorders could potentially yield high-quality abundance-

based data on butterflies. Such a method is also suitable for projects involving citizen scientists.

It should be noted that both line transects and time-constrained counts represent a measure of

butterfly activity rather than true abundance. These methods also cannot be used to estimate

population sizes without a lot more additional data generated through methods such as capture-mark-

recapture. While line transects standardise effort by length of the transect, time-constrained 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 time-

constrained 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, number of surveys per year will need to be optimized 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 time-constrained counts can be formalised, so that the counts are replicable and comparable across space and time. These may include setting up tracks with GPS locations, time of day, sampling frequency, a predefined set of surveyors, repeated sampling, etc., formalised and 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 and 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 time-constrained count method can be formalised and standardised just as well as line transects and other sampling methods for a given project, although it does appear to be more useful in tropical and mountainous terrains, as discussed above. For more question-driven and goal-oriented research projects, time-constrained counts may be used in conjunction with bait-trapping, capture-mark-recapture and other methods to estimate population sizes or community composition and diversity.

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 time-constrained counts are a viable and perhaps even a superior alternative to line transects for conducting butterfly surveys in tropical and mountainous habitats. Statistical methods to analyse data generated through time-constrained counts are not yet as well developed as those for transects, or they have limited statistical models available for estimation of population sizes and community diversity. However, many of the existing methods may be easily adapted. Considering the difficulty of conducting line transects in tropical and mountainous areas, and the need to develop alternative methods such as time-constrained counts, it will serve the scientific and conservation community to urgently develop these methods. This may prove to be especially important at a time when large amounts of data are being generated through citizen science projects. It is easier to train people in conducting time-constrained counts, and the counts are also easier to implement. So, such data may be more easily formalised for subsequent scientific analysis. Smartphones and citizen science platforms can greatly facilitate these steps.

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Table 1: Total monthly sampling effort per habitat and method (line transect: 500 m, 10 min; time-
constrained counts: 30 min). Evergreen and dry deciduous forests were sampled monthly from Feb-
May, the urban site was sampled from March-May.
459

	Time-constrained counts as, total (paths–puddling spots)	Line transects
Evergreen forest		
Feb	7 (3–4)	21
Mar	9 (4–5)	24
Apr	8 (4–4)	24
May	8 (4–4)	24
Dry deciduous forest		
Feb	7	21
Mar	7	21
Apr	6	18
May	6	18
Urban woodland		
Mar	6	18
Apr	6	18
May	6	18

461 **Table 2:** Total number of species, unique species (observed only in that habitat or method), habitat
462 specialists, endemics and rare species observed via line transects and time-constrained counts at the
463 evergreen forest, dry deciduous forest and urban woodland sites. Measurements for puddling spots are
464 also shown for the evergreen site. Number of individuals are shown in parentheses.
465

	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)
Time-constrained counts	121 (1642)	38 (85)	62 (780)	11 (35)	19 (62)
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)
Time-constrained 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)
Time-constrained counts	57 (402)	18 (19)	10 (30)	0 (0)	0 (0)

		Species per sample				Abundance per sample			
	Variable	Estimate	Std. error	z value	P-value	Estimate	Std. error	z value	P-value
Evergreen forest		(negative binomial)				(negative binomial)			
	Intercept	-0.51	0.09	-5.71	< 0.01	0.87	0.15	5.92	< 0.01
	Time-constrained 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	< 0.01	-1.07	0.18	-6.04	< 0.01
	May	-0.56	0.11	-4.94	< 0.01	-1.26	0.17	-7.24	< 0.01
Dry deciduous forest		(poisson)				(negative binomial)			
	Intercept	2.58	0.08	31.82	< 0.01	3.4	0.1	32.51	< 0.01
	Time-constrained 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	< 0.01
	April	0.31	0.09	3.32	< 0.01	0.65	0.12	5.22	< 0.01
	May	0.43	0.1	4.33	< 0.01	0.54	0.13	4.01	< 0.01
Urban woodland		(negative binomial)				(negative binomial)			
	Intercept	2.26	0.12	18.67	< 0.01	3.16	0.17	18.64	< 0.01
	Time-constrained 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

Table 4: Estimated regression parameters, standard errors, z-values and P-values for the GLMs of the abundance and number of species of habitat specialists observed per sample by the two methods, viz. line transects and time-constrained counts in the three habitats, with month of survey (season) as a covariate. 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.

	Species per sample				Abundance per sample			
Variable	Estimate	Std. error	*z* value	*P*-value	Estimate	Std. error	*z* value	*P*-value
				Habitat specialists				
Evergreen forest	(negative binomial)				(negative binomial)			
Intercept	2.02	0.14	14.85	< 0.01	3.32	0.21	16.15	< 0.01
Time-constrained 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	< 0.01	-0.95	0.25	-3.86	< 0.01
May	-0.39	0.16	-2.45	0.01	-0.87	0.24	-3.65	< 0.01
Dry deciduous forest	(poisson)				(negative binomial)			
Intercept	-0.06	0.3	-0.21	0.83	-0.09	0.33	-0.26	0.79
Time-constrained 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	< 0.01
April	0.7	0.33	2.12	0.03	1.49	0.35	4.24	< 0.01
May	0.77	0.34	2.23	0.03	1.18	0.38	3.15	< 0.01
Urban woodland	(poisson)				(negative binomial)			
Intercept	-0.56	0.44	-1.26	0.21	-0.27	0.45	-0.6	0.55
Time-constrained 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	< 0.01

				Rare species (evergreen site)				
	Count model coefficients (poisson)				Count model coefficients (poisson)			
Intercept	0.83	0.29	2.82	<0.01	1.35	0.21	6.43	<0.01
Time-constrained 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	<0.01	-1.29	0.46	-2.8	<0.01
	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
Time-constrained 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

Table 4. (*contd.*)

	Endemic species (evergreen site)							
	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
Time-constrained 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
Time-constrained 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

Fig. 1: Schematic of a landscape, visualizing the two methods for conducting butterfly surveys i.e.,
line transect (a), and time-constrained count (b). Transects are usually straight lines laid near paths (*p*)
and other landscape features, requiring walking at a uniform pace, during which organisms are
sampled in a fixed area during a fixed timespan. The objective of time-constrained counts is to
actively search an area for butterflies (🦋), often sampling different micro-habitats, 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 time-constrained 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
remains more or less the same irrespective of butterfly density, whereas the physical length of a time-
constrained count may be negatively correlated with butterfly density. A comparison of the attributes
of line transects and time-constrained counts is given below (c).
496

| a. Line transect | b. Time-constrained count |

c. Attributes	Line transect	Time-constrained count
Length	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 transect 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
Index measured	Presence-absence, relative abundance, population density	Presence-absence, relative abundance

Fig. 2: Rarefaction curves with 95% CIs, comparing the species richness observed in line transects and time-constrained counts un urban woodland (a), dry deciduous forest (b), and evergreen forest (c, d) habitats. Continuous lines = interpolation, stippled lines = extrapolation.

506 **Fig. 3:** Boxplots showing total number of species (a), habitat specialists (b), endemics (c) and rare
507 species (d) per sample, and conservation values of species (e) observed via two methods, viz. line
508 transects and time-constrained counts in evergreen forest, dry deciduous forest and urban woodland.
509
510
511

512 **Fig. 4:** Monthly variation in number of species observed per sample in line transects and time-
513 constrained counts in the evergreen and dry deciduous forests. While the species per sample reduced
514 from Feb-May in the evergreen forest, it increased during the same period in the dry deciduous forest
515 habitat.
516

517
518

 SUPPLEMENTARY MATERIAL

520 List of species observed in the study, indicating the habitat where they were observed and their habitat
521 specialization, rarity and endemism. Species names follow Kunte et al. (2021), and conservation
522 values are taken from Kunte (2008).
523

Species	Evergreen forest	Dry deciduous forest	Urban woodland	Habitat specialist	Rare/ Uncommon	Endemic	Conservation value
Family Papilionidae							
Graphium agamemnon	1	1	1	1			18
Graphium antiphates	1			1			23
Graphium doson	1	1	1	1			17
Graphium nomius		1	1				16
Graphium teredon	1			1		1	23
Pachliopta aristolochiae	1	1	1				10
Pachliopta hector	1	1	1				13
Pachliopta pandiyana	1			1		1	28
Papilio clytia	1				1		18
Papilio crino		1					18
Papilio demoleus	1	1	1				10
Papilio dravidarum	1			1		1	28
Papilio helenus	1		1	1			19
Papilio liomedon	1			1		1	28
Papilio paris	1			1			19
Papilio polymnestor	1	1		1			20
Papilio polytes	1	1	1				10
Troides minos	1	1		1		1	23
Family Pieridae							
Appias albina	1	1	1	1			17
Appias lyncida	1			1	1		21
Belenois aurota	1	1	1				13
Catopsilia pomona	1	1	1				13
Catopsilia pyranthe		1	1				11
Cepora nadina	1			1			20
Cepora nerissa	1	1	1				16

Species							
Colotis aurora		1					11
Colotis danae		1					11
Colotis etrida		1					13
Delias eucharis	1	1					12
Eurema blanda	1	1					12
Eurema brigitta		1	1				11
Eurema hecabe	1	1	1				9
Eurema laeta	1	1	1				11
Eurema nilgiriensis	1			1	1	1	40
Hebomoia glaucippe	1	1					15
Ixias marianne		1					16
Ixias pyrene		1		1			18
Leptosia nina	1	1	1				12
Pareronia hippia	1	1	1				16
Prioneris sita	1			1		1	26

Family Nymphalidae

Species							
Acraea terpsicore		1	1				15
Ariadne merione		1	1				11
Athyma inara	1			1	1		28
Athyma ranga	1			1			23
Athyma selenophora	1			1	1		25
Charaxes agrarius		1	1				17
Charaxes bharata	1	1					12
Charaxes psaphon	1						15
Charaxes solon		1					16
Cirrochroa thais	1			1			21
Cupha erymanthis	1			1			18
Cyrestis thyodamas	1			1			19
Danaus chrysippus		1	1				10
Danaus genutia	1	1	1				11
Doleschallia bisaltide	1			1	1		26
Dophla evelina	1			1	1		23
Elymnias caudata	1	1				1	21
Euploea spp.	1	1	1				NA
Euthalia aconthea	1	1	1	1			18

Euthalia lubentina	1	1			1		19
Hypolimnas bolina	1	1	1				11
Hypolimnas misippus	1	1	1				11
Idea malabarica	1			1		1	28
Junonia almana		1					12
Junonia atlites	1	1					13
Junonia hierta		1	1				10
Junonia iphita	1	1	1				13
Junonia lemonias	1	1	1				10
Junonia orithya		1					10
Kallima horsfieldii	1			1		1	23
Lethe europa			1				12
Lethe rohria	1						13
Lethe spp.	1						NA
Melanitis leda	1	1	1				9
Moduza procris	1	1		1			18
Mycalesis mineus		1	1				13
Mycalesis orcha	1			1	1	1	35
Mycalesis perseus	1						12
Mycalesis spp.	1						NA
Mycalesis subdita	1	1		1			23
Neptis hylas	1	1	1				13
Neptis jumbah	1	1	1	1			19
Orsotriaena medus	1			1			19
Pantoporia hordonia	1			1			20
Parantica aglea	1			1			18
Parthenos sylvia	1			1	1		25
Phalanta alcippe	1			1			22
Phalanta phalantha	1	1	1				11
Rohana parisatis	1			1	1		24
Symphaedra nais		1	1				17
Tanaecia lepidea	1			1			18
Tirumala limniace	1	1					12
Tirumala septentrionis	1	1					11
Vanessa cardui		1					9
Vindula erota	1			1			20

Species							
Ypthima asterope	1	1					13
Ypthima baldus	1						12
Ypthima huebneri	1	1	1	1			18
Zipaetis saitis	1			1	1	1	38

Family Riodinidae

Abisara bifasciata	1			1			17

Family Lycaenidae

Acytolepis puspa	1	1	1	1			17
Amblypodia anita	1			1			18
Anthene emolus	1			1	1		21
Anthene lycaenina	1			1			18
Arhopala alea	1			1	1	1	30
Arhopala amantes			1				16
Arhopala bazaloides	1			1	1		25
Azanus jesous		1					11
Azanus ubaldus		1					11
Bindahara moorei	1			1	1		24
Caleta decidia	1						13
Castalius rosimon	1	1	1				13
Catochrysops strabo	1	1	1				16
Celastrina lavendularis	1			1			23
Cheritra freja	1			1			20
Chilades lajus	1	1	1				13
Chilades pandava	1	1	1				16
Chilades parrhasius		1	1				11
Curetis siva	1			1		1	29
Curetis thetis	1	1	1				17
Discolampa ethion		1		1			18
Euchrysops cnejus		1					10
Freyeria putli		1					10
Freyeria trochylus		1					10
Horaga onyx	1			1	1		27
Hypolycaena othona	1			1	1		24
Ionolyce helicon	1	1		1	1		26

	C1	C2	C3	C4	C5	
Jamides bochus	1	1	1			15
Jamides celeno	1	1	1			15
Lampides boeticus	1	1	1			9
Leptotes plinius		1	1			12
Loxura atymnus	1			1		18
Nacaduba beroe	1			1		18
Nacaduba spp.	1					NA
Neopithecops zalmora	1			1		23
Petrelaea dana	1			1		17
Prosotas dubiosa	1	1	1			12
Prosotas nora	1	1	1			12
Prosotas noreia	1			1	1	31
Pseudozizeeria maha	1	1	1			10
Rachana jalindra	1			1	1	28
Rapala iarbus		1				16
Rapala manea		1				16
Rathinda amor	1	1		1		21
Spalgis epeus			1			10
Spindasis lohita	1				1	19
Spindasis vulcanus		1				11
Zizeeria karsandra	1	1	1			9
Zizina otis	1	1	1			10
Zizula hylax	1	1	1			10
Family Hesperiidae						
Ampittia dioscorides	1					12
Badamia exclamationis	1	1				14
Baoris farri	1					23
Caprona agama		1			1	23
Celaenorrhinus spp.	1					NA
Coladenia indrani		1				16
Gomalia elma		1			1	14
Halpe porus			1			22
Hasora chromus	1	1	1			15
Hasora vitta	1				1	19
Hyarotis adrastus	1			1	1	25

Species	C1	C2	C3	C4	C5	Value
Iambrix salsala	1	1	1	1		18
Matapa aria		1	1			16
Notocrypta curvifascia	1			1		19
Oriens goloides	1			1		24
Potanthus spp.	1	1				NA
Pseudocoladenia dan	1			1		17
Psolos fuligo	1			1		24
Sarangesa dasahara	1			1		18
Spialia galba	1	1	1			12
Suastus gremius		1				13
Swift spp. (Baorini)	1		1			NA
Tagiades gana	1			1	1	23
Tagiades japetus	1			1		19
Tagiades litigiosa	1			1		20
Tapena thwaitesi	1			1	1	21
Taractrocera ceramas	1					13
Taractrocera maevius		1				13
Telicota bambusae		1				12
Telicota colon		1				12
Udaspes folus	1					16

526 **Fig S1:** Butterfly habitats sampled in this study: (a) Locations of the three study sites. (b) Urban

527 woodland in the Doresanipalya Forest Research Campus, Bengaluru, (c) Dry deciduous forest at

528 Savanadurga, and (d) Evergreen forest in the Brahmagiri Wildlife Sanctuary, Kodagu.

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