

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

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4 **Running Title:** Timed counts for butterfly monitoring

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6 **Authors:** Attiwilli Suman, Nitin Ravikanthachari, Krushnamegh Kunte

7

8 **Affiliation:** National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK
9 Campus, Bellary Road, Bengaluru 560065, India.

10

11 ***Correspondence:** krushnamegh@ncbs.res.in

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13 **Abstract:**

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

32

33 **Keywords:** butterfly monitoring, butterfly conservation, population sampling methods, biodiversity
34 inventories, citizen science

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37 INTRODUCTION

38 Survey and monitoring of insects is fundamental to their conservation (Kim 1993; Clark and
39 Samways 1996; Brown 1997; Rohr et al. 2007; Leather et al. 2008). Spatial distribution maps
40 obtained through ecological surveys can inform conservation planning and layout of reserves by
41 identifying biogeographic units and areas of high species diversity, endemism or rarity (Kremen et al.
42 1993). The baseline data can also be used to set up monitoring programmes and assess the impact of
43 anthropogenic disturbance on insect populations. This is especially relevant in tropical areas, where
44 diversity of insects is extremely high but resources are scarce to undertake detailed studies of
45 individual species (Braschler et al. 2010, Lewis and Basset 2007). Butterflies are a good target taxon
46 for recording and monitoring because their taxonomy is relatively well-known, and they are
47 conspicuous and relatively easy to identify in the field as compared to other insects (Thomas 2005;
48 Basset et al. 2013).

49 Long-term butterfly monitoring programmes have been remarkably successful in the United
50 Kingdom and Europe (Thomas 2005; van Swaay et al. 2008; Schmeller et al. 2009; Brereton et al.
51 2011). Their objective is to assess regional and national-level trends in abundance of butterfly species
52 (van Swaay et al. 2008). All such programmes employ spatially explicit transects—popularly known
53 in butterfly monitoring schemes as ‘Pollard walks’—in which recorders walk the transects at a
54 uniform pace, counting all butterfly individuals observed within a certain width along the transect line
55 (Pollard and Yates 1994). The transects are predefined, i.e., fixed a priori, and revisited every
56 sampling session. The transect method is popular because it is simple to implement in open, relatively
57 flat habitats with fewer butterfly species and lower population densities, and are easily replicable once
58 the line transects have been identified by experienced butterfly watchers. The protocol allows rapid
59 collection of data on relative abundances of butterflies using a fixed effort. Long-term population
60 monitoring using this method has yielded valuable insights into population and community dynamics
61 of British and European butterflies, including changes in community structure and diversity, and the
62 recent alarming population declines, due to climate change, habitat fragmentation, and habitat
63 alterations from land use practices (Roy and Sparks 2000; Van Dyck et al. 2009; Devictor et al. 2012;
64 Botham et al. 2015; Thackeray et al. 2016; McDermott Long et al. 2017; Mills et al. 2017; van Strien
65 et al. 2019; Warren et al. 2021a; Fourcade et al. 2021). Monitoring schemes of comparable magnitude
66 are lacking in tropical countries and habitats, even though the tropics harbour a much larger
67 proportion of butterfly diversity (Bonebrake et al. 2010).

68 The difficulty is that line transects and related statistical methods for data analysis were
69 originally devised to count large mammals and other conspicuous organisms in simpler habitats.
70 These methods have inherent limitations in monitoring insects in more complex habitats (Spitzer et al.
71 1993; Zhang et al. 2018). For example, line transects require the transect line to be more or less
72 straight, which is nearly impossible to achieve in hilly tropical regions with dense vegetation,
73 sometimes with difficult terrain. Moreover, line transects require recorders to cover the transect length
74 at a uniform pace. Since butterflies and certain other insects are often highly clustered, e.g., at

75 puddling sites in hundreds or thousands, the requirement of uniform pace is easily violated. Such
76 highly clustered occurrence is also not easy to account for in the analysis of line transect data.
77 Besides, the fixed-transect method has been criticized for poor detectability of cryptic, rare or
78 sedentary species (Kadlec et al. 2012; Henry et al. 2015). Certain tropical butterfly genera are difficult
79 to identify on the wing or may be easily missed while walking transects, especially in shaded areas
80 (Walpole and Sheldon 1999; Caldas and Robbins 2003). However, line transects have been conducted
81 at certain sites in tropical rainforests as part of previously established permanent vegetation
82 monitoring plots in slightly more comfortable terrain (Basset et al. 2013).

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

99 Time-constrained counts is an alternative method to line transects for conducting butterfly
100 surveys and population monitoring (Beneš et al. 2003; Kadlec et al. 2012; Taron and Ries 2015; Kral-
101 O'Brien et al. 2021). In time-constrained counts, effort is standardised by time rather than by length of
102 the transect and area under the belt transect. It involves walking a wandering, often a zig-zag path
103 rather than a fixed (more or less) straight line, thoroughly searching an area in the stipulated time,
104 with the goal of maximizing the number of species and individuals observed (Fig. 1). This is
105 accomplished by visiting resource patches—puddling sites, canopy gaps, roosting sites, etc., that are
106 frequented by a diversity of butterfly species—and recording every individual of every species that is
107 encountered. Unlike line transects, the survey path need not be fixed a priori, so it offers more
108 flexibility for rapid surveys at new or even well-established field sites. Time-constrained counts also
109 offer flexibility to navigate difficult terrain because a uniform pace and linear paths are not required,
110 but they can still record spatial and temporal distribution of butterflies or their resources. Time-
111 constrained counts may be especially advantageous in complex, dynamic landscapes, and even in
112 smaller habitat fragments (Taron and Ries 2015). Similar to line transects, time-constrained counts

113 assume that: (a) detectability is certain on the path, (b) counts are exact, (c) variation in the number of
114 individuals counted at different sites or in different seasons truly reflect differences in their population
115 sizes, and (d) butterflies are detected at their initial location (Taron and Ries 2015; Glennie et al.
116 2015). Other assumptions and violations of line transects should also apply, e.g., (a) individual
117 organisms are not going back and forth on sampling paths, therefore they are likely to be counted only
118 once, and (b) species with certain biological characteristics such as crepuscular activity patterns and
119 excellent camouflage, are under-represented. It may be possible to apply some of the statistical
120 methods and models originally developed for data generated through line transects to those generated
121 through time-constrained counts. However, this needs to be specifically tested, and perhaps new
122 statistical models and methods need to be developed for the time-constrained count method as the
123 method becomes more popular with both research scientists and citizen scientists, and large-scale data
124 become available.

125 Our study was motivated by a need to develop and test standardised methods for conducting
126 butterfly surveys in tropical areas such as India, with its complex landscapes and high butterfly
127 diversity. While India is home to four globally recognized biodiversity hotspots and over 1,400
128 butterfly species, large-scale data on the population dynamics of butterflies through seasons and space
129 are scarce, even as anthropogenic pressures on butterfly habitats are mounting. This situation is
130 widespread in other tropical countries as well. At the same time, with the rise in popularity of social
131 media and citizen science initiatives, there is renewed interest in natural history, and an opportunity to
132 engage enthusiastic naturalists to obtain large-scale data on butterfly diversity using standardised
133 protocols. Towards this end, we compared two methods for butterfly surveys (line transects and time-
134 constrained counts) in three habitats: (1) an evergreen forest, (2) a dry deciduous forest, and (3) an
135 urban woodland, in southern India. We evaluated the efficacy of these methods to record the number
136 of species and individuals as well as numbers of rare, endemic or specialist species.

137

138 **MATERIALS AND METHODS**

139 **Survey methods:** We conducted butterfly surveys in three habitats (evergreen forest, dry deciduous
140 forest, urban woodland) (Fig. S1). All three study sites were located in Karnataka state of southern
141 India (Fig. S1). The evergreen forest site (Brahmagiri Wildlife Sanctuary, 181.8 km², altitude 100-
142 1,600 m) is hilly with evergreen and semi-evergreen forests at low and mid-elevations, and grasslands
143 and montane forest patches at higher altitudes. It is a protected area located in the Western Ghats
144 biodiversity hotspot. The dry deciduous forest site (Savandurga State Reserve Forest, 26.6 km²,
145 altitude 750-900 m) is located on the Dakhan (=Deccan) plateau. The urban woodland (Doresanipalya
146 Forest Campus, 0.4 km², altitude ~ 900 m), a reserved forest in the midst of the metropolitan city of
147 Bengaluru, has a mix of native and exotic trees and mixed understorey, criss-crossed by paths used by
148 citizens for morning walks.

149 The three sampling locations have been extensively surveyed for butterfly diversity over the
150 past 11 years, with their butterfly faunas enumerated by a collaborative of professional and citizen

151 scientists (Kunte and Ravikanthachari 2020; Kunte et al. 2020). Building on this robust experience,
152 we wanted to compare the efficacy of the two survey methods in recording species and individuals in
153 representative habitat patches within the three sites. Accordingly, we demarcated survey areas near 19
154 km and 10 km stretches of roads and forest paths at the evergreen and dry deciduous forest sites,
155 respectively. The urban woodland was small and fully accessible and most of it was covered with both
156 the survey methods. At each of the study sites, we surveyed butterflies using two methods for
157 comparison: a) line transects (500 m in length, more or less in a straight line, 10 m in width, 10 m in
158 height, covered in 10 mins), and b) time-constrained counts (length not fixed, covered in 30 mins)
159 (Taron and Ries 2015) (Fig. 1). A single surveyor (NR) with 10 years of experience of watching and
160 sampling butterflies at these locations, walked the line transect and count trails at a steady pace,
161 noting down all the individuals of each species observed. We used GPS (Garmin eTrex Vista HCX) to
162 record the location of the line transects, which were laid near forest trails (Fig 1). In the 30-min time-
163 constrained counts, the surveyor (NR) walked a wandering path depending on the accessibility of
164 terrain, adjusting the pace to the encounter rates of butterflies or their resources, often lingering
165 around host plants, forest streams or canopy gaps that are frequented by butterflies (Fig. 1). To
166 equalize the effort between the two methods, we walked three 10-min line transects immediately
167 before or after every 30-min time-constrained count. We alternated between the two methods in each
168 sampling session and in each habitat patch so that habitat variability did not affect results of a single
169 method.

170 We carried out surveys between 0900 and 1300 hrs on clear, sunny days. We visited the
171 sampling locations for 2–3 days each month and repeated the sampling four times at each location
172 from February to May 2018 (Table 1). The total sampling effort for line transects and time-
173 constrained counts for each habitat is shown in Table 1. The species recorded, their habitat-wise
174 occurrence and conservation values are given in supplementary Table S1. Sampling datasets will be
175 made available on Dryad upon provisional acceptance of the paper.

176 **Statistical analysis:** We used rarefaction to compare the overall number of species observed via time-
177 constrained counts vs. line transects. We used iNext package (Hsieh et al. 2016) in R 3.4.2 (R core
178 team 2017) to compute rarefaction curves with 95% confidence intervals. The sample size-based
179 rarefaction curves with bootstrapped confidence intervals can be used to quantify and compare species
180 richness observed between samples (Chao et al. 2014). We pooled the data from the three 10-min line
181 transects walked immediately before or after the time-constrained counts, and used 30 min as a
182 uniform sampling effort to compare results of the two sampling methods. We computed rarefaction
183 curves for the combined data from the four months of the survey. We used generalized linear models
184 (GLMs) to compare number of species and number of individuals of butterflies recorded per sample
185 (i.e., per 30 mins of line transect or time-constrained count) by the two methods (METHOD: *time-*
186 *constrained counts* vs. *line transect*) in each of the three habitats, with survey month as a co-
187 explanatory variable. For further analysis, we classified butterfly species encountered at the three
188 study sites on the basis of endemism (Western Ghats endemics), rarity (rare or uncommon in the

189 Western Ghats) and habitat specialisation (habitat preference for the endangered evergreen, semi-
190 evergreen, riparian moist deciduous forests, and montane forests and grasslands), and assigned
191 conservation value to each species as calculated by Kunte (2008). We ran regression models on the
192 number of habitat specialists, endemics and rare species per sample similar to above with METHOD
193 and MONTH as explanatory variables. Since both response variables were counts (of either
194 individuals or species) we used poisson regression models with log-link function and negative
195 binomial in case of overdispersion (Table 3-4). Since the dataset of endemics and rare species had
196 excess of zero observations, we ran zero-inflated poisson (ZIP) models using the pscl package in R.
197 The zero-inflated poisson model has two parts: a poisson count model and a logit model for predicting
198 excess zeros. It is thus appropriate to model count data that have an excess of zero counts. We used
199 non-parametric, two-sample Wilcoxon signed-rank test to compare conservation values of species
200 observed in pairs of sampling methods in each of the three habitats.

201

202 **RESULTS**

203 Number of individuals, species, habitat specialists, endemics and rare species observed during
204 the survey are summarized in Table 2. Measures of species diversity, endemism and other parameters
205 relevant for butterfly sampling across the two sampling methods are analysed and compared below.

206 **Species richness:** Species richness was similar in time-constrained counts and line transects in two
207 habitats: urban woodland (time-constrained counts = 57 species, lower confidence limit (LCL) = 49.4,
208 upper confidence limit (UCL) = 64.6; line transects = 51 species, LCL = 46.2, UCL = 55.8), and dry
209 deciduous forest (time-constrained counts = 87 species, LCL = 79.3, UCL = 94.7; line transects = 87
210 species, LCL = 79.4, UCL = 94.7) (Fig. 2a-b). Species richness was higher in time-constrained counts
211 as compared to line transects at the evergreen forest site (time-constrained counts = 122 species, LCL
212 = 111.3, UCL = 133.5; line transect = 102 species, LCL = 93.8, UCL = 110.2) (Fig. 2c). This could be
213 partly due to higher number of species observed in the time-constrained counts at mud-puddling spots
214 and small openings along forest paths as compared to time-constrained counts and line transects along
215 shaded forest paths (time-constrained counts at mud-puddling spots and forest openings = 92 species,
216 LCL = 83.1, UCL = 101.3; time-constrained counts along forest paths = 81 species, LCL = 71.6, UCL
217 = 90.4; line transects = 73 species, LCL = 66.6, UCL = 80.3) (Fig. 2d).

218 **Numbers of species and individuals per sample:** Numbers of species and individuals per sample
219 were similar between time-constrained counts and line transects in all three habitats (Table 3, Fig. 3).
220 However, there was significant monthly variation in species and abundance per sample in the
221 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
222 deciduous forests (species: $\chi^2(3) = 20.57$, $p<0.00$; abundance: $\chi^2(3) = 22.76$, $p<0.00$; Fig.4; Table 3).
223 While the species per sample reduced from Feb–May in the evergreen forest, it increased during the
224 same period in the dry deciduous forest habitat (Fig. 4; Table 3).

225 **Habitat specialists, rare and endemic species:** Numbers of species and individuals of habitat
226 specialists observed *per sample* were higher in time-constrained counts only in the evergreen forest

227 (no. of species: $Est_{\text{timed}}=0.27\pm 0.12$, $z=2.31$, $p=0.02$; no. of individuals: $Est_{\text{timed}}=0.35\pm 0.17$, $z=2.02$,
228 $p=0.04$) (Table 4, Fig. 3). For rare and endemic species, since the overall abundance in the dry
229 deciduous forest and urban woodland was extremely low (rare species: dry deciduous forest=7, urban
230 woodland=0; endemic species: dry deciduous forest=0, urban woodland=0; Table 2), we conducted
231 further analysis for these species only for the evergreen forest. A greater number of endemic species
232 (but not their abundance) per sample was observed in time-constrained counts as compared to line
233 transects (Poisson count model coefficients for no. of endemic species: $Est_{\text{timed}}=0.83\pm 0.41$, $z=2.02$,
234 $p=0.04$), while no difference was found for rare species (Table 4, Fig. 3).

235 **Conservation value:** We observed no difference in conservation values of species encountered by the
236 two methods in any of the three habitats (Fig. 3). However, evergreen forest had a greater number and
237 abundance of species with a high conservation value as compared to dry deciduous forest (Wilcoxon
238 rank sum test: $W=7880$, $p<0.00$) and urban woodland (Wilcoxon rank sum test: $W=5532.5$, $p<0.00$),
239 as revealed by both the survey methods (Fig. 3).

240

241 **DISCUSSION**

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

246 We compared two visual-count survey methods, namely, line transects and time-constrained
247 counts, in three different habitats: (1) evergreen forest, (2) dry deciduous forest, and (3) urban
248 woodland. We observed similar species richness via time-constrained counts and line transects in the
249 urban woodland and dry deciduous forest. However, we observed greater species richness via time-
250 constrained counts in the evergreen forest. We also observed greater number of species and
251 abundance of habitat specialists, and greater number of species of habitat specialists and endemics *per*
252 *sample*, in time-constrained counts as compared to line transects in evergreen forest. These results are
253 parallel to those from other studies at different scales and habitats (Kadlec et al. 2012; Kral-O'Brien et
254 al. 2021).

255 Species richness is a widely used index in ecology and conservation, but surprisingly difficult
256 to measure accurately (Gotelli and Colwell 2001). Raw species counts underestimate species richness
257 due to many species remaining undetected. Moreover, detectability varies between species and
258 observers and over space, time and habitats (Kéry and Plattner 2007; Nowicki et al. 2008; Isaac et al.
259 2011; Pellet et al. 2012). Time-constrained counts may improve detectability of species by enabling
260 the surveyor to search a habitat more thoroughly at a pace adapted for local habitat conditions or to
261 species being sampled, and spending more time where butterflies may be concentrated. This may be
262 especially true for rare, cryptic or specialist species, and those that are difficult to identify in flight.
263 Our study detected higher number of habitat specialist and endemic species per sample in time-
264 constrained counts in the more complex evergreen forest habitat. This was partly due to inclusion of

265 puddling spots in the surveys, which sampled overall greater numbers of species, habitat specialists,
266 endemics and rare species as compared to line transects (Table 2). Puddling spots attract
267 concentrations of many species since they are a crucial resource for butterflies, including species that
268 may be easily missed in line transects, such as smaller-sized, fast-flying or largely canopy species. On
269 the other hand, the results of time-constrained counts vs. line transects were similar in less structurally
270 complex habitats (dry deciduous forest and urban woodland), where the possibility of missing canopy
271 species is smaller, and there are fewer species that can be identified only with close inspection. Thus,
272 taking a non-linear path, paying particular attention to butterfly resources such as nectar/host plants,
273 wet soil, tree sap, and rotting fruit, crabs or fish may indeed improve species detection and lead to
274 better estimates of species richness in complex, species-rich habitats.

275 Traditionally, bait traps have been used commonly for butterfly surveys in tropical regions,
276 e.g., to evaluate effects of natural disturbance such as tree-fall gaps (Hill et al. 2001; Pardonnet et al.
277 2013), vertical stratification of butterfly communities (Fermon et al. 2003; Molleman et al. 2006),
278 forest fragmentation (Uehara-Prado et al. 2007), and intensification within agroecosystems (Mas and
279 Dietsch 2003). However, bait-trapping is suitable to surveying a narrow range of subfamilies and
280 genera within one family (Nymphalidae). This method is not suitable to sample larger butterfly
281 communities, and this method can also not scale up over large areas. Hence, bait-trapping is
282 complementary to visual census methods such as transect counts (Sparrow et al. 1994; Jakubikova and
283 Kadlec 2015; Kral et al. 2018). Given that time-constrained counts are more efficient at detecting
284 species and simpler to conduct in complex terrain, this method is particularly suited for studies
285 requiring occupancy surveys and for mapping butterfly diversity at large scales. Since the survey path
286 need not be fixed in time-constrained counts, recorders may vary in their search efficiency and
287 attention paid to particular resources. Observer bias can be minimized by training surveyors prior to
288 conducting the surveys, and by noting down GPS tracks of surveys. For ecological studies at smaller
289 spatial scales, given better detectability via time-constrained counts as compared to line transects even
290 at relatively small study plots (Kadlec et al. 2012), a grid-based, area-proportionate scheme of time-
291 constrained counts by a team of well-trained recorders could potentially yield high-quality abundance-
292 based data on butterflies. Such a method is also suitable for projects involving citizen scientists.

293 It should be noted that both line transects and time-constrained counts represent a measure of
294 butterfly activity rather than true abundance. These methods also cannot be used to estimate
295 population sizes without a lot more additional data generated through methods such as capture-mark-
296 recapture. While line transects standardise effort by length of the transect, time-constrained counts do
297 so by time expended. Thus, many of the methodological factors that influence counts of butterflies in
298 line transects (including pollard walks, discussed in Basset et al. 2013) are equally applicable to time-
299 constrained counts. For example, environmental factors such as ambient temperature, wind velocity
300 and elevation, may need to be either controlled for during survey efforts (van Swaay et al. 2008), or
301 measured and accounted for during statistical analysis (Basset et al. 2013). Seasonal variation can also
302 considerably affect butterfly numbers. We found significant seasonal variation in butterfly abundance

303 at our study sites. Thus, depending on the goals of the study, number of surveys per year will need to
304 be optimized for adequate representation of seasonal variation (Basset et al. 2013). Similarly, for large
305 areas, sampling locations must be representative of all the habitats in the area (Basset et al. 2013). For
306 mapping and monitoring studies at local and/or large spatial scales, protocols for time-constrained
307 counts can be formalised, so that the counts are replicable and comparable across space and time.
308 These may include setting up tracks with GPS locations, time of day, sampling frequency, a
309 predefined set of surveyors, repeated sampling, etc., formalised and agreed to by a research team for
310 long-term monitoring. The strictness of the methodological criteria for monitoring should depend on
311 the scope of the monitoring programme (Lindenmayer and Likens 2010), such as whether it is
312 conducted at local or regional scales (Chiarucci et al. 2011; Scheiner et al. 2011), and whether
313 professional or citizen scientists are involved in a formalised, centrally coordinated project. In
314 general, more question-driven and goal-oriented monitoring programmes would require stricter design
315 criteria. In any case, the time-constrained count method can be formalised and standardised just as
316 well as line transects and other sampling methods for a given project, although it does appear to be
317 more useful in tropical and mountainous terrains, as discussed above. For more question-driven and
318 goal-oriented research projects, time-constrained counts may be used in conjunction with bait-
319 trapping, capture-mark-recapture and other methods to estimate population sizes, community
320 composition, and species diversity (Taron and Ries 2015).

321 Based on our findings as well as those of other recent studies (Kadlec et al. 2012; Kral-
322 O'Brien et al. 2021), we conclude that time-constrained counts are a viable and perhaps even a
323 superior alternative to line transects for conducting butterfly surveys and to monitor butterfly
324 populations in tropical and mountainous habitats. Statistical methods to analyse data generated
325 through time-constrained counts are not yet as well developed as those for transects, or they have
326 limited statistical models available for estimation of population sizes and community diversity.
327 However, many of the existing methods may be easily adapted. Considering the difficulty of
328 conducting line transects in tropical and mountainous areas, and the need to develop alternative
329 methods such as time-constrained counts, it will serve the scientific and conservation community to
330 urgently develop these methods. This may prove to be especially important at a time when large
331 amounts of data are being generated through citizen science projects. It is easier to train people in
332 conducting time-constrained counts, and the counts are also easier to implement. So, such data may be
333 more easily formalised for subsequent scientific analysis. Smartphones and citizen science platforms
334 can greatly facilitate these steps.

335

336 **Acknowledgements:** We thank Tarun Karmakar, Minoti Asher, Swathi H. A., Santosh Hatti, and
337 Nagesh Gowda for assistance in the field, and Karnataka Forest Department for research permission
338 (letter no. PCCF/WL/E2/CR/227/2014-2015 dated 26/05/2017) to carry out this study, for which we
339 thank the Principal Chief Conservator of Forest (Wildlife) and field officers of the state. This work
340 was funded by an NCBS Bridging Fellowship to SA, and a research grant from NCBS to KK.

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- 485

486 **Table 1:** Total monthly sampling effort per habitat and method (line transect: 500 m, 10 min; time-
487 constrained counts: 30 min). Evergreen and dry deciduous forests were sampled monthly from Feb-
488 May, the urban site was sampled from March-May.
489

	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

490

491 **Table 2:** Total number of species, unique species (observed only in that habitat or method), habitat
 492 specialists, endemics and rare species observed via line transects and time-constrained counts at the
 493 evergreen forest, dry deciduous forest and urban woodland sites. Measurements for puddling spots are
 494 also shown for the evergreen site. Number of individuals recorded are shown in parentheses after the
 495 species numbers.
 496

	Total no. of species (individuals)	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)

497

498 **Table 3:** Estimated regression parameters, standard errors, z-values and P-values for the GLMs of the
 499 abundance and number of species observed per sample by the two methods, viz. line transects and
 500 time-constrained counts at the three habitats, with month of survey (season) as a covariate. Intercept
 501 represents line transects in February for evergreen and dry deciduous forest and March for urban
 502 woodland.
 503

		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

504

505

506 **Table 4:** Estimated regression parameters, standard errors, z-values and P-values for the GLMs of the
 507 abundance and number of species of habitat specialists observed per sample by the two methods, viz.
 508 line transects and time-constrained counts in the three habitats, with month of survey (season) as a
 509 covariate. The same analysis was repeated for rare and endemic species at the evergreen forest site
 510 using zero-inflated poisson (ZIP) regression. Intercept represents line transects in February for
 511 evergreen and dry deciduous forests and March for urban woodland.
 512


		Species per sample				Abundance per sample			
Variable		Estimate	Std. error	z value	P-value	Estimate	Std. error	z value	P-value
<i>Habitat specialists</i>									
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
<i>Rare species (evergreen site)</i>									
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	

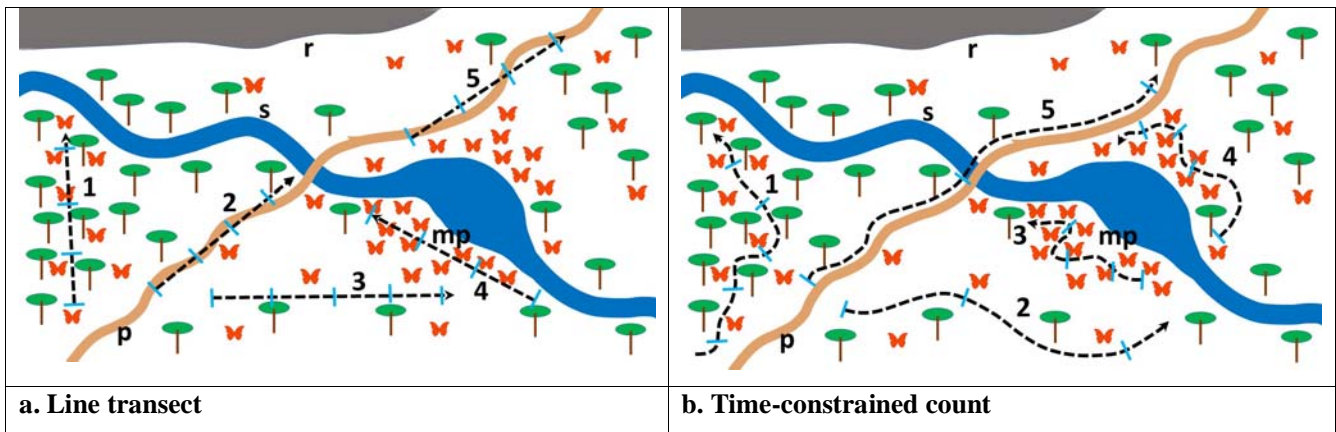
Table 4. (*contd.*)

<i>Endemic species (evergreen site)</i>								
	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

513

514

515 **Fig. 1:** Schematic of a landscape, visualizing the two methods for conducting butterfly surveys i.e.,
 516 line transect (a), and time-constrained count (b). Transects are usually straight lines laid near paths (*p*)
 517 and other landscape features, requiring walking at a uniform pace, during which organisms are
 518 sampled in a fixed area during a fixed timespan. The objective of time-constrained counts is to
 519 actively search an area for butterflies () , often sampling different micro-habitats, such as vegetation,
 520 rocky outcrops (*r*), stream-sides (*s*) and mud-puddling spots (*mp*), while keeping a fixed length of
 521 time as a unit of sampling but not the area. In a time-constrained count, a surveyor would spend more
 522 time in a patch where butterfly density is higher, whereas in a line transect the surveyor would
 523 normally be expected to maintain pace irrespective of butterfly density. As a result, the transect length
 524 remains more or less the same irrespective of butterfly density, whereas the physical length of a time-
 525 constrained count may be negatively correlated with butterfly density. A comparison of the attributes
 526 of line transects and time-constrained counts is given below (c).
 527



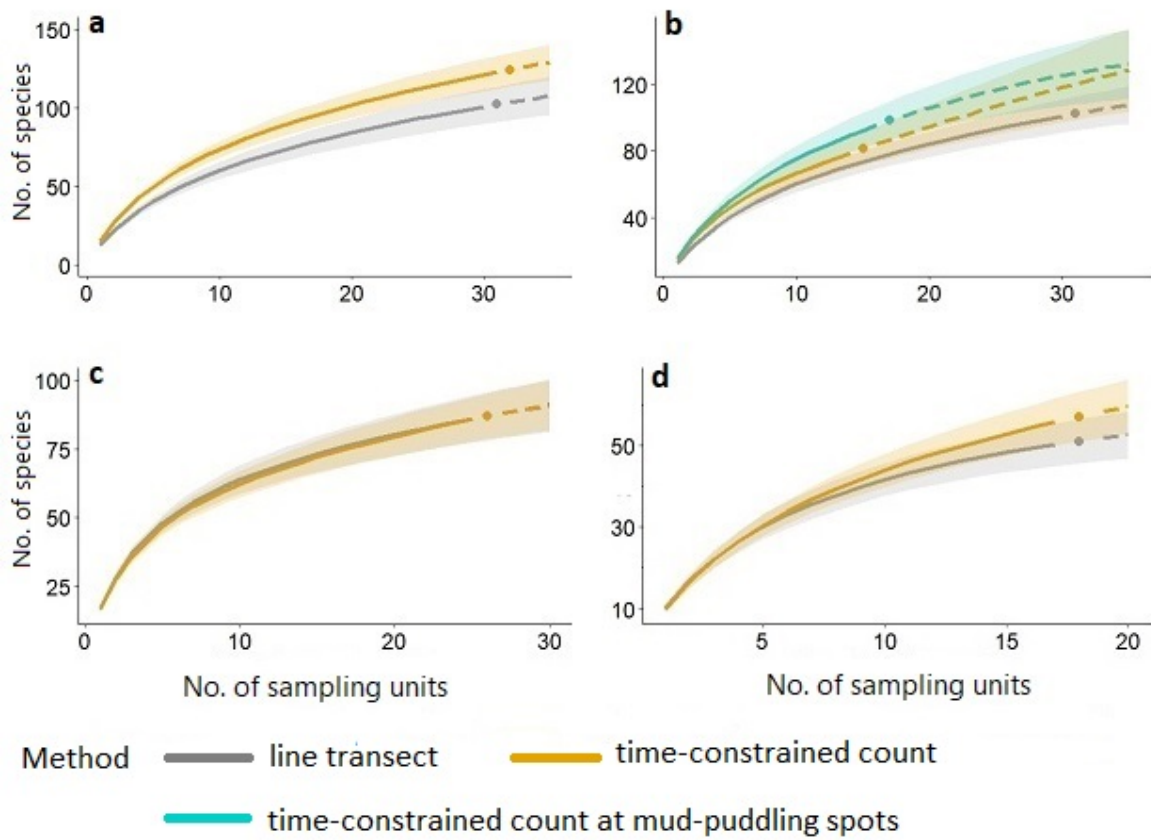
528

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

529

530

531 **Fig. 2:** Rarefaction curves with 95% CIs, comparing the species richness observed in line transects
532 and time-constrained counts un urban woodland (a), dry deciduous forest (b), and evergreen forest (c),
533 d) habitats. Continuous lines = interpolation, stippled lines = extrapolation.
534

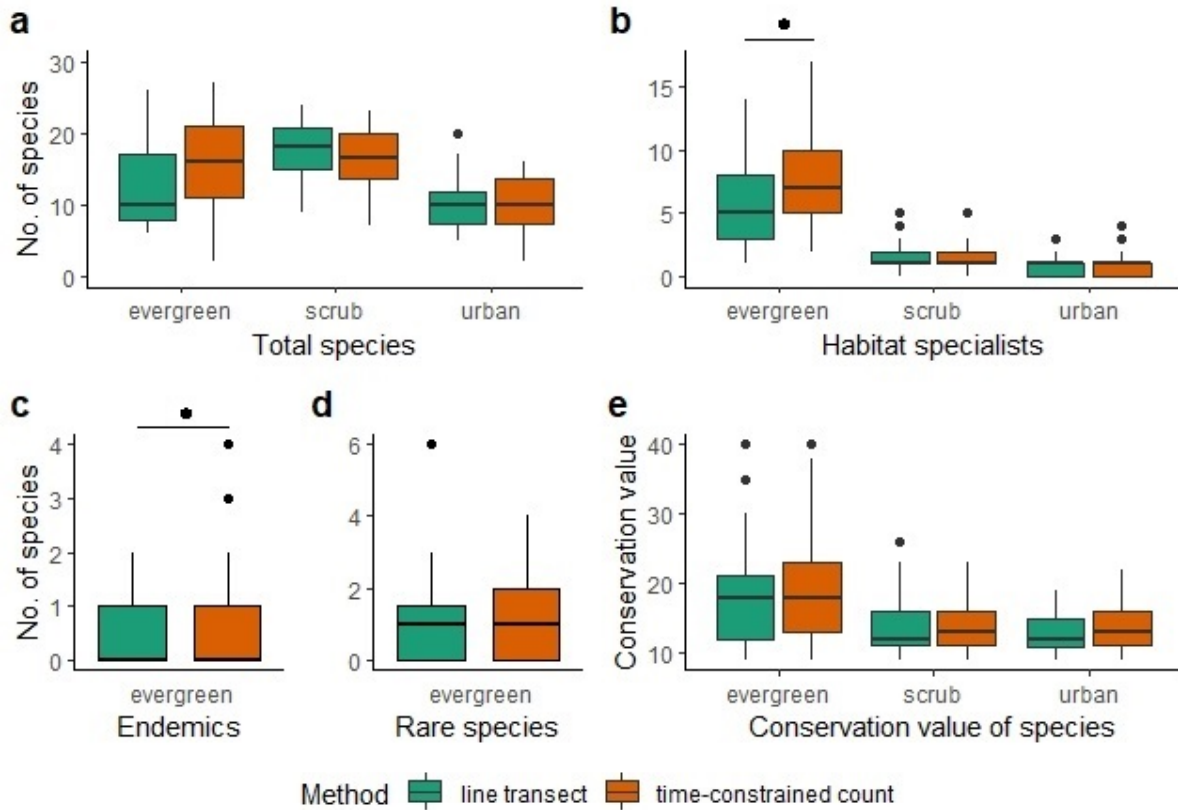


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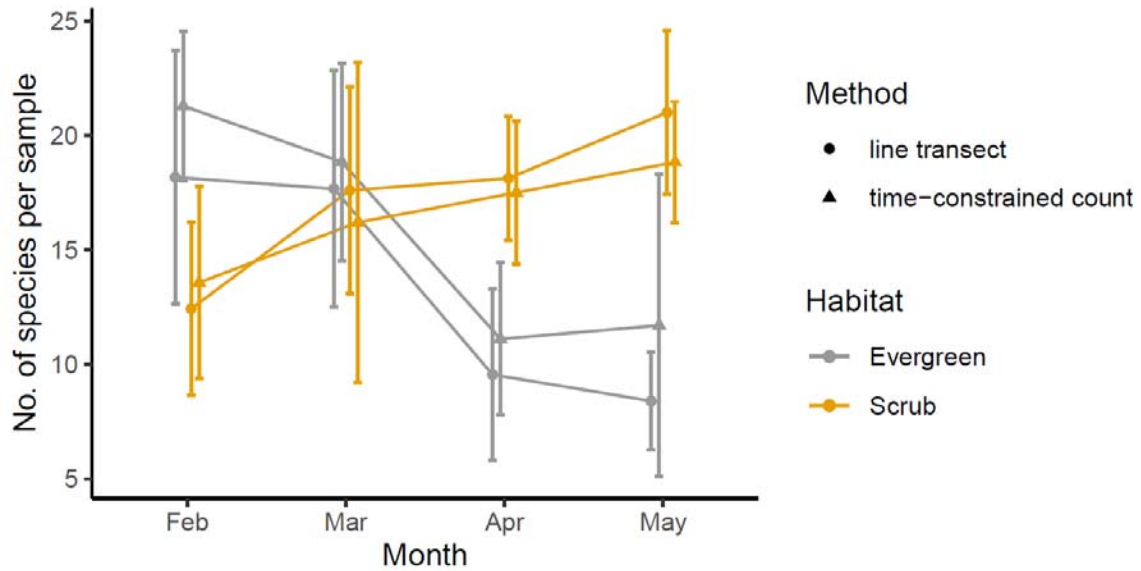
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537 **Fig. 3:** Boxplots showing total number of species (a), habitat specialists (b), endemics (c) and rare
538 species (d) per sample, and conservation values of species (e) observed via two methods, viz. line
539 transects and time-constrained counts in evergreen forest, dry deciduous forest and urban woodland.
540

541
542



543 **Fig. 4:** Monthly variation in number of species observed per sample in line transects and time-
544 constrained counts in the evergreen and dry deciduous forests. While the species per sample reduced
545 from Feb-May in the evergreen forest, it increased during the same period in the dry deciduous forest
546 habitat.
547



548

549

550 **SUPPLEMENTARY MATERIAL**

551

552 **Table S1.** List of species observed in the study, indicating the habitat where they were observed and
 553 their habitat specialization, rarity and endemism. Species names follow Kunte et al. (2021), and
 554 conservation values are taken from Kunte (2008).
 555

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

<i>Cepora nerissa</i>	1	1	1				16
<i>Colotis aurora</i>		1					11
<i>Colotis danae</i>		1					11
<i>Colotis etrida</i>		1					13
<i>Delias eucharis</i>	1	1					12
<i>Eurema blanda</i>	1	1					12
<i>Eurema brigitta</i>		1	1				11
<i>Eurema hecabe</i>	1	1	1				9
<i>Eurema laeta</i>	1	1	1				11
<i>Eurema nilgiriensis</i>	1			1	1	1	40
<i>Hebomoia glaucippe</i>	1	1					15
<i>Ixias marianne</i>		1					16
<i>Ixias pyrene</i>		1		1			18
<i>Leptosia nina</i>	1	1	1				12
<i>Pareronia hippia</i>	1	1	1				16
<i>Prioneris sita</i>	1			1		1	26
Family Nymphalidae							
<i>Acraea terpsicore</i>		1	1				15
<i>Ariadne merione</i>		1	1				11
<i>Athyma inara</i>	1			1	1		28
<i>Athyma ranga</i>	1			1			23
<i>Athyma selenophora</i>	1			1	1		25
<i>Charaxes agrarius</i>		1	1				17
<i>Charaxes bharata</i>	1	1					12
<i>Charaxes psaphon</i>	1						15
<i>Charaxes solon</i>		1					16
<i>Cirrochroa thais</i>	1			1			21
<i>Cupha erymanthis</i>	1			1			18
<i>Cyrestis thyodamas</i>	1			1			19
<i>Danaus chrysippus</i>		1	1				10
<i>Danaus genutia</i>	1	1	1				11
<i>Doleschallia bisaltide</i>	1			1	1		26
<i>Dophla evelina</i>	1			1	1		23
<i>Elymnias caudata</i>	1	1				1	21
<i>Euploea spp.</i>	1	1	1				NA

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

<i>Vindula erota</i>	1			1			20
<i>Ypthima asterope</i>	1	1					13
<i>Ypthima baldus</i>	1						12
<i>Ypthima huebneri</i>	1	1	1	1			18
<i>Zipaetis saitis</i>	1			1	1	1	38
Family Riodinidae							
<i>Abisara bifasciata</i>	1			1			17
Family Lycaenidae							
<i>Acytolepis puspa</i>	1	1	1	1			17
<i>Amblypodia anita</i>	1			1			18
<i>Anthene emolus</i>	1			1	1		21
<i>Anthene lycaenina</i>	1			1			18
<i>Arhopala alea</i>	1			1	1	1	30
<i>Arhopala amantes</i>			1				16
<i>Arhopala bazaloides</i>	1			1	1		25
<i>Azanus jesous</i>		1					11
<i>Azanus ubaldus</i>		1					11
<i>Bindahara moorei</i>	1			1	1		24
<i>Caleta decidia</i>	1						13
<i>Castalius rosimon</i>	1	1	1				13
<i>Catochrysops strabo</i>	1	1	1				16
<i>Celastrina lavendularis</i>	1			1			23
<i>Cheritra freja</i>	1			1			20
<i>Chilades lajus</i>	1	1	1				13
<i>Chilades pandava</i>	1	1	1				16
<i>Chilades parrhasius</i>		1	1				11
<i>Curetis siva</i>	1			1		1	29
<i>Curetis thetis</i>	1	1	1				17
<i>Discolampa ethion</i>		1		1			18
<i>Euchrysops cnejus</i>		1					10
<i>Freyeria putli</i>		1					10
<i>Freyeria trochylus</i>		1					10
<i>Horaga onyx</i>	1			1	1		27
<i>Hypolycaena othona</i>	1			1	1		24

<i>Ionolyce helicon</i>	1	1		1	1	26
<i>Jamides bochus</i>	1	1	1			15
<i>Jamides celeno</i>	1	1	1			15
<i>Lampides boeticus</i>	1	1	1			9
<i>Leptotes plinius</i>		1	1			12
<i>Loxura atymnus</i>	1			1		18
<i>Nacaduba beroe</i>	1			1		18
<i>Nacaduba</i> spp.	1					NA
<i>Neopithecops zalmora</i>	1			1		23
<i>Petrelaea dana</i>	1			1		17
<i>Prosotas dubiosa</i>	1	1	1			12
<i>Prosotas nora</i>	1	1	1			12
<i>Prosotas noreia</i>	1			1	1	31
<i>Pseudozizeeria maha</i>	1	1	1			10
<i>Rachana jalindra</i>	1			1	1	28
<i>Rapala iarbus</i>		1				16
<i>Rapala manea</i>		1				16
<i>Rathinda amor</i>	1	1		1		21
<i>Spalgis epeus</i>			1			10
<i>Spindasis lohita</i>	1				1	19
<i>Spindasis vulcanus</i>		1				11
<i>Zizeeria karsandra</i>	1	1	1			9
<i>Zizina otis</i>	1	1	1			10
<i>Zizula hylax</i>	1	1	1			10

Family Hesperidae

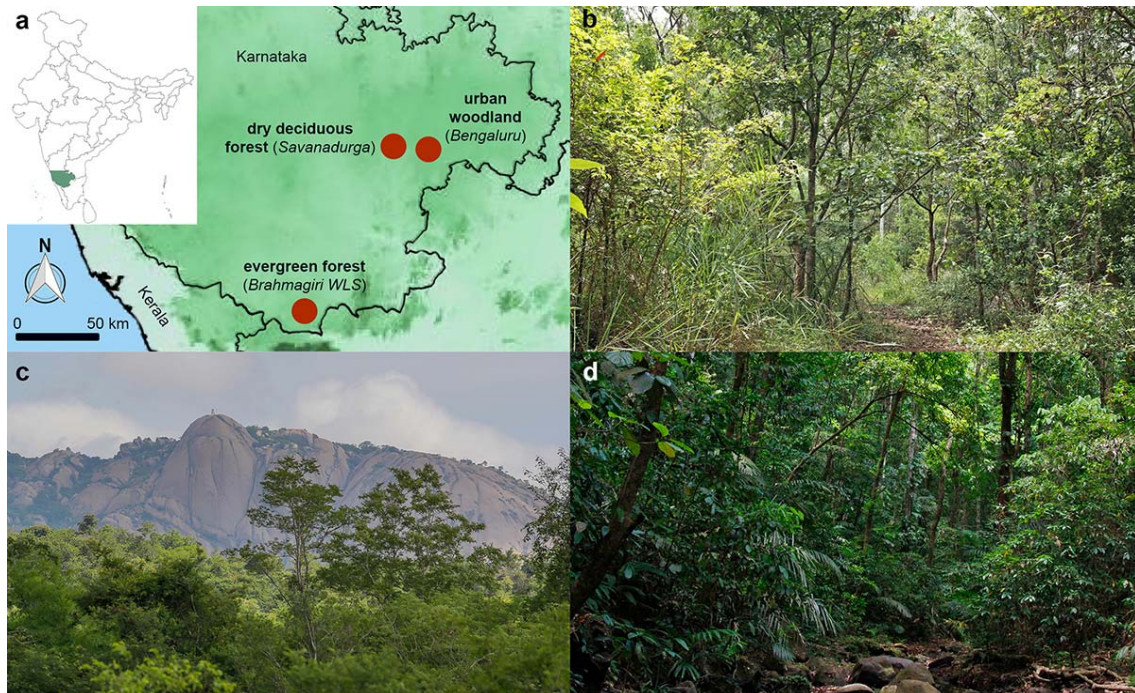
<i>Ampittia dioscorides</i>	1					12
<i>Badamia exclamationis</i>	1	1				14
<i>Baoris farri</i>	1					23
<i>Caprona agama</i>		1			1	23
<i>Celaenorrhinus</i> spp.	1					NA
<i>Coladenia indrani</i>		1				16
<i>Gomalia elma</i>		1			1	14
<i>Halpe porus</i>			1			22
<i>Hasora chromus</i>	1	1	1			15
<i>Hasora vitta</i>	1				1	19

<i>Hyarotis adrastus</i>	1			1	1	25
<i>Iambrix salsala</i>	1	1	1	1		18
<i>Matapa aria</i>		1	1			16
<i>Notocrypta curvifascia</i>	1			1		19
<i>Oriens goloides</i>	1			1		24
<i>Potanthus</i> spp.	1	1				NA
<i>Pseudocoladenia dan</i>	1			1		17
<i>Psolos fuligo</i>	1			1		24
<i>Sarangesa dasahara</i>	1			1		18
<i>Spialia galba</i>	1	1	1			12
<i>Suastus gremius</i>		1				13
Swift spp. (Baorini)	1		1			NA
<i>Tagiades gana</i>	1			1	1	23
<i>Tagiades japedus</i>	1			1		19
<i>Tagiades litigiosa</i>	1			1		20
<i>Tapena thwaitesi</i>	1			1	1	21
<i>Taractrocera ceramas</i>	1					13
<i>Taractrocera maevius</i>		1				13
<i>Telicota bambusae</i>		1				12
<i>Telicota colon</i>		1				12
<i>Udaspes folus</i>	1					16

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558 **Fig S1:** Butterfly habitats sampled in this study: (a) Locations of the three study sites. (b) Urban
559 woodland in the Doresanipalya Forest Research Campus, Bengaluru, (c) Dry deciduous forest at
560 Savanadurga, and (d) Evergreen forest in the Brahmagiri Wildlife Sanctuary, Kodagu.
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