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RESEARCH ARTICLE

Butterflies respond to habitat disturbance in tropical forests through activity shifts

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Abstract

1. Habitat disturbance can alter the dynamics of the forest microclimate by disrupting the canopy structure, particularly in structurally complex tropical forests. These changes may impact ectotherms, of which performance and fitness are highly sensitive to climatic conditions. Behavioural responses, such as changes in activities, may help buffer forest ectotherms like butterflies from microclimate changes in disturbed tropical forests.
2. Using field surveys from four tropical forest sites in Asia, we compared flight activity peaks, durations and intensity for populations of 21 forest-associated butterfly species between open-canopy and closed-canopy forests. We then compared the temperature and illumination that each species experienced during its activity period between the two forest types.
3. Although butterfly populations began their activity earlier and reached peak levels sooner in open-canopy forests compared to closed-canopy forests, the duration and intensity of activity remained similar across populations. Despite these shifts in activity timing between forest types, butterflies experienced comparable temperature conditions in both forest types, but were exposed to higher illumination levels in open-canopy forests.
4. Overall, we demonstrate that tropical butterflies can compensate for microclimate changes in tropical forests by shifting their activity patterns. This may help butterflies buffer against temperature increases but not against higher illumination levels following forest canopy opening due to habitat disturbance. Our results emphasize the importance of understanding how animal activity responds to habitat disturbance.

KEYWORDS
activity pattern, habitat disturbance, insects, microclimate, tropical forest

1 | INTRODUCTION

The structure and microclimates of intact forests are complex and diverse (Scheffers et al., 2017). High microclimate heterogeneity of intact forests provides thermal refugia for diverse groups of forest dwellers (Senior et al., 2018; Woods et al., 2015), particularly in the tropics where ectotherms are under greater thermal stress under climate change (Giam, 2017; Hoang & Kanemoto, 2021; Scheffers et al., 2014; Zellweger et al., 2020). However, this buffering effect may diminish with habitat disturbance caused by human activity and extreme climatic events (Marsh et al., 2025; Senior et al., 2017; but see Senior et al., 2018), which can reduce canopy cover and vegetation complexity, thereby simplifying the biotic and abiotic environments within forests (Santos et al., 2024; Senior et al., 2017).

When forest canopies become open, more sunlight heats the forest understories, and the buffering effects of closed-canopy forests are diminished (Senior et al., 2018). In general, open-canopy forests are hotter and brighter than intact forests with closed canopies (Pfeifer et al., 2019; Senior et al., 2017). Additionally, due to the buffering effect of multiple layers and complex vegetation structures, the peak of daily temperature usually lags behind daily illumination peaks in the understorey of tropical forests (von Arx et al., 2012). However, such mismatches between temperature peaks and illumination peaks are expected to be smaller in open-canopy forests (Reserve & Reserve, 2005; Figure 1a,b).

For many species, both temperature and illumination are important abiotic factors shaping performance, especially for ectotherms. Extreme high temperatures may alter activity patterns (i.e. peak/duration/intensity in activity) across a wide range of taxa including tiger beetles (Dreisig, 1979); tenebrionid beetles (Kenagy & Stevenson, 1982); ants (Wetterer, 1990); stingless bees (Heard & Hendrikz, 1993); lizards (Grant & Dunham, 1988); and butterflies (Agosta et al., 2017; Roland, 1982). While air temperature is known to be a key factor shaping activity intensity and duration for ectotherms (Franzén et al., 2022; Gunderson & Leal, 2015; Xing et al., 2016), the effects of solar radiation—the primary driver of air temperature changes (hereafter referred to as illumination)—on ectotherm activity have been largely overlooked (Niesenbaum & Kluger, 2006). Compared to temperature, illumination can affect ectotherm activity differently, which often serves as a cue for initiating and ceasing activities (Liao et al., 2017; Saunders, 2009; Seymoure, 2018). For diurnal ectotherms, activity often starts earlier or ceases later under higher illumination (Liao et al., 2017). However, the role of air temperature and illumination, together with their interactions, in influencing species activity patterns along forest canopy openness is understudied.

The activity of a species is closely linked to vital ecological processes that impact its performance and fitness, such as dispersal and mating (Kingsolver, 1983; Saastamoinen & Hanski, 2008). Species can also adjust their activity patterns to optimize resource use based on the suitability of environmental conditions (Vitt et al., 2005). Activity responses of ectotherms to microclimate changes suggest that species may exhibit a certain level of thermoregulatory behaviours, allowing them to adapt to a limited range of environmental fluctuations (Abram et al., 2017; Huey et al., 2003; Logan et al., 2015). Many insects, particularly butterflies, are not only known to be sensitive to temperature and illumination changes but can also adjust their behaviour to buffer extreme temperatures (Laird-Hopkins et al., 2023; Wenda et al., 2021). Through behaviour responses such as microclimate selection, basking and activity shifts (Abram et al., 2017), ectothermic species are able to cope with environmental changes such as climatic stress from microhabitat to elevational scale (Sun et al., 2020; Wang et al., 2024; Wenda et al., 2021), as well as climate change impacts (Bladon et al., 2020; Bonebrake et al., 2014). Understanding how activity patterns change in response to microclimate alterations caused by habitat disturbance may reveal the mechanisms through which such disturbances impact population dynamics, species performance, and ultimately, its ecological function (Bladon et al., 2020; Cosset et al., 2021). Here, we surveyed forest-associated butterflies in understories of four tropical forest sites. Using hourly-repeated field surveys, we quantified the differences in butterfly activity patterns between cooler and dimmer closed-canopy forests (hereafter referred to as closed forests) and adjacent hotter and brighter open-canopy forests (hereafter referred to as open forests). We compared flight activity peak, duration and intensity for each butterfly species between populations from closed and open forest, and explored whether such activity differences were likely in response to different temperature or illumination profiles within these forests. We expected that changes in temperature and light condition regimes with forest openness may alter the activity patterns of butterflies. We hypothesized that: (1) forest-associated butterfly species shift activity times earlier (start activity earlier, peak earlier) in open forests than in closed forests (Figure 1c); (2) forest-associated butterfly species exhibit differences in activity duration and intensity between closed and open forests (Figure 1d); and (3) the above differences in activity patterns between forest types are non-random and associated with air temperature and/or illumination differences (Figure 1e).

2 | MATERIALS AND METHODS

2.1 | Study sites and field sampling

We conducted intensive surveys of flight activities for adult butterflies at four lowland sites in tropical Asia. These sites are biodiversity hotspots and widely distributed across tropical Asia: Tai Po Kau Nature Reserve, Hong Kong S.A.R, China (TPK; 22° N 114° E); Xishuangbanna Tropical Botanical Garden, Yunnan, China (XTBG; 21° N 100° E);

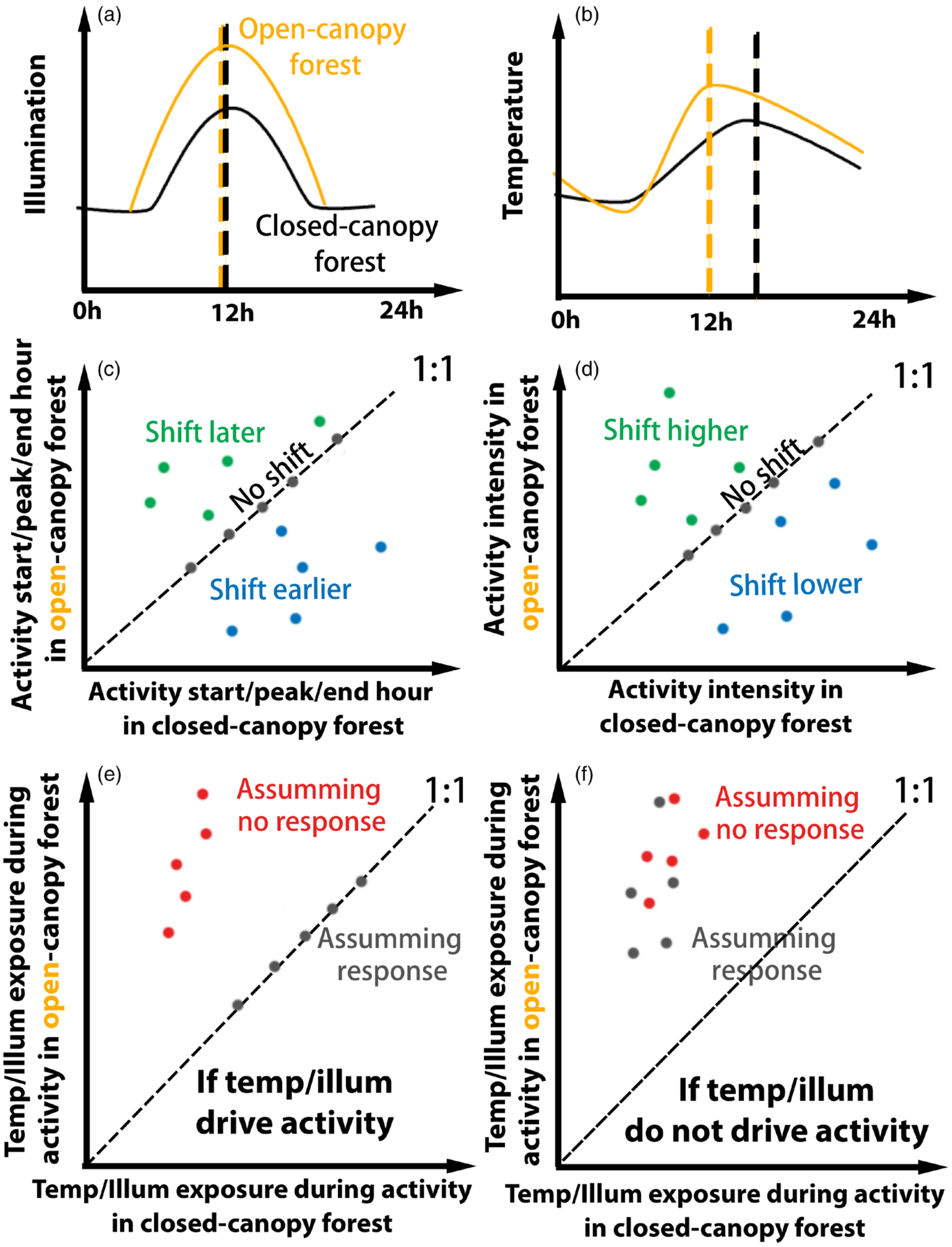

FIGURE 1 Hypothetical illustrations of abiotic environment and activity differences between open and closed forests. Each dot represents a butterfly population of the same species found in both forest types at the same locality. (a) Hypothetical diel illumination and (b) temperature profiles of open (orange) and closed forests (black); (c, d) Hypothetical activity patterns with different shift scenarios indicated with different colours. In our hypotheses, we posit that butterfly activity shifts earlier and activity intensity higher in open forests; (e) Hypothetical illumination and temperature exposures during activity if species respond to illumination and/or temperature or (f) not. If butterfly populations are adapted to changes in temperature and illumination regimes, their exposure to temperature and illumination during their activities should match between closed and open forests as illustrated in (e).

Khao Chong, Trang Province, Thailand (KHC; 7°N 99°E); Maliau Basin Conservation Area, Sabah, Malaysia (MBCA; 5°N 117°E; Figure S1). We recorded butterfly activities in both closed forests and adjacent (~1 km) open forests within each site. Our closed forests were either primary tropical rainforest with little disturbance (XTBG, MBCA and KHC) or old regenerated (~70 years) secondary subtropical evergreen forests (TPK). Our open forests were those located near the closed forest sites but with a more open canopy from disturbance due to road construction (TPK, XTBG and MBCA). For KHC, the open forest was due to disturbance by a seasonally flooded stream. At each site, we set up butterfly survey transects of 400–600 m in length in each forest type (two transects in MBCA and XTBG; one transect in TPK and KHC). The transects were generally flat and on similar hill aspects, so that the microclimate does not vary much within the same transect.

Each transect is ~1km away from each other. For closed forest transects, the transects are narrow trails in the forest, while for open forests, we selected transects depending on the way the forest canopy became opened. In TPK, XTBG and MBCA, our open forest transects were forest edges along a concrete road. In KHC, the open forest transect is one of the butterfly monitoring transects along a seasonally flooded stream in the forest.

We surveyed butterflies in each location when adult butterflies were most abundant: that is, in the middle of the wet season in July 2016 in TPK; in October–November 2017 in MBCA (no distinct wet and dry seasons in MBCA); in the beginning of the wet season in June 2019 in XTBG; and in the middle of the wet season in July 2019 in KHC. We conducted surveys on sunny and windless days. Sampling efforts at each site are detailed in Table 1. In each study site, two experienced observers recorded butterfly species and abundance using adjusted Pollard walks (30min at a constant pace, recording butterflies encountered within 5m of established transects; Basset et al., 2013) at each transect every hour from morning (about half to 1h after sunrise) to dusk (about half to 1h before sunset). At each site, butterfly observers were the same and were randomly switched between forest types or surveys to minimize bias caused by different observers. We recorded the presence of active (displayed flying, feeding, mud puddling, territorial behaviour, mating and ovipositing) butterfly individuals during the sampling. We used hand-held butterfly nets to capture butterflies and 300mm digital single-lens reflex cameras to record butterflies for species identification. In TPK and XTBG, where taxonomy is relatively well resolved, butterflies were identified with local field guides (Zhou, 1994). At MBCA and KHC, we also used local field guides (Ek-Amnuay, 2012; Otsuka, 2001) but excluded records of cryptic species, such as *Arhopala* spp. and *Euthalia* spp., which are relatively common but difficult to identify to species level in the field.

To measure the microclimate difference between forest types, we placed 1–2 data loggers (Onset HOBO UA-002-64) in each habitat suspended 1m above-ground under vegetation (for avoiding direct solar radiation). These data loggers recorded air temperature (°C) and illumination (Lux) at every 5-min interval in TPK and KHC, at 1-min intervals in XTBG and MBCA. We aggregated (averaged across) 1-min interval recordings to 5-min intervals to make recordings in different sites comparable and used these 5-min interval recordings in the subsequent analyses.

TABLE 1 Number of species used in this study for intra-specific comparison and recordings in different sites and forest types.

Sites	Forest types	Number of species occurring in both habitats	Total records
TPK	Open-canopy	8	293
	Closed-canopy		530
XTBG	Open-canopy	7	84
	Closed-canopy		185
MBCA	Open-canopy	1	14
	Closed-canopy		47
KHC	Open-canopy	6	117
	Closed-canopy		147

2.2 | Quantification of microclimates

We identified maximum temperature (T_{max}), mean temperature (T_{mean}), maximum illumination ($Illm_{max}$) and mean illumination ($Illm_{mean}$) for each sampling day. We averaged the above daily values in each forest type in each site as corresponding temperature and illumination profiles for the subsequent analysis.

2.3 | Quantification of activity

We used the R package 'activity' to quantify butterfly activity patterns (Rowcliffe et al., 2014). This package uses modified kernel estimation with truncation and options for bootstrapping to obtain activity probability density functions (i.e. activity curve). Although designed for processing camera trap data, the package also applies to other datasets from temporally standardized observations confined to fixed areas, such as hourly repeated transect walks in our case (Rowcliffe et al., 2014). For better model performance, only species with eight or more recordings per forest type per site were used, as recommended by Rowcliffe et al. (2014). Since our transect walks were in 1-h intervals and not continuous as in camera trap data, we adjusted the bandwidth of the kernel estimation by visually checking the best fits to our data (Zoller et al., 2020). We bootstrapped the activity curve 100 times to obtain confidence intervals (Rowcliffe et al., 2014).

For the activity peak, we used the highest value estimated from the activity curve. We only used the first peaks for populations with a bimodal activity curve (Figure S2), as the change of temperature and illumination was stronger in the morning than in the afternoon (Figure 2). For activity duration, we defined the lower quantile of the activity curve as activity start time (H_{start}) and the upper quantile of the activity curve as activity end time (H_{end}). We calculated the time between the upper and lower quantiles of the activity curve as activity duration.

We also quantified the activity intensity as the area under the activity curve. Apart from the whole activity duration, we also calculated the activity intensity during the hottest time of the day (10:00AM–02:00PM). We calculated activity peak, duration, intensity and the activity intensity during the hottest time of the day separately for each population of each forest type in each site.

2.4 | Quantification of temperature and illumination exposure during activity

We quantified the microclimate conditions that each butterfly population experienced. We first summed the microclimate values (temperature and illumination) measured at 5-min intervals during the

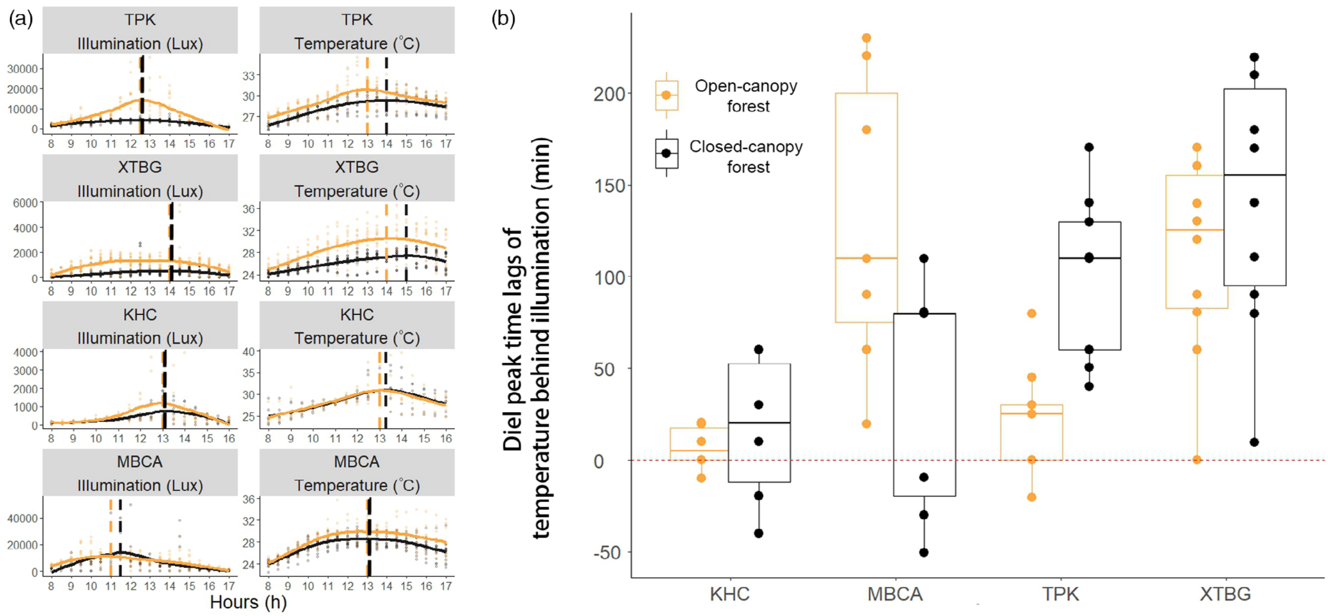

FIGURE 2 (a) Recorded diel illumination and temperature profiles in each study site, points are mean values of illumination or temperature every 30 min within each day and lines connect the mean values through time. Vertical dash lines indicate peak times. All times are based on UTC+8. (b) Peak time lags of temperature behind illumination (diel peak temperature time- peak illumination time). Each dot indicates one sampling day. Values higher than zero (red dashed line) indicated peak temperature time occurred later than illumination peak. Different colours indicate different forest types.

activity time. Since these values are inherently higher for populations with longer activity durations, we divided the cumulative microclimate values by activity duration as follows:

$$T_{\text{its}} = \frac{\sum \text{temperature}}{|H_{\text{end}} - H_{\text{start}}|}$$

$$I_{\text{its}} = \frac{\sum \text{illumination}}{|H_{\text{end}} - H_{\text{start}}|}$$

where T_{its} and I_{its} are, respectively, the exposure of temperature and illumination each butterfly population experienced from H_{start} to H_{end}.

2.5 | Statistical analyses

To test if the effects of illumination were confounded with temperature, we ran pair-wise correlations between T_{max}, T_{mean}, Illm_{max} and $\text{Illm}_{\text{mean}}$ each day using Kendall's rank test with tau-b (Kendall, 1945). We used non-parametric correlation tests as none of the temperature and illumination variables were normally distributed despite log transformation and identical values occurring in some sites. To test whether open forest had higher temperature and illumination, we used generalized linear mixed models (GLMM) with forest type as the fixed factor and site as a random factor using the R package *glmmTMB* (Brooks et al., 2017). We separately examined T_{max}, T_{mean}, Illm_{max}, $\text{Illm}_{\text{mean}}$ and the time differences between daily temperature and illumination peaks.

To test the differences in intra-specific activity patterns between populations from closed and open forests, we used generalized linear mixed effect models (GLMM) with the R package *glmmTMB* for activity peak, duration and intensity metrics separately. To account for potential site variation and confine the comparison of populations within species pairs within the same species and site, we set forest type (closed vs. open) as a fixed factor, and species and site as random factors.

To test whether activity responses were associated with temperature and/or illumination, we compared the temperature and illumination exposure during butterfly activities in two forest types using the same GLMM model structure for intra-specific activity pattern comparison. Specifically, we considered two scenarios: (1) Comparing the exposure of temperature and illumination between two forest types standardized by the observed activity duration and (2) comparing the exposure of temperature and illumination standardized by the same duration regardless of the actual activity duration of populations (assuming that open forest populations keep the same activity time as populations in the closed forest, thus butterfly populations had the same H_{start} and H_{end} regardless of habitat types). All analyses were conducted in R 4.3.2 (R Core Team, 2023).

3 | RESULTS

For a total of 49 sampling days, we recorded 4824 observations of active butterfly presence from 252 species. Among those, 1417 observations (909 from closed and 508 from open forests) and 22 conspecific population pairs of 21 species (one species occurred in both XTBG and TPK) met our criteria for intra-specific comparison

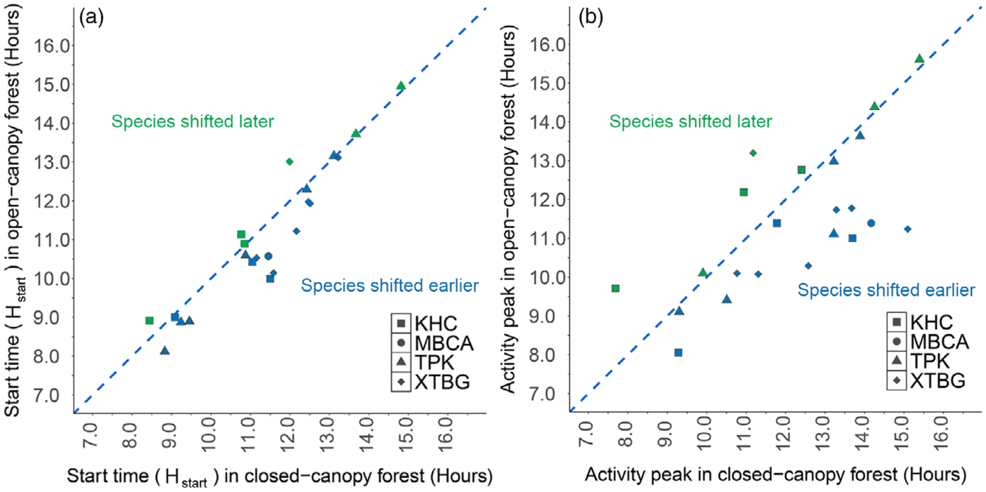

FIGURE 3 Intra-specific comparison of (a) activity peaks and (b) start times (H_{start}) of butterfly populations in open forest to those in closed forest, dashed blue lines indicate 1:1 relationship. Each point represents one species, with sites indicated by different shapes.

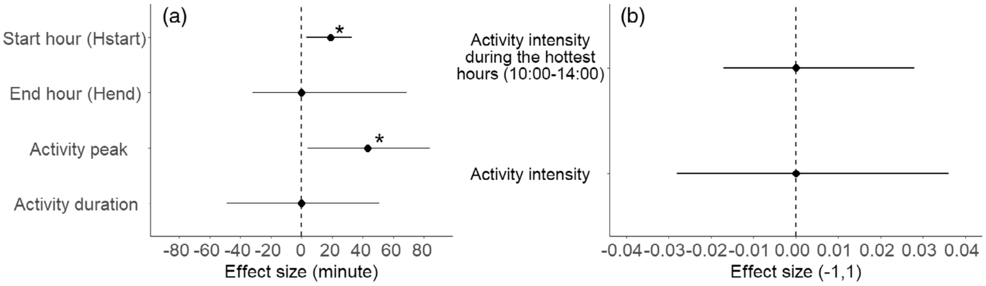

FIGURE 4 Mean shifted value (effect size) of different activity metrics of butterflies from closed to open forests with 95% confidence intervals. (a) for time metrics and (b) for activity intensity metrics. Significant results ($p < 0.05$) from GLMM are indicated with *.

(Table 1). Species list and abundance measures in each habitat are detailed in Table S1. Activity curves from kernel estimation and activity patterns calculated for each species are illustrated in Figures S2 and S3.

Illumination was significantly and positively correlated with temperature (T_{mean} vs. $Illm_{mean}$: $\tau_{b(148)} = 0.32$, $p < 0.001$; see Supporting Information for more details). Within the same site, T_{max} and T_{mean} in closed forests were significantly lower ($\chi^2 = 24.96$, $p < 0.001$ and $\chi^2 = 19.75$, $p < 0.001$) than open forests (Figure 2a). $Illm_{max}$ and $Illm_{mean}$ in closed forests were also significantly lower ($\chi^2 = 6.36$, $p = 0.01$ and $\chi^2 = 4.62$, $p = 0.03$) than open forests. Across four sites and forest types, temperature peak times lagged behind illumination peak times in both forest types ($\chi^2 = 68.38$, $p < 0.001$). With the exception of MBCA, the overall time lags between temperature peak time and illumination peak time were greater in closed forests than open forests ($\chi^2 = 9.08$, $p = 0.002$; Figure 2b).

For activity pattern comparison, we found that populations in open forests had earlier start times (H_{start}) ($\chi^2 = 6.99$, $p = 0.008$; Figures 3a and 4). Populations in open forests also had earlier activity peaks than in closed forests ($\chi^2 = 5.46$, $p = 0.019$; Figures 3b and 4). However, activity duration and end times (H_{end}) were similar between populations from different forest types ($\chi^2 = 0.0009$, $p = 0.98$; $\chi^2 = 0.61$, $p = 0.44$; Figure 4). No significant difference was found for the activity intensity throughout the whole active period and during the hottest time of the day between the two forest types ($\chi^2 = 0.07$, $p = 0.78$; $\chi^2 = 3.77$, $p = 0.052$; Figure 5).

For the standardized temperature and illumination exposure profile during activity, we found that observed populations were exposed to the same standardized temperature exposure in two forest types ($\chi^2 = 0.49$, $p = 0.48$; Figure 6a) but were exposed to significantly higher standardized illumination exposure in open forests ($\chi^2 = 8.15$, $p = 0.004$; Figure 6b). Assuming populations from open forests did not change their H_{start} and H_{end}, both standardized temperature exposure ($\chi^2 = 15.01$, $p < 0.001$; Figure 6c) and illumination exposure were higher in open forests than in closed forests ($\chi^2 = 10.86$, $p < 0.001$; Figure 6d).

4 | DISCUSSION

Our results demonstrate that butterfly species shift their activity time to an earlier schedule, with earlier start times and peak times in open-canopy forest. However, we observed a similar activity duration and activity intensity between closed and open-canopy forests. By comparing temperature and illumination experienced by active butterflies, we found that by shifting activities earlier in

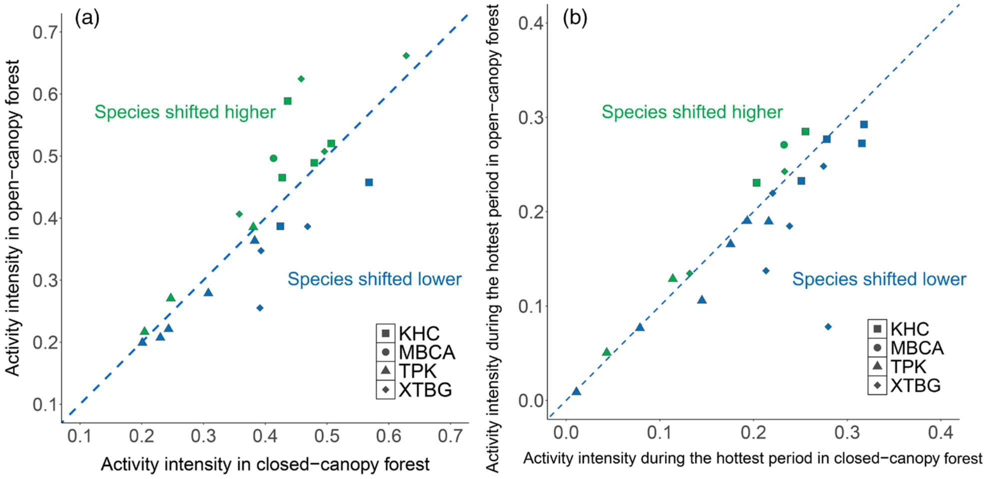

FIGURE 5 Intra-specific comparison of (a) activity intensity (area under activity curve) and (b) activity intensity during the hottest time of the day (10:00 AM–02:00 PM) of butterfly populations in open forest to those in closed forest, dashed blue lines indicate 1:1 relationship, each point represents one species, with sites indicated by different shapes.

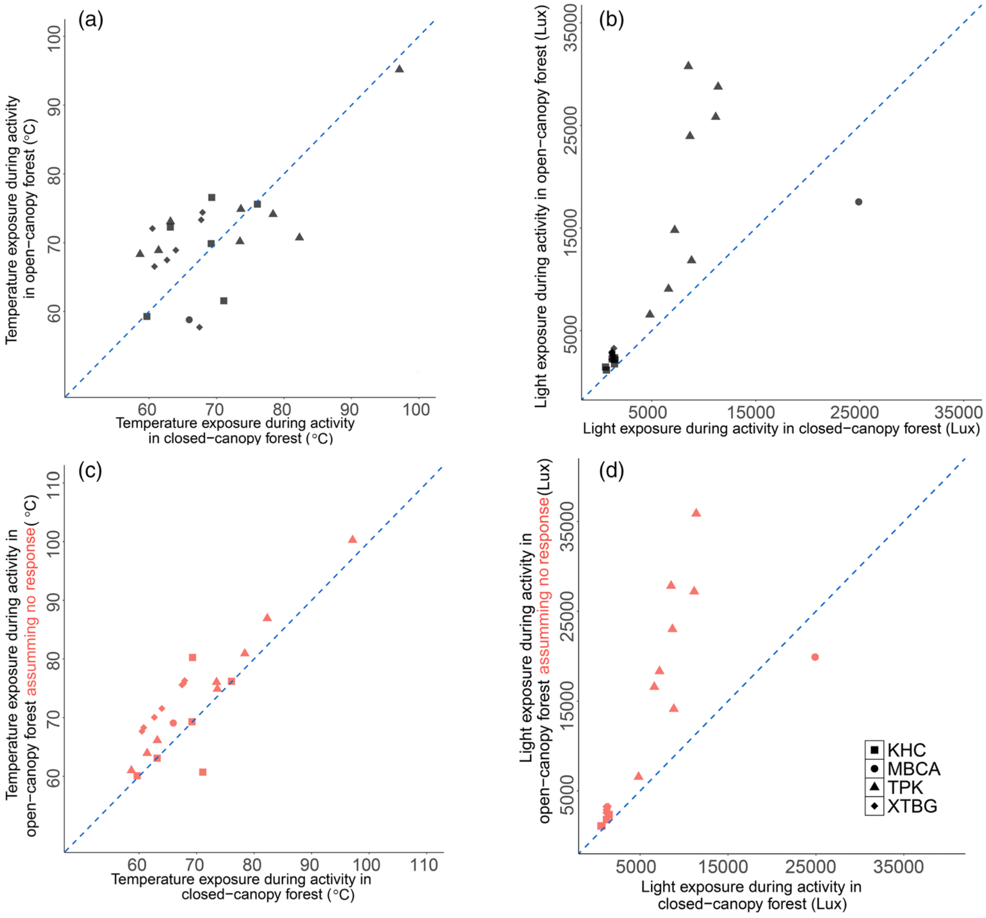

FIGURE 6 Comparison of temperature exposure (a, c) and illumination exposure (b, d) butterfly populations experienced between different forest types during activity. (a) and (b) are from our observation, (c) and (d) are hypothetical scenario when activity does not change with forest canopy become open (also in red to compared with our hypothesis in Figure 1). Dashed blue lines indicate 1:1 relationship. Each point represents one species, with sites indicated by different shapes. Points below the dashed line are the species that experienced lower temperature or illumination exposure in open forests.

open-canopy forest, butterflies were exposed to stronger light conditions but similar temperature exposure relative to those in closed forests, suggesting maintaining similar temperature conditions is more important than illumination. Although complex interactions between temperature and illumination contributed to the changes in activity pattern, the earlier active start and peak times in open-canopy forest are consistent across all tropical sites. Our findings indicate the flight activity of butterflies responds to habitat disturbance, and the altered temperature conditions could explain butterfly activity change.

The climatic profiles presented across our four study sites suggest that compared with closed-canopy tropical forest, open-canopy tropical forest consistently exhibit higher air temperature and illumination conditions with larger variation. We demonstrate that temperature peaks generally lag behind illumination peaks, and the lag is generally higher in closed forest compared to that in open forest. While previous studies have largely focused on the differences in mean microclimatic conditions between closed and open forests (Xing et al., 2016, 2018), our data show that the temporal dynamics of microclimate within and across habitats are also an important dimension and need further examination (Stark et al., 2023). Although our temperature and illumination profiles reflect the general climatic conditions experienced by forest butterflies in each habitat, they may not fully capture the heterogeneity of the microclimate shaped by the complex vegetation structure. As such, the climatic profiles presented in our study should be interpreted as the baseline environmental conditions for each habitat, rather than precise representations of the microclimate experienced by each species. To better capture the complexity of the microclimate affecting butterflies and other ectotherms, future research utilizing ecologically relevant, mechanistic microclimatic models (Maclean & Klinges, 2021) could provide more comprehensive insights (Wang et al., 2024).

As expected, we observed that butterfly populations shifted their activity peak time and start time with the change of temperature and illumination profiles. However, we found that butterfly activity duration and intensity remained stable across forest types. This suggests that butterflies do not strictly follow pre-set circadian rhythms and show changes in activity patterns in response to microclimate change at the habitat scale. While environment-associated activity shifts have been shown in previous studies using laboratory experiments or model predictions, mostly focusing on single species (Jiang et al., 2023; Landry Yuan et al., 2018), our results confirmed such phenomena in the field and across multiple species. Nevertheless, such ecophysiological responses have a limited capacity to buffer ectotherms from environmental changes in the long term due to increasing energy costs (Buckley et al., 2015; Jiang et al., 2023). Shifting activity may also generate extra costs for butterflies who may be under higher predation risk or phenological mismatch with plant nectar secretion rhythm (Freimuth et al., 2022; Kharouba & Vellend, 2015). Moreover, for many forest species, behavioural response depends on available microclimate heterogeneity (Senior et al., 2018; Woods et al., 2015; Zellweger et al., 2020). Understanding the holistic microclimate impact on ectotherms also requires relevant information across different life stages. For instance, Agosta et al. (2017) found that the performance of *Rothschildia lebeau* caterpillars was reduced in secondary forest compared to closed-canopy forest, which is associated with differences in climate between the habitats. Future studies should further investigate the extent to which forest ectothermic species can buffer changes in both average microclimate conditions and heterogeneity, and how these shifts may influence their performance across life cycles and population dynamics (Agosta et al., 2017; Senior, 2020).

In particular, by comparing the exposure of temperature and illumination butterfly populations experienced between closed and open forests during activity, we found the shift in butterfly activity patterns did not cause any changes in the exposure of temperature that the species experienced, but the exposure of illumination experienced was higher (Figure 6a,c). While in the absence of activity response, butterflies would inevitably be exposed to higher temperature and illumination levels (Figure 6b,d). This suggests that activity shifts effectively mitigate the intensity of temperature, but not illumination exposure for forest-associated butterflies. Those findings all together indicate that although temperature and illumination are highly correlated in tropical forests, temperature is likely a more important factor in influencing the activity pattern of forest butterfly species. This is expected as for tropical butterflies, flight activity is closely related to low temperatures and may be even limited by them (Wenda et al., 2021). However, our results do not rule out the importance of illumination for forest butterflies, which can also affect butterfly performance depending on their morphological traits such as body size and body colour (Xing et al., 2016, 2018). In addition, higher illumination exposure in open forests may pose species under additional abiotic or biotic pressures such as climatic extremes or higher predation rates (Cheng et al., 2018; Nokelainen et al., 2022; Sunday et al., 2014).

With considerable field sampling across multiple sites, our species pool covers the major butterfly families and includes most common forest-associated species in the region. However, further observations covering more rare species would provide valuable insights in the future (Leitao et al., 2016). Although we observed consistent patterns of activity shifts between forest types across the four sites, specific site characteristics should be considered. For example, in TPK, we recorded notably higher illumination exposure in open forests (Figure 6c), which may be due to a larger difference in illumination between forest types at this old regenerated secondary subtropical forests site (Figure 2a). This suggests that the magnitude of microclimate exposure could be influenced by local climatic conditions and geographical variation. While the limited number of sites in our study restricts a comprehensive analysis of site-specific effects, future research investigating how butterfly responses to habitat disturbance-induced microclimate differences vary across broader geographical scales could offer valuable insights into these patterns. Furthermore, other abiotic factors, such as humidity and wind speed, may also play a role. For example, studies in temperate regions show that damp wings can reduce flight performance

(Ide, 2010). In more open habitats with fewer obstacles, wind speed may be stronger (Laurance & Curran, 2008), potentially enhancing cooling mechanisms for butterflies (Kingsolver & Moffat, 1982) and counteracting the effects of higher temperatures on their thermoregulation. Additionally, biotic factors, such as diel variations in flower closure times (Schwarz et al., 2021), may influence butterfly activity patterns. However, these effects are likely species-specific and difficult to quantify across species to establish a general pattern but should be considered in the future.

5 | CONCLUSIONS

By examining changes in activity patterns for multiple forest butterfly species in four tropical sites, we demonstrated activity shifts in butterfly species across close and open-canopy tropical forest. Our work highlights how changes in microclimate due to changes in forest structure can lead to changes in butterfly activity pattern, an important ecological mechanism through which species respond to forest environmental changes. Such behavioural response can help mitigate the impact of temperature changes on butterfly activity, but it has limited capacity to buffer changes in illumination. Our study highlights both the sensitivity and resilience of some tropical butterfly species to forest disturbance through changes in their activity pattern and also the importance of monitoring and understanding changes in animal activity in anthropogenic disturbance in the future.

AUTHOR CONTRIBUTIONS

Cheng Wenda and Shuang Xing designed the work, Cheng Wenda, Shuang Xing and Chung-Lim Luk collected the data, Cheng Wenda did the analysis and Cheng Wenda and Shuang Xing drafted the manuscript; Suzan Benedick, Akihiro Nakamura, Yves Basset, Timothy C. Bonebrake, Brett R. Scheffers and Louise A. Ashton helped with data collection and provided substantive editing and revision of the manuscript.

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CONFLICT OF INTEREST STATEMENT

All authors agree with the contents of the manuscript and approved the submitted version of the manuscript. No conflict of interest is to be declared.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository. https://doi.org/10.5061/dryad.prr4xgxzc (Wenda et al., 2025).

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SUPPORTING INFORMATION

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

Figure S1. Sampling sites in our study.

Figure S2. Activity patterns of the 22 butterfly populations used in the study.

Figure S3. Activity peak and duration distribution in different times of the day of our 22 butterfly population pairs.

Figure S4. NMDS results of butterflies recorded from intact forests (blue) and degraded forests (yellow).

Figure S5. Model diagnostics for the best model testing the effect of habitat (open forest vs. closed forest) on intra-specific butterfly activity peak comparisons.

Figure S6. Model diagnostics for the best model testing the effect of habitat (open forest vs. closed forest) on intra-specific butterfly activity start time comparisons.

Table S1. Sampling efforts for different sites and forest types.

Table S2. Detailed 21 Species (22 populations) and numbers of recordings in different forest types and sites used for the analysis.

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