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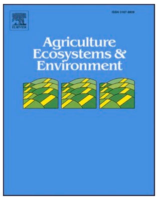

Nocturnal insect communities altered by land-use change contribute little to coffee pollination in the Western Ghats, India

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A B S T R A C T

Wild insects pollinate numerous agricultural crops, but the role of nocturnal pollinators, while increasingly acknowledged, remains poorly understood. We examined nocturnal insect communities and pollination in agroforests of robusta coffee (*Coffea canephora*) – a crop that exhibits floral traits suggestive of nocturnal pollination – in India's Western Ghats mountains. Specifically, we (1) compared nocturnal insect communities of a shaded robusta coffee agroforest and a nearby secondary tropical rainforest using light screens, and (2) assessed nocturnal and diurnal pollination of coffee using floral exclosure experiments in the agroforest and in a former coffee agroforest located within the secondary rainforest. Nocturnal pollinators visiting light screens were 21 % fewer in the agroforest than the rainforest, mainly due to reduced numbers of Lepidoptera, Coleoptera, and Diptera in the former. Lepidoptera and Coleoptera differed in genus richness and composition between habitats, with the agroforest having fewer Lepidoptera and more Coleoptera genera than the rainforest. Coffee pollination success was largely attributable to diurnal pollinators in both the agroforest and rainforest. While nocturnal pollination effects were absent in the agroforest, we found some evidence of nocturnal pollination in the secondary rainforest, where coffee flowers accessible to diurnal and nocturnal pollinators had higher pollination success (60 %) than flowers accessible to diurnal pollinators alone (46 %). In summary, the nocturnal insect community of coffee agroforestry, which is distinct from the rainforest community, contributes little to coffee pollination. However, a greater contribution of nocturnal pollination under less intensive coffee cultivation is a possibility that warrants further exploration.

1. Introduction

There is growing evidence that insect species and populations are in a general state of decline (Dirzo et al., 2014; Sánchez-Bayo and Wyckhuys, 2019), with some terming this the insect apocalypse (Wagner et al., 2021). Land-use change and in particular the expansion of intensive agriculture and pesticide use are recognized as major global drivers of insect declines (Wagner, 2020; Wagner et al., 2021). As insects contribute to numerous ecosystem services such as pollination, pest control, and nutrient recycling, their ongoing declines are not only a major biodiversity conservation concern but also have direct implications for human well-being (Chaplin-Kramer et al., 2014; Losey and Vaughan, 2006)

The production of a wide range of agricultural goods – including most food crops – is known to depend on cross-pollination by managed and wild insects (Garibaldi et al., 2013; Klein et al., 2007; Rader et al., 2016). Habitat loss, fragmentation, and agricultural land-use can, therefore, have significant ecological and economic consequences (Gallai et al., 2009; Potts et al., 2010). For example, deforestation-driven pollinator declines have been shown to substantially increase production costs and drive farmers to switch to less pollination-dependent crop varieties (Partap and Ya, 2012). Studies also show that pollinator declines and crop pollination losses are potentially mitigated by proximity to remnant forests (Ricketts et al., 2004) and agroforestry systems such as shade coffee, which are known to perform better at sustaining pollinators and pollination functions than open agriculture (Centeno-Alvarado et al., 2024). However, land-use change impacts on pollinators and pollination are largely understood through the lens of

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diurnal insects, although emerging research suggests an important role for nocturnal insect pollination in many crop varieties (Buxton et al., 2022).

More than half of all insect species are nocturnally active, and many species within mega-diverse insect orders such as Lepidoptera, Coleoptera, Hymenoptera, and Diptera are known to pollinate plants at night (Borges et al., 2016; Hölker et al., 2010). Among plants, around 30 % of all families are known to comprise species that are nocturnally pollinated (Borges et al., 2016). In agricultural systems, floral interactions with potential nocturnal pollinators have been documented for around 50 crop plant families (Buxton et al., 2022). Recent studies have established the importance of nocturnal pollination for major crops such as apple, avocado, and strawberry (Buxton et al., 2022; Fijen et al., 2023; Robertson et al., 2021). However, the role of nocturnal pollination and its vulnerability to land-use change have not been examined for the majority of candidate crops (Buxton et al., 2022).

Coffee is among the most highly traded crops globally and its agroforests are considered refuges for biodiversity beyond protected areas across several global biodiversity hotspots (Jha et al., 2014; Manson et al., 2024; Murrieta-Galindo et al., 2013; Perfecto et al., 1996). Two coffee species – arabica (*Coffea arabica*) and robusta (*Coffea canephora*) – comprise nearly all the coffee grown commercially (Bunn et al., 2015). While both species benefit from insect cross-pollination, robusta coffee is associated with greater self-incompatibility and is consequently more dependent on insect-mediated cross-pollination than arabica coffee (Crane and Walker, 1984; Free, 1993). While the role of diurnal insects – especially bees – in *C. canephora* pollination is well-established (Klein et al., 2003; Krishnan et al., 2012; Willmer and Stone, 1989), the species exhibits a number of floral traits suggestive of nocturnal pollination (Borges et al., 2016; Samnegård, 2020; Sinaga et al., 2024). These include a large floral display and prominent, fragrant, easily accessible white flowers (Borges et al., 2016). It is worth investigating, therefore, how nocturnal insect communities respond to coffee agroforestry, and whether they provide additional or complementary pollination services to diurnal insects in these agroforests.

Nocturnal insects can contribute to robusta coffee pollination if (1) coffee agroforests harbor communities and populations of nocturnal insects that potentially visit coffee flowers, and (2) nocturnal floral visits increase pollination success. We investigated both aspects using a field study on nocturnal pollinator communities and pollinator exclusion experiments in the Western Ghats mountains of south India. The Western Ghats are both a global biodiversity hotspot and a major coffee-producing region (Murugan et al., 2022). We hypothesized that land-use change from forest to coffee would reduce nocturnal insect abundances and alter community composition (Hawes et al., 2009; Millard et al., 2021; Vanbergen et al., 2005). To evaluate this hypothesis, we compared the nocturnal insect communities of a shade-coffee agroforest and a relatively undisturbed natural habitat (40 + year old secondary tropical rainforest). We expected the secondary rainforest and coffee agroforest to have distinct nocturnal insect communities, with the latter habitat having lower abundance and diversity of disturbance-sensitive insect groups such as Lepidoptera, Coleoptera, and Hymenoptera, while we expected Diptera – a group often associated with disturbed habitats – to increase in the coffee agroforest (Collyer et al., 2023; Millard et al., 2021; Ohler et al., 2023; Sahrir et al., 2024). Next, we hypothesized that nocturnal pollinators can complement diurnal pollinators and enhance robusta coffee pollination. To evaluate this, we conducted a pollinator exclusion experiment to estimate the standalone and combined effects of nocturnal and diurnal insect pollinators on coffee pollination success. We expected pollination success to be higher under nocturnal pollination than ambient (wind) pollination alone, and under nocturnal plus diurnal pollination than diurnal pollination alone. We conducted the exclusion experiment within an actively managed coffee agroforest, and on remnant coffee bushes in a part of the secondary rainforest in which robusta coffee was previously cultivated. The former experiment aimed to investigate coffee pollination associated with an insect community potentially modified by land-use change, and the latter investigated coffee pollination under a potentially more intact native nocturnal insect assemblage.

2. Methods

2.1. Study site

This study was conducted at a robusta coffee farm and a secondary tropical rainforest in the Sakleshpur Taluk, Karnataka State, located in the Western Ghats biodiversity hotspot, southern India (Figure S1). In the robusta coffee farm, situated on private property in the Kumbardi village (12.93° N, 75.73° E), coffee is grown alongside pepper vines under a diverse shade tree canopy comprising at least 57 native tree species; this habitat resembles the traditional polyculture coffee garden described in Moguel and Toledo (1999). The secondary rainforest was situated on a private property in the Kadamane village (12.92° N, 75.67° E), formed part of a c. 1600 ha complex of fragmented rainforests interspersed with tea fields and montane grasslands. This site is contiguous with a larger swathe ($>$1000 km^2) of state-protected rainforests to its west, and a coffee agroforestry landscape in other directions (Figure S1). Utilized for selective-logging and shade robusta coffee cultivation until the 1980s and then abandoned, these rainforests are recovering under protection from the landowners (Nandakumar et al., 2024).

The study area ranges from 900 m to 1000 m asl in elevation and receives approximately 5000 mm of rainfall annually (Nandakumar et al., 2024). The dominant land-use is shade coffee (*C canephora* and *C arabica*), interspersed with secondary and degraded primary tropical rainforest fragments, open croplands, and built-up areas (Figure S1). The rainforests are classified as mid-elevation wet-evergreen forests of the *Mesua ferrea*–*Palaquium ellipticum* type (Pascal, 1986).

2.2. Insect sampling

We compared the nocturnal flying insect communities of the robusta coffee agroforest and secondary tropical rainforest during March - April 2022. Our sampling coincided with the flowering season of robusta coffee across the landscape (February-March), which is the warm and dry season that precedes the wet southwest monsoon season (June-Oct). Flowering in coffee is initiated by summer rains/ irrigation preceded by about 3 months of moisture stress. We focused on four nocturnal flying insect orders that are recognized as potential nocturnal pollinators – Coleoptera, Lepidoptera, Hymenoptera and Diptera (Borges et al., 2016). Nocturnal insects were sampled using light screens, which comprised a vertical white 3.24 m^2 screen illuminated by four ultraviolet LEDs, two blue LEDs, and one green and white LED (Fig. 1a), following Brehm (2017). We set up two light screens per night over 12 nights in each habitat, maintaining at least 200 m between screens on any given night for spatial independence (Truxa and Fiedler, 2013), for a total of 24 screen nights each in the coffee agroforest and rainforest. Screens were set up at different locations each night over approximately 250 ha each in the coffee agroforest and rainforest.

Light screens were set up at dusk (1800 h) and nocturnal insects were inventoried between 2330 and 0130 h. The timing of data collection was determined based on a pilot study in the rainforest comprising 12 screens monitored hourly from 1830 to 0630 h, in which insect accumulation was observed to peak during 2330–0130 h (Figure S2). At each screen, we performed a snapshot count of insects larger than 0.5 cm in head-to-abdomen length and belonging to the four focal orders. For Lepidoptera and Coleoptera, we further classified individuals larger than 0.5 cm into visually distinct genus or morpho-genus groups and photographed representative individuals of each group using one of two cameras – Canon 80D with 100 mm Lens and Nikon Coolpix B500 for further identification and/or confirmation. No insect specimens were collected.

Fig. 1. (a) Set up of the light screen used for sampling nocturnal insects. (b) A flowering branch of robusta coffee covered with a mesh bag to exclude insect pollinators. (c) An image captured through a fluorescence microscope of the lower stylar region of a coffee flower showing individual pollen tubes that fluoresce brightly when successfully pollinated.

To verify if the four focal insect orders are potential pollinators of coffee, we scanned coffee flowers for nocturnal insect visitors. Floral scans comprised 20-second visual searches of individual floral clusters for insects, which if present were identified to the order level and counted (Table S1). Scans were performed using a head torch with a red filter, and only insects seen in direct contact with the reproductive organs of coffee flowers were recorded as potential pollinators (Knop et al., 2018). Floral scans covering 500 floral clusters in the actively managed agroforest confirmed that coffee attracts and is potentially nocturnally pollinated by orders Lepidoptera, Coleoptera, Diptera, and Hymenoptera (Table S1).

2.3. *Moth and beetle classification*

Moths and beetles photographed on light screens were identified to the genus or morpho-genus level with the help of field guides (Vaylure, 2018), photographic checklists from the region (Balakrishnan Valappil, 2020; Gupta et al., 2014; Poorani, 2002; Rajagopal et al., 2023; Sondhi et al., 2018), insect taxonomy websites (Pyralids of Borneo, 2025; Sondhi et al., 2024) and species descriptions (Bingham et al., 1906; Hampson et al., 1892; Moore and Moore, 1880), and automated identification aids on the iNaturalist platform (“iNaturalist,” 2024). We uploaded images that could not be unambiguously identified to the genus level by these methods to iNaturalist and invited experts in moth and beetle taxonomy to provide and/or confirm identifications. For moths, after excluding images of four micromoth families (Gelechiidae, Lecithoceridae, Tineidae, Tortricidae) that were not possible to reliably classify further from photographs, we identified 298 genera or morph-genera from the 317 morphologically distinct taxa photographed, and the rest remained unidentified. Among beetles, 106 out of a total of 111 unique taxa photographed were identified to the genus or morpho-genus level. Our decision to avoid specimen collection precluded species level identification in most cases and reduced our ability to detect more subtle differences in diversity and community composition, but enabled our attempt at compassionate entomological research (Gray, 2024).

2.4. *Pollinator exclusion experiments*

We conducted a pollinator exclusion experiment to quantify and contextualize the effects of nocturnal pollinators on coffee pollination success. We conducted the experiment on robusta coffee in the coffee agroforest during the coffee flowering season (March - April) of 2022, and repeated it in the abandoned coffee (robusta) area of the rainforest during the coffee flowering season of 2023. The former experiment investigated pollination (nocturnal and diurnal) by insect communities associated with the actively managed coffee agroforest, while the latter investigated coffee pollination associated with less-modified native insect communities of the rainforest.

Insect pollinators were excluded using 1 mm nylon mesh bags tied around flowering branches with wire frames used as structural reinforcements to prevent contact between flowers and the mesh (Fig. 1b). The experiment comprised the following treatments: (1) complete insect exclusion (Negative control), (2) pollinator exclusion by day (0630–1830h) and open at night (1830–0630h; Night - accessible), (3) pollination exclusion by night and open in the day (Day - accessible), and (4) no exclusion (Positive control). To avoid inadvertent pollination during bagging and unbagging, the researcher (HRN) rinsed their hands with an alcohol-based sanitizer after handling each bag. Bags were not interchanged between branches and bushes during the experiment.

The experiments were conducted on 25 adult robusta coffee bushes in the coffee agroforest and 24 abandoned robusta bushes in the rainforest. Four branches with floral buds were selected on each bush and randomly assigned to the experimental treatments. Previous studies indicate that coffee flowers are most attractive to pollinators on the day they bloom (Alvim, 1985; Ngo et al., 2011), and pollen tubes reach the ovary within 49 h of pollination (Krishnan et al., 2012). Accordingly, our experiments were initiated at the advanced bud stage (a day before blossom) and maintained for 72 h following blossom (Krishnan et al., 2012). Ten floral styles selected at random were collected from floral clusters within each treatment and immediately fixed in Farmer’s solution (one-part glacial acetic acid and three-part absolute ethanol) for subsequent laboratory analyses (Shivanna and Tandon, 2014).

Additionally, we conducted a separate experiment to test for any effects of the experimental procedure (hardware plus handling during bagging and unbagging) on coffee pollination. We selected 25 additional coffee bushes in the active agroforest, on which two branches were selected at random and assigned to the following treatments: (i) experimental procedure, in which flowers were fitted with experimental hardware and in the open position, and the procedure of bagging followed immediately by unbagging was carried out once a day, and (ii) controls, in which flowers were not manipulated in any way. As with the main experiment, this experiment was initiated when coffee flowers were at an advanced bud stage and ran for 72 h. We found no differences in pollination success between procedural and control flowers (Figure S3; see 2.5 for methodological details), which confirmed that the outcomes of our main experiments were not biased by procedural effects.

2.5. Pollination success

The collected styles were thoroughly washed and then softened by soaking in 8 N NaOH for 18 h. Softened styles were rinsed in water and stained in decolorized aniline blue solution (0.1 % solution of aniline blue dye in 0.1 M K_3PO_4) (Kearns and Inouye, 1993; Krishnan et al., 2012). The stained tissues were examined under an epifluorescence microscope (Olympus IX-81) with a UV filter (excitation wavelength of 450–490 nm) for fluorescence, where linear fluorescence patterns created by pollen tube linings (Fig. 1c) indicated pollen tube development (Kearns and Inouye, 1993). We recorded the number of pollen tubes at the lower stylar region of each style, and styles with two or more pollen tubes were considered to be successfully pollinated (Krishnan et al., 2012). Pollination success estimated by this method is known to be a reliable proxy for final fruit set (Krishnan et al., 2012). To eliminate unconscious observer biases, we masked treatment identities while observing pollen tubes under the microscope (Popovic et al., 2024).

2.6. Statistical analysis

All data analyses and visualizations were performed using R version 4.2.2 (R Core Team, 2022). We compared light screen encounter rates of nocturnal pollinators between the agroforest and rainforest using generalized linear models (GLM) from the R package MASS (Ripley et al., 1998). We modeled encounter rates (individuals/screen) of all nocturnal insects, and Coleoptera, Diptera, Hymenoptera, and Lepidoptera individually as response variables, and habitat type (coffee agroforest vs. rainforest) as the predictor variable. As the response data were counts and initial Poisson models suggested overdispersion, we ran negative binomial GLMs. We examined model-estimated mean encounter rates and 95 % confidence intervals (CIs) of each response in the coffee agroforest and rainforest, and interpreted the absence of overlap between means of each habitat and 95 % CIs of the other as indicating consistent differences in encounter rates between habitats (Nakagawa and Cuthill, 2007).

We compared Lepidoptera and Coleoptera taxonomic richness at the genus level between coffee agroforest and rainforest, standardized for coverage, using the R package iNEXT (Chao et al., 2014; Hsieh et al., 2022). We generated bootstrap 95 % CIs of the genus-level richness based on 50 iterations and interpreted the lack of overlap between means of each habitat and 95 % CIs of the other as indicative of differences in genus-level richness between the agroforest and the rainforest (Cumming et al., 2007).

We used Non-Metric Dimensional Scaling (NMDS) to visually represent the dissimilarity of Lepidoptera and Coleoptera genus-level composition between agroforest and rainforest habitats. We performed a three-dimensional ordination based on the Bray-Curtis dissimilarity index using the metaMDS function in the 'vegan' R package (Oksanen et al., 2022). We estimated the magnitude and statistical significance of community differences between the agroforest and rainforest using a non-parametric Analysis of Similarities (ANOSIM), using the 'anosim' function in the R package 'vegan'.

For the pollination exclusion experiments, we used generalized linear mixed-effects models (GLMM) with a binomial error distribution to compare pollination success (a binary variable) across the different exclusion treatments and controls. We ran separate models for the 2022 experiment in the coffee agroforest and the 2023 one in abandoned coffee bushes within the rainforest. Each model comprised the exclusion treatments and controls as fixed effects and bush ID as a random effect. GLMMs were run using the 'lme4' R package (Bates et al., 2015). We estimated marginal means and associated 95 % CIs of each treatment using the 'ggeffects' R package (Lüdecke et al., 2024). We interpreted the absence of overlap between means of any given treatment with 95 % CIs of the other, and vice-versa, as indicating consistent differences in pollination success between those treatments (Nakagawa and Cuthill, 2007). We only interpreted patterns and differences in pollination success across treatments within each experiment and avoided comparing pollination success across experiments. This was because the latter could be confounded by other factors such as experiment year (2022 vs. 2023), coffee floral density (higher in the coffee agroforest than rainforest: HRN pers. obs.), and irrigation (a few experimental bushes received blossom-inducing sprinkler irrigation in the coffee agroforest).

3. Results

3.1. Nocturnal insect communities in coffee and rainforest

Over 24 light screen nights each in the rainforest and robusta coffee agroforest habitats, we encountered 2424 (Lepidoptera - 1163; Coleoptera - 801; Hymenoptera - 195; Diptera - 265) and 1929 (Lepidoptera - 814; Coleoptera - 531; Hymenoptera - 407; Diptera - 177) individual insects, respectively. The overall encounter rate of nocturnal insects per light screen was 20 % lower in the coffee agroforest (mean = 80.4/screen, 95 % CI = 67.1–96.2) than the rainforest (mean = 101.0, 95 % CI = 84.5–120.7); we interpreted this as a consistent difference in encounter rates as the CIs associated with each habitat did not overlap with the means of the other (Fig. 2; Table S2). Similarly, Coleoptera, Diptera, and Lepidoptera encounter rates were 34 %, 33 %, and 31 % lower in the coffee agroforest than rainforest, while Hymenoptera encounter rates in the agroforest were more than twice that of rainforest (Fig. 2; Table S2).

Overall, we identified 214 and 180 moth taxa to the genus or morpho-genus level at light screens in the rainforest and coffee agroforest, respectively. The standardized genus-level richness of Lepidoptera was higher in the rainforest (mean = 213.86, 95 % CI = 170.84–256.60) than in agroforest (mean = 156.50, 95 % CI = 131.90–181.10). The number of beetle genera or morpho-genera encountered in the rainforest and agroforest were 53 and 82, respectively. The standardized genus-level richness of Coleoptera was higher in the agroforest (mean = 81.22, 95 % CI = 62.61–99.82) than in rainforest (mean = 29.11, 95 % CI = 24.65–33.57).

Erebidae, Geometridae, and Crambidae were the most abundant Lepidoptera families (excluding unidentified micromoth families) in the coffee agroforest (Erebidae: 46 %, Geometridae: 12 %, and Crambidae: 13.81 %), and comprised three of the four most abundant families in the rainforest (Nolidae: 22 %, Erebidae: 20 %, Geometridae: 12 %, and Crambidae: 7 %; Table S3). These three families were also the most diverse families in both habitats, comprising 33 %, 23 %, and 16 % of all genera in the rainforest and 33 %, 15 %, and 25 % of genera in coffee agroforest, respectively (Table S3).

Aquatic beetles (Gyrinidae: 43 %, Hydrophilidae:18 %) were the most abundant beetle families in the rainforest, followed by Scarabaeidae (8 %) and Elateridae (7 %), while Tenebrionidae (29 %), Scarabaeidae (27 %), and Hydrophilidae (10 %) dominated beetle abundance in the agroforest (Table S3). Tenebrionidae was the most diverse family (17 % of all genera) in the rainforest followed by Scarabaeidae and Elateridae (15 % each), while Carabidae was the most diverse family in the agroforest (16 %) followed by Scarabaeidae and Tenebrionidae (11 % each; Table S3).

Coleoptera and Lepidoptera communities at genus level in the coffee agroforest and in the rainforest occupied distinct positions over the first three NMDS axes, with NMDS stress values of 0.19 and 0.15, respectively (Fig. 3a, b). The ANOSIM test indicated significant differences between the rainforest and coffee agroforest communities of both Lepidoptera (Anosim Static R = 0.47, $P < 0.01$) and Coleoptera (Anosim Static R = 0.32, $P < 0.01$).

3.2. Pollination success

In the pollinator exclusion experiment in the coffee agroforest, pollination success was lowest in night-accessible flowers (mean =

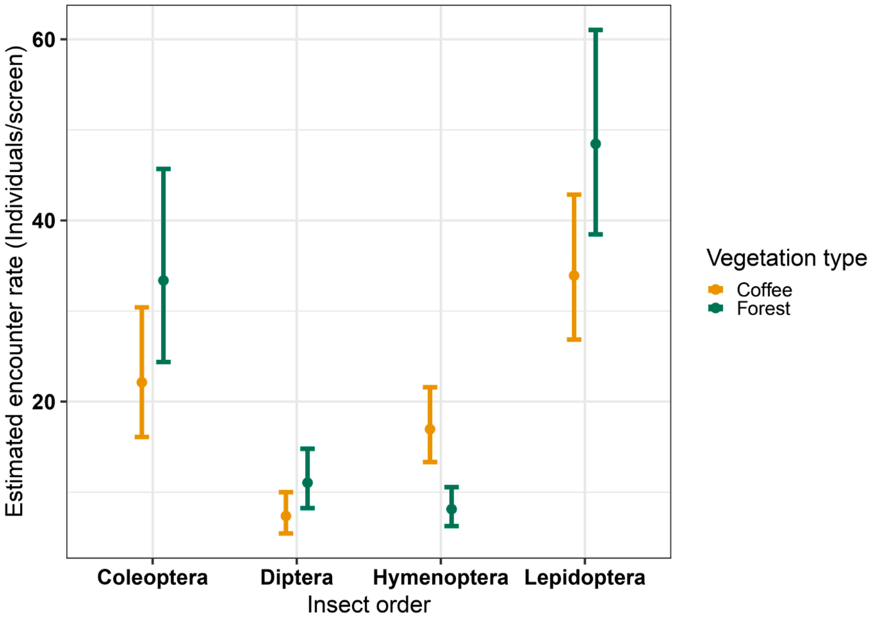

Fig. 2. Encounter rates per light screen of the four focal insect orders and 95 % confidence intervals estimated from generalized linear models.

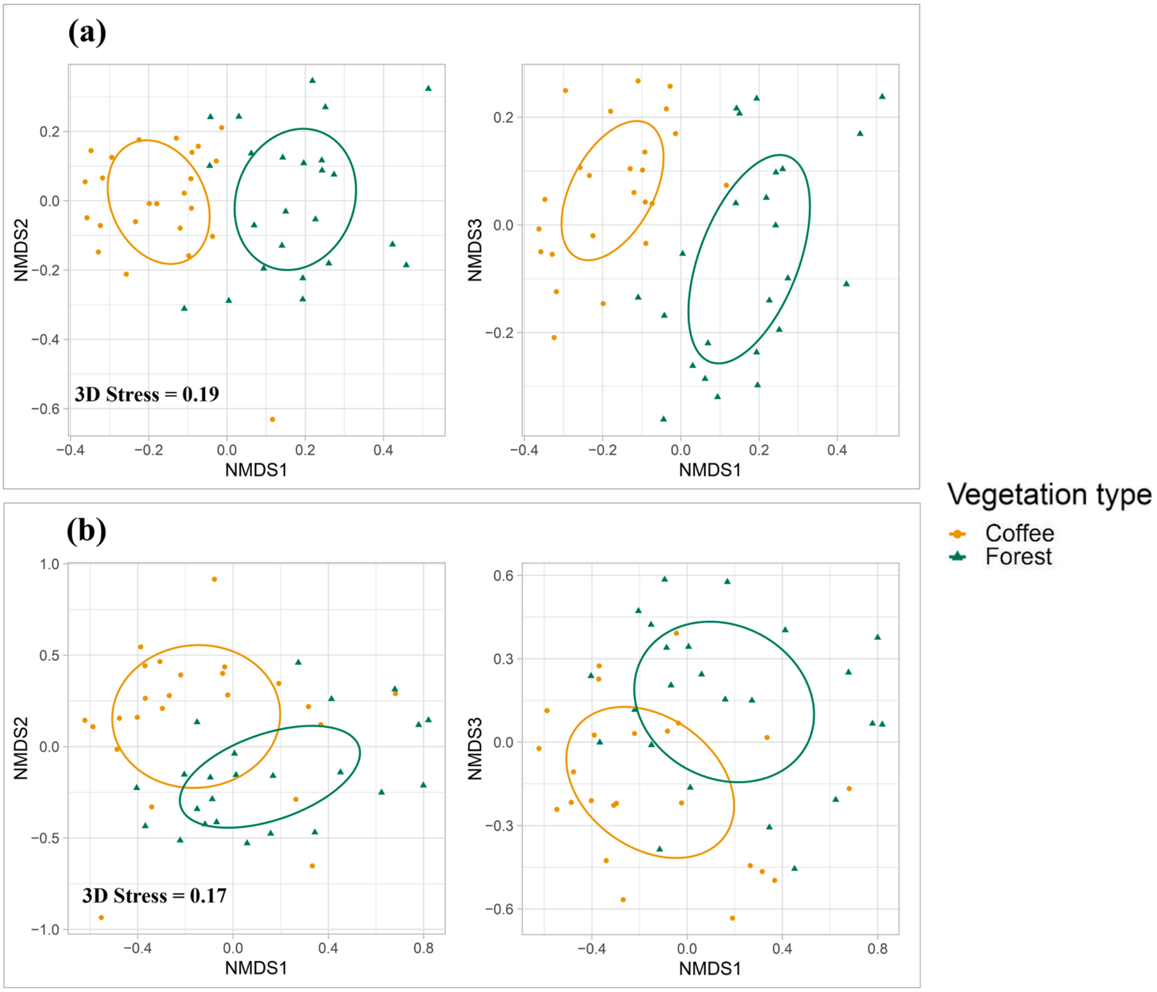

Fig. 3. Three-dimensional non-metric multidimensional scaling (NMDS) plots depicting the dissimilarity at the genus level of (a) Lepidoptera and (b) Coleoptera communities between coffee agroforest and secondary rainforest. Ellipses indicate 95 % confidence intervals associated with each habitat.

10 %, 95 % CI = 5 %–18 %) and negative controls (day- and night-inaccessible; mean = 8 %, 95 % CI = 4 %–15 %), with complete overlap of the 95 % CIs of each treatment with the means of the other indicating no difference in pollination success between the two treatments (Fig. 4a; Table S4). Pollination success was significantly higher in positive control (day- and night-accessible; mean = 24 %, 95 % CI = 14 %–38 %) and day-accessible flowers (mean = 19 %, 95 % CI = 11 %–32 %), with no statistical differences in success between these two treatments (Fig. 4a; Table S4). In this experiment, the fixed effect (treatments) explained relatively little variation in pollination success compared to the bush-level differences incorporated in the random effect term (marginal $R^2 = 0.05$; conditional $R^2 = 0.40$; Table S4). In the experiment on remnant coffee bushes in the secondary rainforest, by contrast, pollination success was higher in positive controls (mean = 60 %, 95 % CI = 49 %–70 %) than day-accessible (mean = 47 %, 95 % CI = 36 %–58 %) flowers (Fig. 4b; Table S4). While pollination success of night-accessible flowers remained relatively low (mean = 4 %, 95 % CI = 2 %–7 %), it was marginally higher than negative control flowers (mean = 2 %, 95 % CI: = 1 %–5 %; Fig. 4b; Table S4). Unlike the experiment in the coffee agroforest, a substantial amount of variation in pollination success was explained by treatment effects in the experiment in the secondary rainforest (marginal $R^2 = 0.47$; conditional $R^2 = 0.56$; Table S4).

4. Discussion

Our study from the Western Ghats is among the first to investigate nocturnal insect communities in coffee agroforests and their contribution to coffee pollination. Our light screen study showed that nocturnal insects were less abundant and compositionally distinct at the genus level in coffee relative to secondary rainforest, broadly resembling previous findings on tropical insect community responses to land-use change and intensification (Millard et al., 2021; Raven and Wagner, 2021). Our pollinator exclusion experiments did not detect nocturnal pollination of robusta coffee in the active agroforest, while uncovering some evidence for nocturnal pollination in unmanaged coffee bushes in the secondary rainforest. Our findings suggest that robusta coffee is primarily cross-pollinated by diurnal insects, but if buffered from the impacts of land-use change, nocturnal insects could also offer small enhancements to coffee pollination (Samnegård, 2020).

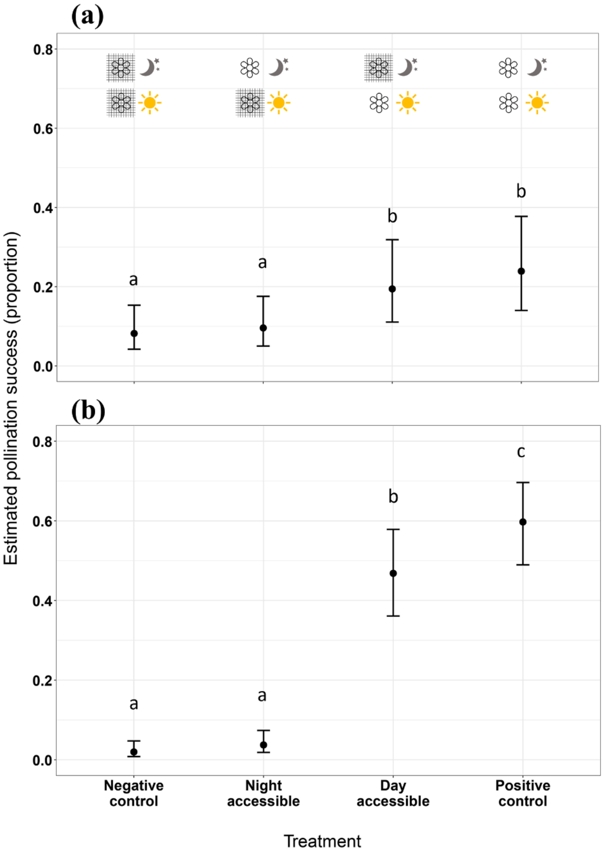

Fig. 4. Pollination success associated with night- and day-access treatments and controls in the pollinator exclusion experiments conducted in (a) robusta coffee agroforest and (b) an area of remnant robusta coffee in the secondary rainforest. Points and error-bars represent pollination success means and 95 % confidence intervals estimated from generalized linear mixed-effects models.

4.1. *Coffee agroforestry and nocturnal insect communities*

Nocturnal insects were less abundant in the coffee agroforest than the secondary rainforest, and differences in community composition were evident at the level of taxonomic order and genus. Coffee harbored relatively fewer Lepidoptera, Coleoptera and Diptera but more Hymenoptera, and while Lepidoptera genera were fewer and Coleoptera genera more numerous in coffee, both orders differed markedly in genus-level composition between the coffee agroforest and rainforest. Such changes – i.e., varying responses of abundance and diversity across insect orders leading to broad divergence in nocturnal insect community composition between coffee and rainforest – are consistent with known effects of land-use change on insects (Fisogni et al., 2025; Gossner et al., 2023, 2016; Millard et al., 2021; Pires et al., 2022) and other taxa such as birds (Bohada-Murillo et al., 2020) and amphibians (Murrieta-Galindo et al., 2013; Sankararaman and Miller, 2024).

The responses of nocturnal insect abundance, genus richness, and genus-level composition to land-use change largely followed expected lines (Millard et al., 2021), but a few exceptions warrant further exploration. For example, coffee unexpectedly harbored higher abundances of Hymenoptera. While we did not attempt systematic identification to the genus level for this group as visual methods alone are unreliable for doing so, we did observe that the majority of Hymenoptera recorded in coffee belonged to two parasitoid wasp families – Ichneumonidae and Braconidae (HRN pers. obs.). There is some evidence from previous studies of parasitoid wasps not being negatively affected by land-use change to tropical agroforestry, including coffee (Klein et al., 2002; Pak et al., 2015). Another result that contradicted initial expectations was the high genus-level richness of Coleoptera in coffee relative to rainforest. While we lack ecological trait data at the genus level, secondary information at the family level suggests that this pattern might be associated with the responses of disturbance-sensitive versus disturbance-tolerant taxa. For example, many beetle genera in coffee belonged to Carabidae (Table S3), which is a family that is known to comprise many disturbance-sensitive genera (Arenas-Clavijo and Armbrecht, 2019). Meanwhile, the aquatic Gyrinidae – which is known to be a forest specialist that responds negatively to disturbance (Subramanian et al., 2005) – was relatively abundant in the rainforest but absent from coffee agroforest. Similarly, among Lepidoptera, while a similar suite of families dominated both habitats in terms of abundance and diversity, the family Geometridae – which is known to comprise several disturbance-sensitive genera (Alonso-Rodríguez et al., 2017; Fiedler et al., 2007; Klein et al., 2002) – was relatively less abundant in coffee agroforest, while Crambidae and Erebidae, which comprise genera having affinity for open and disturbed habitats (Alonso-Rodríguez et al., 2017; Fiedler et al., 2007), were relatively more abundant in coffee than the rainforest (Table S3).

Collectively, these patterns suggest that although not a substitute for natural forests, coffee grown under structurally complex and floristically diverse tree shade could offer relatively hospitable conditions for certain native nocturnal insect groups. While our assessment focused on the flowering season in a traditional coffee agroforest, seasonal variation in nocturnal insect communities, and their responses in more intensively-managed coffee agroforests, require further investigation. There is also a need for traits-based studies to better understand the drivers and implications of nocturnal insect community responses to land-use change (Wong et al., 2019), which in turn requires efforts to build ecological trait datasets for nocturnal insects.

4.2. Coffee pollination success

Our pollinator exclusion experiments (which tested and ruled out the influence of procedural effects) suggest that robusta coffee is predominantly diurnally pollinated, despite exhibiting certain floral traits suggestive of nocturnal pollination (Borges et al., 2016; Samnegård, 2020). Our results from the experiment in the secondary rainforest do suggest, however, that nocturnal insects can augment coffee pollination by diurnal insects under certain circumstances. Previous studies from coffee agroforests have shown that diurnal pollinator diversity, floral visitation rates, and pollination success decrease with increasing farm management intensity and/or distance from remnant natural forests (Hipólito et al., 2018; Klein, 2009; Krishnan et al., 2012). Similar factors could explain why the positive controls that were accessible for diurnal and nocturnal pollination had higher pollination success than the day-accessible treatment (60 % vs 46 %) in the unmanaged secondary rainforest, but not in the more intensively-managed active agroforest that harbored lower numbers and an altered community of nocturnal insects. The same could also explain overall higher coffee pollination success in the secondary rainforest (60 %) than active agroforest (24 %), although such absolute differences in pollination success could also be due to other factors such as coffee density and year of experiment.

5. Conclusions

Our findings suggests that in comparison to secondary rainforests, robusta coffee agroforestry reduces nocturnal insect abundances, reduces the richness of Lepidoptera genera but not Coleoptera genera, and alters genus-level community composition to the apparent advantage of disturbance-adapted generalists over rainforest specialists. Our findings imply, therefore, that while traditional polyculture shade coffee agroforests cannot substitute for rainforests as refuges for nocturnal insect communities as a whole, they can represent a relatively hospitable habitat for certain groups within this community. Further research and a better understanding are needed of why certain groups decline while others persist, and the roles of local- and landscape- factors such as native tree diversity (Boreux et al., 2013; Fisher et al., 2017; Jha and Vandermeer, 2010), pesticide management (Tuell and Isaacs, 2010), and proximity to natural ecosystems (Centeno-Alvarado et al., 2024) in making coffee agroforestry systems more nocturnal insect-friendly.

Our pollination experiments showed that unlike crops such as apple and strawberry that experience substantial nocturnal pollination (Fijen et al., 2023; Robertson et al., 2021), nocturnal pollination in robusta coffee may be low and context-dependent. Our experiments confirmed the predominant role of diurnal insects in coffee cross-pollination while providing some support for the hypothesis that nocturnal insects can make a minor contribution to coffee pollination (Samnegård, 2020). Nocturnal pollination effects were evident only in abandoned coffee bushes in the secondary rainforest and not in the coffee agroforest, and one possible explanation for this difference is the observed decline in potential nocturnal pollinator abundances in the more intensively-managed habitat. Collectively, our findings lead to the hypothesis that if robusta coffee is cultivated using methods that minimize the disruption of nocturnal insect communities, then nocturnal insects could enhance and complement pollination services provided by diurnal pollinators. This hypothesis warrants rigorous evaluation through standardized exclusion experiments along gradients of farm management intensity and proximity to forest remnants, as previous studies have done for diurnal pollination, in different coffee-growing regions (Geeraert et al., 2020; González-Chaves et al., 2020; Krishnan et al., 2012; Pereira Machado et al., 2024; Saturni et al., 2016).

CRediT authorship contribution statement

Smitha Krishnan: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Anand M Osuri:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **H Rama Narayanan:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109966.

Data availability

The datasets and codes used in this study are openly available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.6djh9w18f.

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