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Brief Report

Artificial Light at Night (ALAN) Influences Understory Plant Traits through Ecological Processes: A Two-Year Experiment in a Rubber Plantation in China

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Abstract: Artificial light at night (ALAN) demonstrated a new ecological factor that influences organisms through a multi-approach. Yet, the impacts of ALAN on understory plants remain largely unknown. We evaluated whether ALAN would affect the leaf mass per area (LMA) of understory plants through a two-year field light experiment in a tropical rubber plantation in south China. We hypothesized that ALAN could impact the understory in two ways: by directly supplementing light to aboveground plant parts (which increases LMA) and indirectly affecting soil nutrient composition by attracting insects (which decreases LMA). We selected two species: *Colocasia gigantea*, representing shade-tolerant species, and *Melastoma candidum*, representing light-demanding species. We measured canopy openness, LMA, soil nutrients, and individual distance away from light resources. Our Bayesian linear mixed model showed a negative relationship between LMA and the strength of ALAN, indicating that ALAN may influence LMA more indirectly by enhancing soil nutrient availability rather than directly acting as a light resource. This relationship was significant for *Colocasia gigantea* but not for *Melastoma candidum*. These results suggest that ALAN might have complex and species-specific impacts on the understory ecosystem. Our study underscores the need for continued research and informed management of anthropogenic ecosystems.

Keywords: *Colocasia gigantea*; *Melastoma candidum*; artificial light at night; functional traits; leaf mass per area; specific leaf area; understory

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1. Introduction

Artificial light at night (ALAN), a leading contributor to light pollution, has disrupted ecological processes since the early 20th century [1–3]. A recent study estimated that around 23% of the world's inhabited land surfaces, accounting for over 80% of the global population, are subject to the adverse effects of light pollution [4]. Although the intensity of ALAN varies several orders of magnitude from faint skyglow reflected from distant cities to direct illumination of urban and suburban vegetation [1], ALAN influences the behavior or physiology of broad ranges of taxonomic groups, including mammals, birds, reptiles, amphibians, fish, invertebrates, and plants [5–8]. It could also alter ecosystem functions [5,8]. For example, ALAN attracts insects and interferes with their movement, foraging, reproduction, and development [9–11]. These interferences have been linked to declines in insect populations [9]. Unlike animals, only a handful of studies have been published on the effects of ALAN on plants [1,12,13]. Speißer et al. (2021) conducted plant growth experiments with and without weak ALAN (28 lux: within the range of light intensities at ground level under street lights) and showed that ALAN increases the biomass of herbaceous plants. Those previous studies suggest that even low-intensity

ALAN can influence plant biomass [9,13]. However, few studies have examined the effects of ALAN on plant functional traits in conditions close to their natural environment.

ALAN might, directly and indirectly, affect plant leaf functional traits. First, ALAN might directly affect plant leaf functional traits, such as leaf mass per area (LMA), because ALAN could work as an additional light resource. LMA is the key trait in the leaf economics spectrum, spanning from leaves that are low-cost and short-lived to those that are high-cost and long-lived [14–16]. Although LMA is driven by inherent genetic mechanisms [17], environmental stresses (temperature, water, and light) also shape LMA. Plants can sense light through photoreceptors, allowing them to respond to four parameters of their light environment: light spectral quality, light intensity, light direction, and light duration [8,18]. Terashima et al. (2006) [19] showed that the light-saturated rate of leaf photosynthesis per unit area is highly correlated with leaf structural parameters such as leaf thickness, leaf mass per area, mesophyll surface area, and chloroplast surface area, resulting in sun leaves being thicker than shade leaves as the height of the palisade tissue in sun leaves is greater than that in shade leaves. For individual species, LMA was proportional to species distributions along the insolation gradient and was significantly higher in evergreen versus deciduous species [20–22]. Moreover, among a local community, Ackerly et al. (2002) demonstrated that the average values of LMA significantly increased with increasing potential diurnal insolation (PDI).

On the other hand, ALAN might indirectly affect plant leaf functional traits because ALAN has the potential to increase soil fertility by attracting insects. Many insects orient themselves by maintaining a constant angle to light rays and are attracted by light [23,24]. Previous studies showed that 30–40% of insects die soon after approaching street lamps due to collision, overheating, dehydration, or predation [25,26]. Since nitrogen (N) and phosphorus (P) are the nutrients most frequently limiting primary productivity in forest ecosystems [27], dead insects killed by ALAN could be important nutrient inputs for soil nutrients [28]. Soil resources, especially N and P availability, are known to affect LMA and leaf N and P contents [16,29,30], and those effects are known to be opposite to the effects of light [20,31] (i.e., strong light increases LMA but high levels of N availability decrease LMA).

In this study, we investigated the effects of ALAN on the LMA of understory plants through a two-year experiment in a tropical rubber plant forest in south China. Rubber plantations, one of the main drivers of deforestation in Southeast Asia [32], coupled with low canopy closure and sparse shrub density, can represent anthropogenic ecosystems under land use. A previous study conducted under the same experimental setup at this site demonstrated that ALAN attracts ants [11]. We selected two understory species as subjects of this experiment, each representing a light-demanding and shade-tolerant species, to discern differences in their responses to ALAN. Our hypothesis proposes that ALAN would influence the understory plants via two distinct pathways. The first would be a direct effect, with ALAN serving as a supplementary light resource for plants, increasing LMA. The second pathway would be an indirect effect, where ALAN enhances soil nutrient availability, decreasing LMA. To determine the relative importance of these two pathways, we estimated the influences of ALAN, daylight, and their interaction on the LMA of the understory plants.

2. Materials and Methods

2.1. Experimental Setup

ALAN field experiments were located within the Xishuangbanna Tropical Botanical Garden (XTBG), China, in a rubber tree forest (N21°54′ E101°16′; elevation: 560 m; Figure 1), where we set 5 plots and selected two plots for this experiment based on the natural distribution of the target plant species. The rubber trees were planted 2 m apart within rows, with inter-row spacing ranging from 4 m to 12 m.

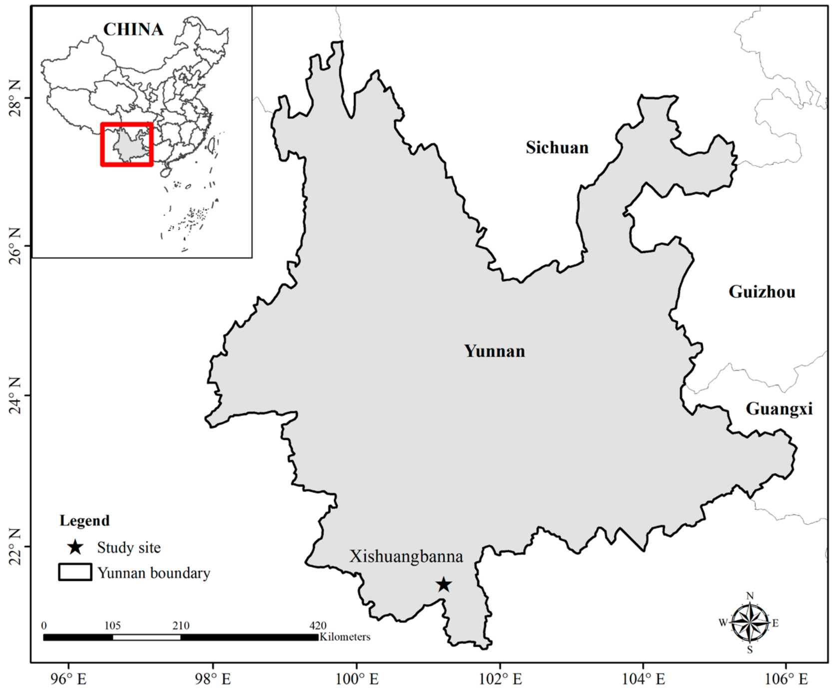

Figure 1. Geographic location of the study site (star).

The overstory stands at approximately 20 m in height, while the understory exhibits a notably lower density compared to that of the primary forest. In the study area, the average yearly temperature is recorded at 21.7 °C, accompanied by an average annual precipitation of 1557 mm. No fertilizer was used in the study area. LED lights (10 W; Tc = 6696 K) were used to create an artificial light environment in all plots at night (Figure 2). The LED system was programmed to function automatically from 8 p.m. to 5 a.m. daily. A rechargeable lithium battery (12 V/30 Ah) and an electric timer controlled the timing and duration of the LED operation at night. The battery and LEDs were connected by electric wire and hung from a tree branch with a lampshade approximately 2 m from the ground. The light intensity of LED lights at the light sources was 372.8 ± 66.6 (mean ± SE) lux. The light intensity decreased with distance: 190.2 ± 26.5 lux at a radius of 1 m, 62.0 ± 4.9 lux at a radius of 2 m, and 9.9 ± 0.7 lux at a radius of 4 m. The light intensity was almost undetectable at 0 lux beyond 10 m. Thus, we treated distance as a continuous variable in our analysis to capture the gradient effect of ALAN on plants. Additionally, plant individuals at greater distances (e.g., beyond 5 m) can be conceptually viewed as controls. The experiment was set up in November 2019, and leaf disc samples were collected two years later, in November 2021.

2.2. Species Selection

We considered the understory conditions to select species, ensuring that at least 15 mature individuals were present from the light source to 10 m away from it. Essential criteria also included the species being part of functional groups, specifically evergreen species, and not belonging to nitrogen-fixing families such as Leguminosae. As a result, we chose two species, each from a different plot, for our study: *Colocasia gigantea*, representing shade-tolerant species, and *Melastoma candidum*, representing light-demanding species.

Figure 2. Photographs of the experimental setup during daytime (**A**) and nighttime (**B**) in a rubber tree forest within the Xishuangbanna Tropical Botanical Garden (XTBG), China. One of the target species, *Colocasia gigantea*, is visible in both pictures.

2.3. Measurements

We measured the horizontal distance and geographic orientation of each individual away from the LED using a tape measure representing the relative effects of ALAN. We used a fish-eye lens to quantify canopy openness, indicative of individual daylight interception [33–35]. The canopy openness of each individual was photographed on the top of each individual by Nikon COOLPIX4500 with a fish-eye lens (Nikon FC-e8, Tokyo, Japan) and then measured using the R package LeafArea (version: 0.1.8) [36].

For leaf mass per area (LMA), we used a 1-cm-diameter puncher instead of using whole-leaf LMA values, avoiding veins and leaf margins [37]. We chose five healthy leaves from each individual *M. candidum* plant and between three and five healthy leaves from each individual *C. gigantea* plant. We then punched five leaf discs from each *M. candidum* leaf and seven leaf discs from each leaf of *C. gigantea*. In total, we sampled 165 leaves from 35 *C. gigantea* individuals and 95 leaves from 19 M. candidum individuals. For soil nutrients (N, C, P), we collected surface soil samples (0–10 cm depths) in five plots in June 2019 and June 2022 to investigate the general trends in soil nutrients. We took three replicates at the place under ALAN and 10 m away from ALAN, separately from each plot. After sampling, the soils were air-dried at room temperature for one week, then sieved through 0.85-mm and 0.15-mm mesh, finally used for total N, C measurements by combustion using an elemental analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Langenselbold, Germany) and total P measurement by inductively coupled plasma atomic-emission spectrometer (iCAP7400, Thermo Fisher Scientific, Waltham, MA, USA). We then calculated the relative percentage change of each nutrient between the values in 2019 and 2022 to compare the soil nutrient change with ALAN's effect (sampled under ALAN) and without ALAN's effect (sampled 10 m away from ALAN).

2.4. Data Analysis

To analyze the effects of ALAN, daylight, and their interaction on *M. candidum* and *C. gigantea*, we fitted a Bayesian linear mixed-effects model for each species. The leaf mass per area (LMA) of each leaf of each individual was modeled as a function of the distance from the ALAN source for each individual, the canopy openness of each individual, and the interaction between the distance from the ALAN source and the canopy openness. We transformed the distance from the ALAN source for each individual using a log and reciprocal function, as the intensity of ALAN diminishes non-linearly with distance. Hereafter, we refer to the distance from the ALAN source for each individual as the ALAN effect and the canopy openness of each individual as the daylight effect. To account for non-independence among individuals of the same species, we included individuals as a random intercept in our models.

Posterior distributions of all parameters were estimated using the Hamiltonian Monte Carlo algorithm (HMC) implemented in Stan [38] using weakly-informative priors [39]. The convergence of the posterior distribution was assessed with the Gelman-Rubin statistic with a convergence threshold of 1.1 [40] and effective sample sizes > 400 [41] for all parameters. All statistical analyses were conducted in R version 4.2.0 [42] using the R package targets version 1.2.0 for workflow management [43]. Codes are available at https://github.com/congz007/light_project (accessed on 1 November 2023).

3. Results

The influence of artificial light at night (ALAN) and daylight on LMA had significant effects on the species *Colocasia gigantea*, while for *Melastoma candidum*, these effects were not significant (Figure 3). In the case of *C. gigantea*, ALAN led to a significant decrease in the average individual leaf mass per area (LMA) value (Table 1, slope: −0.1052 [95% CI: −0.1500, −0.0613]). Although *M. candidum* showed a similar decrease in LMA value in response to ALAN (Table 1, slope: −0.0434 [95% CI: −0.1147, 0.0278]), this change was not statistically significant. The interaction of the effects of ALAN and daylight did not yield any significant results for both species (Table 1).

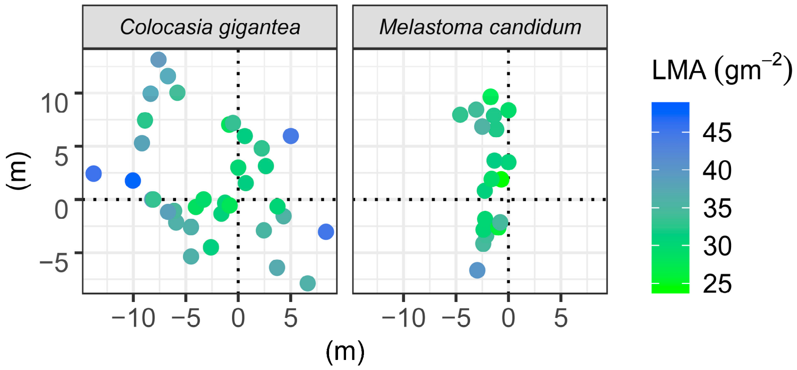

Figure 3. Spatial map showing leaf mass per area (LMA) values for the two experimental species, *C. gigantea* and *M. candidum*. Each species naturally occurred in one of the two plots. The ALANs are located in the center of the maps (0, 0). Color represents the LMA values. Note that the apparent linear distribution of *M. candidum* is due to its occurrence along a slope within the plot.

Table 1. Summary of Bayesian linear mixed-effect models testing the effects of artificial light at night (ALAN), daylight, and their interaction on leaf mass per area (LMA) values. Posterior means and 95% credible intervals (CI) are shown. Intervals that do not include zero are highlighted in bold.

Variables	Mean	95% CI
Melastoma candidum		
ALAN	−0.0434	[−0.1147, 0.0278]
Daylight	0.0006	[−0.0736, 0.0768]
ALAN × Daylight	−0.0309	[−0.0840, 0.0233]
Colocasia gigantea		
ALAN	−0.1052	**[−0.1500, −0.0613]**
Daylight	0.0489	**[0.0036, 0.0934]**
ALAN × Daylight	−0.0113	[−0.0436, 0.0216]

Soil nutrients decreased from 2019 to 2022 [$X_{2022}/X_{2019} < 1$, where X represents carbon I, nitrogen (N), and phosphorus (P); Figure 4] across all of the locations, regardless of the distance away from ALAN. However, the relative percentage change in each soil nutrient demonstrated that the locations under ALAN sustained more nutrients in 2022

(C_{2022}/C_{2019} = 0.919, N_{2022}/N_{2019} = 0.948, P_{2022}/P_{2019} = 0.537) compared to the locations 10 m away from ALAN (C_{2022}/C_{2019} = 0.663, N_{2022}/N_{2019} = 0.695, P_{2022}/P_{2019} = 0.492) in the plot where *C. gigantea* was investigated. In the plot where *M. candidum* was investigated, we found less pronounced differences between the locations under ALAN (C_{2022}/C_{2019} = 0.677, N_{2022}/N_{2019} = 0.761, P_{2022}/P_{2019} = 0.729) and those 10 m away from ALAN (C_{2022}/C_{2019} = 0.712, N_{2022}/N_{2019} = 0.746, P_{2022}/P_{2019} = 0.742).

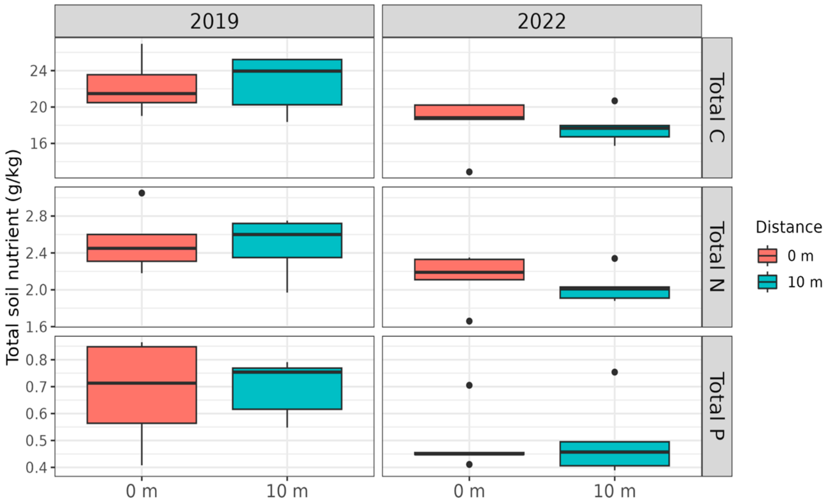

Figure 4. Soil nutrients across five plots under the ALAN and 10 m away from the ALAN in 2019 and 2022.

4. Discussion

Our findings support the hypothesis that artificial light at night (ALAN) can influence leaf mass per area (LMA) in understory plants, but the response appears to vary among species. We observed a significant decrease in LMA in response to ALAN in the shade-tolerant species *Colocasia gigantea*, but not in the light-demanding species *Melastoma candidum*. Below, we elaborate on the insights gained from our experiment and the implications of our results for the effects of ALAN.

We observed an apparent decline in soil nutrient content from 2019 to 2022. This trend could be primarily attributed to the nutrient absorption characteristics of the rubber trees [44] and the absence of fertilizer applications at our study site. Rubber trees are known for their high nutrient uptake, which can lead to significant soil nutrient depletion over time. This effect was evident in our study, with noticeable decreases in soil nutrient levels over two years in both ALAN-influenced and non-influenced areas. This soil nutrient decline seemed less pronounced near ALAN in the plot populated by *C. gigantea*. This trend suggests a potential positive impact of ALAN on soil nutrient content, likely mediated by the attraction of insects. ALAN is known to attract insects, which, upon death due to collision, overheating, or predation, could contribute additional nutrient inputs into the soil, such as N and P [25,26]. This ALAN-induced insect influx could help offset the nutrient depletion caused by the nutrient-intensive rubber trees, thereby helping to maintain soil nutrient levels under ALAN exposure.

The significant decreaIe in LMA for *C. gigantea* under ALAN could be predominantly driven by indirect effects mediated through changes in soil nutrient availability rather than direct effects of ALAN acting as a light resource because sunlight increased LMA (Table 1). Indirect effects on LMA, rather than direct effects observed in the previous study [13], might also lead to enhanced plant growth rates, potentially increasing biomass. The presence of ALAN is known to attract a higher density of insects, many of which may die due to collision, overheating, dehydration, or predation [25,26]. The decomposition of these deceased insects could lead to considerable enrichment of soil nutrients, particularly N and P [28,45–47], which are fundamental to plant growth. Although the precise quantity of dead insects and the resultant increase in soil nutrient content are subjects for further detailed study, this enhanced nutrient availability could potentially shift the resource allocation strategy of *C. gigantea*. Additionally, increased soil nutrient availability, particularly N, could increase the photosynthetic capacity of *C. gigantea*. The enhanced nutrient availability may enable *C. gigantea* to allocate more resources to rapid leaf growth rather than structural tissue, leading to a decrease in LMA [14,31].

On the other hand, ALAN did not have a significant effect on LMA in the light-demanding species *M. candidum*. Light-demanding species receive stronger sunlight than shade-tolerant species, which might result in a small effect of ALAN on their LMA. Because the effect of daylight was not significant either, intraspecific trait variability (ITV) itself for light-demanding species may inherently be smaller than for shade-tolerant species. Although many studies have explored ITV within different functional groups, such as herbs and trees [48], there needs to be more research into the ITV differences between light-demanding species and shade-tolerant species. Additionally, the less pronounced soil nutrient differences between ALAN-influenced and non-influenced areas in the plot with *M. candidum* compared to the plot with *C. gigantea* may explain the lack of significant change in LMA for *M. candidum*. The ALAN treatment was set up on a slope in this plot, and therefore, increased soil nutrients resulting from dead insects attracted by ALAN might be more likely to be washed off and not persist in the soil [49–51]. Alternatively, ALAN's attraction to insects might be spatially dependent, which leads to certain locations attracting fewer insects and consequently experiencing a diminished soil fertilization effect.

Although our results partially support our hypothesis, we acknowledge several areas of potential improvement and offer suggestions for future work. First, we focused on a limited number of species in our study. Collecting a large number of individuals from the same species is challenging in field experiments. Bayesian hierarchical models offer the flexibility to accommodate more species. Considering species-level parameters rather than fitting each species separately can deal with a limited dataset [40]. Future studies should include more species to assess generality better. Second, the accuracy and uniformity of leaf-scale measurements need enhancement. The shading of some leaves by their neighbor could result in sporadic exposure to ALAN. Furthermore, the angle of the leaf blade influences light interception, warranting its incorporation in analyses. Future studies might need to consider leaf-level fisheye cameras or light data loggers to more precisely quantify light interception at the leaf level. Third, we also recognize the importance of Photosynthetic Photon Flux Density (PPFD) [52] and photosynthetic compensation points in determining plant responses to light and overall photosynthetic performance. Integrating these metrics into future research will provide a more comprehensive perspective on plant-ALAN interactions and adaptations to varying light conditions. Finally, while our study focused on a single trait (i.e., LMA), which is the key trait for the leaf economic spectrum, we acknowledge that there are other important traits for resource acquisition and defense strategies.

ALAN, an increasingly prevalent aspect of our anthropogenic world, can have complex and nuanced impacts on forest ecosystems. Although it has been demonstrated that insolation (i.e., natural light) increases LMA [20,21], our research indicates that ALAN may influence LMA more indirectly by enhancing soil nutrient availability rather than directly acting as a light resource. ALAN may unexpectedly impact forest health and productivity by affecting understory plant functional traits and possibly soil nutrient dynamics. Controlled experiments potentially underestimate species interactions and unpredictable environmental heterogeneity because many irreplaceable features of field conditions, such as subtle nutrient change, herbivores, and competitors, are usually absent in the controlled experiments. Thus, robust tests of the ALAN effects on the understory will require more experimental work under field conditions. Further investigations into the intricate relationships between ALAN, plant functional traits, and soil nutrient dynamics are warranted to enable the development of comprehensive forest management strategies that consider the broad implications of artificial lighting.

5. Conclusions

Artificial light at night (ALAN) is an emerging concern with wide-ranging and species-specific effects on understory vegetation. In this two-year field experiment conducted in a rubber plantation in southern China, we examined the responses of two plant species (*C. gigantea* and *M. candidum*) to ALAN. We observed different responses in the LMA of these species, with nutrient dynamics affecting *C. gigantea*. These results suggest that it is imperative to recognize species-specific responses and the potential effects of ALAN on nutrient dynamics. Our study underscores the need for continued research and informed management of anthropogenic artificial ecosystems.

Author Contributions: C.Z. and M.K. conceived the study; A.N. and X.S. set up the ALAN experiments; C.Z. and X.S. collected data; C.Z. performed the analysis; C.Z. and M.K. led the writing of the paper; and all authors contributed to revisions. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data and codes for this study are publicly available at https://github.com/congz007/light_project (https://zenodo.org/doi/10.5281/zenodo.10060043, accessed on 1 November 2023).

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Conflicts of Interest: The authors declare no conflict of interest.

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