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Research article

Declining floral color diversity alters bee color preferences in fragmented habitats☆

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ABSTRACT

Habitat fragmentation reduces floral color diversity in plant communities, thus resulting in a shift in bee pollinator color preferences, as shown by altered visitation frequency. We conducted a two-year survey of plant-bee interactions on 41 islands and adjacent mainland habitats in a reservoir island system of eastern China. Results showed that bee-blue-green and bee-blue dominated the floral color composition and that a reduction in island area significantly reduced floral color diversity. Visitation frequencies to bee-blue-green, bee-ultraviolet-blue, and bee-ultraviolet-green flowers declined significantly as island area decreased. These changes in floral color diversity altered the color preferences of bees, as shown by the significantly impacted total floral visitation frequencies. The preference for bee-blue-green flowers increased as island area increased, while floral resources showed no significant effect on visitation frequencies. In sum, these results improve our understanding of how pollinators adapt their behavior in fragmented habitats and provide important insights supporting the conservation of floral color diversity as well as the plant species associated with the colors that correspond to a high visitation frequency.

1. Introduction

Pollinators exhibit distinct preferences for floral colors, which alert pollinators of certain floral traits, provide the most accurate and stable signal for flower localization and play a unique role in pollinator attraction (Carvalho et al., 2012; Fenster et al., 2004; Francisco and Ascensao, 2024; Shrestha et al., 2013). One of the most vital pollinators, bees possess trichromatic color vision with photoreceptors maximally sensitive in the ultraviolet, blue, and green wavelengths of light (Chittka, 1992; Peitsch et al., 1992), but they display limited responsiveness to long-wavelength red light. Consequently, bees exhibit a pronounced preference for blue and purple flowers (Briscoe and Chittka, 2001; Dyer et al., 2021; Raine and Chittka, 2007; Streinzer et al., 2021; van der Kooi et al., 2021). Floral color is closely linked to bee foraging efficiency, and bees forage on blue flowers more rapidly and accurately than on red ones (Telles et al., 2017). Furthermore, bee-seeking flowers typically exhibit enhanced short-wavelength reflectance and heightened color contrast in the range of a bee's visual perception (de Camargo et al., 2019). These features contribute to differences in bee visitation frequencies across floral colors. At the same time, bees often prefer colors corresponding to plant species that offer essential nutrition (Chittka et al., 1999; Viana et al., 1997), and they tend to serve as key pollinators for these plants (Ballantyne et al., 2017; Kandori, 2002; Vázquez et al., 2005). Thus, conserving plants with floral colors that correspond to high visitation frequencies is critical for sustaining bee diversity and the stability of plant-bee mutualistic interactions.

The frequency of bee visits to specific flowers is influenced by multiple factors, with floral color diversity (FCD) (Chittka et al., 1999; Tai et al., 2020) and floral resources (Marques et al., 2018; Samnegard et al., 2015) being particularly important. Conservation efforts should focus on

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both characteristics of flowers. FCD exhibits variation that generally correlates positively with plant species richness at the habitat level (Binkenstein et al., 2013). Similarly, floral resources correlate strongly with plant abundance because higher abundance increases resource availability and consequently enhances pollinator visitation (Ebeling et al., 2008; Lazaro et al., 2020). However, most extant studies have focused on total floral resources, which highlights the need for finer-scale investigations partitioned by specific traits such as floral color. Importantly, habitat fragmentation can exert combined effects on FCD and floral resources through modifying species composition and diversity (Haddad et al., 2015; Thornton et al., 2011). Nevertheless, the current body of research lacks data on how habitat fragmentation alters FCD and floral resources in terms of floral colors and how they collectively shape bee visitation patterns.

Habitat fragmentation alters species diversity and composition through its effects on habitat area and isolation. It has been shown to reduce species persistence and movement among patches, consequently lowering interaction richness and abundance between plants and pollinators (Haddad et al., 2015; Santamaria et al., 2018). For bees, habitat fragmentation disrupts the functionality of pollination services (Mayer et al., 2012; Smith and Mayfield, 2018; Warzecha et al., 2016). Correspondingly for plants, habitat fragmentation disrupts their reproductive success (Lazaro et al., 2020). Such shifts in community composition have gradually induced floral color homogenization (Shrestha et al., 2016), thereby resulting in diminished FCD and floral resources. These changes may further modify bee visitation frequencies and preferences across floral colors in fragmented habitats. Collectively, these pieces of evidence highlight the necessity to investigate how variations in floral color traits and floral resources jointly influence bee visitation patterns in fragmented habitats.

Fragmentation alters species composition along with FCD and floral resources in habitats. These combined effects modify bee foraging behavior and color preferences, as reflected in differential bee visitation frequencies across floral colors. Plant species richness and abundance generally increase as habitat area increases (Hu et al., 2019; Liu et al., 2019; Wilson et al., 2020), suggesting a positive correlation between FCD and habitat area. Habitat fragmentation will alter the floral resources and the relative abundance of floral colors, even promoting dominance of specific colors. By analyzing variation in FCD, floral resources, the relative abundance of floral colors and bee visitation frequencies in fragmented habitats, we can assess whether habitat fragmentation induces shifts in bee color preferences and uncover the mechanisms behind such behavioral changes. This approach could advance our understanding of pollinator behavioral adaptations in fragmented landscapes, support predictions of plant-pollinator interactions, and inform targeted conservation strategies tailored to habitat-specific floral color composition and visitation dynamics.

Here, we hypothesize that habitat fragmentation alters floral color composition within habitats through its area and isolation effects, thereby reducing FCD and floral resources, which subsequently drives a shift in bee color preferences. In this study, we aim to determine whether bee color preferences have changed and to examine the mechanisms by which fragmentation influences bee visitation frequencies, with an emphasis on indirect effects mediated by FCD and floral resources. Then, we discuss how best to conserve plant-bee interactions and associated plant species in fragmented landscapes by adjusting the floral color composition.

2. Materials and methods

2.1. Study site

This study was conducted in the Thousand Island Lake (TIL), an artificial reservoir formed in the 1950s by the construction of the Xin'anjiang Dam in Chun'an County, Hangzhou, Zhejiang Province, China (29°22′-29°50′N, 118°34′-119°15′E). The lake has a surface area of ~581 km^2 (water area: ~540 km^2; island area: ~41 km^2). At the water level of 108 m elevation, there are 1078 islands larger than 0.25 ha in the reservoir (Si et al., 2024). The boundaries of forested islands are distinct, with the surrounding matrix composed entirely of water, and the habitats exhibiting relative environmental homogeneity. The isolation and formation time of habitats across different islands remains largely consistent throughout. These islands originated during the partitioning of a discontinuous mainland and became isolated as islands of varying size and isolation levels when the water level rose in 1959. Notably, the vegetation has experienced synchronous development across the islands and in the mainland under identical initial environmental conditions, making this an ideal system in which to study habitat fragmentation (Si et al., 2024; Zhong et al., 2021).

We selected 41 islands (seven large islands (>20 ha) and 34 small islands) and 16 mainland sampling sites for field surveys (see Fig. 1 for the spatial distribution of sampling sites and Table S1 for island attributes). The selected islands spanned the broadest gradients of area and isolation, and the mainland sites covered extensive spatial ranges and contained similar types of vegetation to the islands. Fixed transects were established at both the edge and interior of each sampling site, with surveys conducted over two consecutive years.

2.2. Surveying bee visitation and floral resources

We conducted biweekly surveys at each site from March 22 to July 15, 2023, and from March 26 to July 23, 2024. In each year, we ran seven replicated surveys. Each survey was carried out on days without rain or strong winds during two time slots: 8:30–12:00 and 13:00–17:00. At each site, we established fixed transects (100 m length × 4 m width) in edge habitats with high flowering herb richness and in interior habitats extending inward from the edge. At each visit, edge transects were surveyed for 15 min and interior transects for 10 min. We recorded bee visitations, which were defined as contact with anthers or stigmas on flowers of herbs, shrubs, and trees within a vertical layer of 3.5 m above ground. We identified bee species and estimated their abundance by recording the visiting behavior through photographs or videos. We also recorded flowering plant species and total floral area and collected flowers to measure colors.

Due to limited manpower for the survey, we did not directly measure the quantities of pollen or nectar for each kind of flower. However, we observed that the quantities of each floral resource correlated positively with floral size. Because larger flowers typically allocate more resources than smaller ones, a greater floral size (floral area) or number leads to an increase in total plant community resources (Dorado and Vazquez, 2014; Ortiz et al., 2021). Therefore, we used floral area as a proxy to represent the amount of floral resources (Ren et al., 2023; Sponsler et al., 2023). Floral area was subsequently categorized by color type to quantify both the area and floral resources of distinct floral colors. We quantified floral area using methods adapted to plant growth forms (Dorado and Vazquez, 2014; Sutter et al., 2017). Specifically, floral area of herbaceous species with dense floral aggregations (e.g., *Pseudognaphalium affine* and *Cnidium monnieri*) was quantified as the ground cover area, while floral area of sparse-flowering species (e.g., *Duchesnea indica*) and large-flowered taxa (e.g., *Rosa laevigata* and *Gardenia jasminoides*) was measured as perianth expansion area. In compact-flowered shrubs and small trees with high floral density (e.g., *Symplocos paniculata*), we modeled the canopies as spherical or conical three-dimensional geometric shapes and calculated floral display area as the total surface area of the idealized structure. Some lianoid species (e.g., *Callerya dielsiana* and *Wisteria sinensis*) and plants bearing elongated inflorescences (e.g., *Monochasma savatieri* and *Scutellaria indica*) were analyzed by modeling them as cylinders based on the radius-length of their inflorescence, with floral area derived from the lateral surface area of these cylinders.

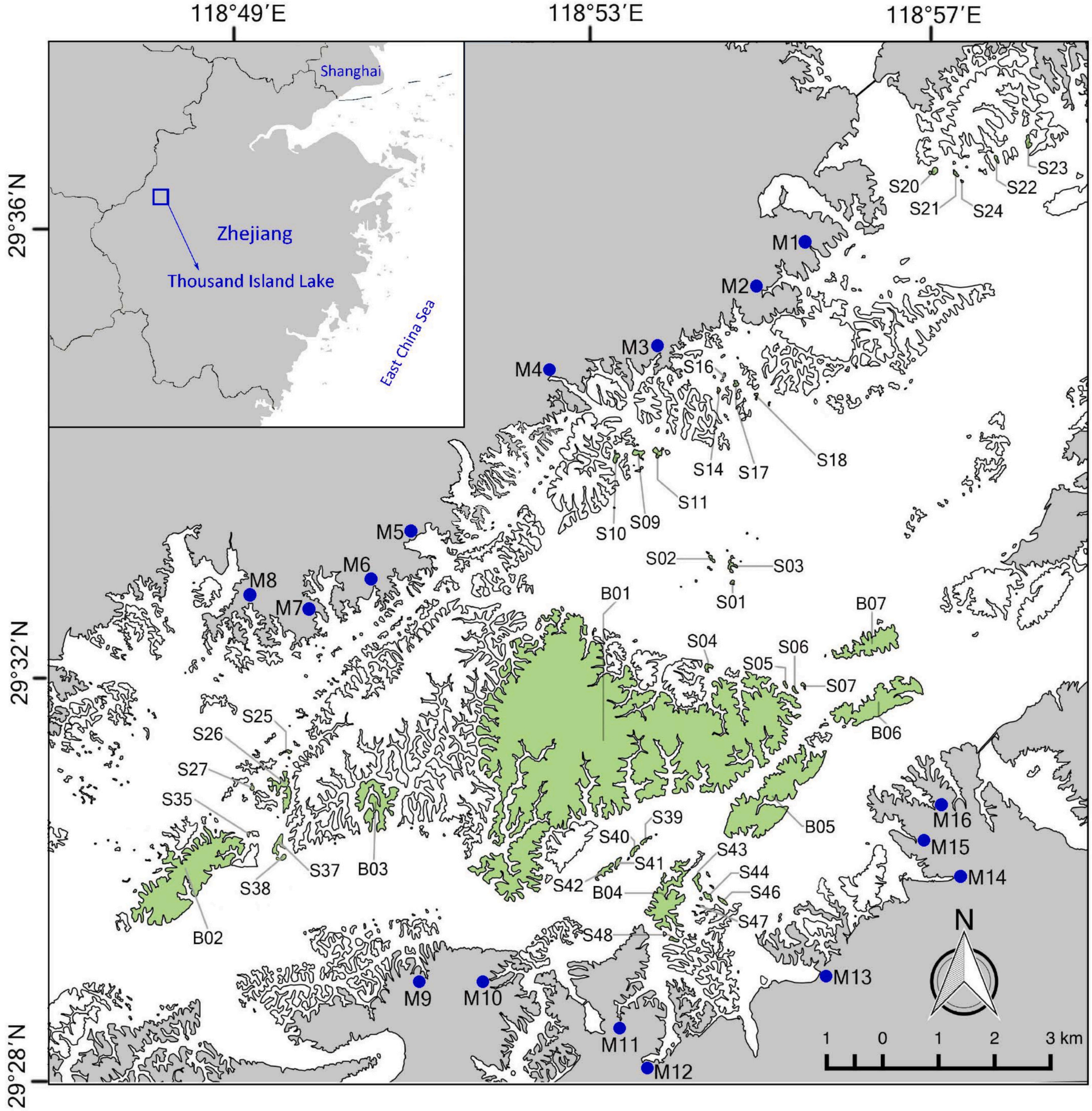

Fig. 1. Sampling sites at the Thousand Island Lake, China, showing 41 island study sites (in green) and 16 mainland sampling sites (blue dots). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. *Measurement of floral color*

Reflectance spectra of the samples were measured using an Ocean Insight portable spectrometer (model SR-6UVV400–25; wavelength range: 180–850 nm) with Ocean View software. The spectrometer system consists of a deuterium-halogen light source (AvaLight-DHc: 200–2500 nm), a fiber optic probe, and a standardized white panel for calibration. The experimental setup included the standard daylight function (D65) for illumination and a green-leaf spectral reflectance function (AV400) to define the background. Reflectance measurements adopted a 90° angle, with PTFE as the white reference and a black chamber as the black reference. Reflectance spectra were recorded over the 300–700 nm wavelength range. Software parameters were set to automatically save measurements every 100 ms, with six consecutive scans collected and stored for each sample, thus resulting in six technical replicates.

We used a customized three-layer dark cardboard box to minimize ambient light interference when measuring flower color. The bottom layer supported the samples, and the middle layer had a circular aperture approximately 1 cm in diameter to expose the samples. The top layer reinforced with three sheets of cardboard contained a 2 mm aperture that aligned with the middle layer opening. This configuration maintained a consistent 2–3 mm distance between the fiber optic probe (positioned flush against the top layer) and the sample surface. All box layers featured a hinged design to facilitate efficient sample replacement.

Measurements focused primarily on petal surfaces; though other pigmented floral structures (receptacles, stamens, and pollen) were also analyzed if visually conspicuous (Tai et al., 2020). For heterogeneously colored samples, the color patches most dominant throughout the floral area were selected. Reflectance values from multiple points were averaged to generate composite spectral data for each flower (Shrestha et al., 2024).

The color hexagon model (the CH model; schematic Fig. S1), which is a graphical representation of bee visual perception (Chittka, 1992), was applied to categorize floral colors. This validation framework generalizes among all hymenopteran pollinators, thus allowing all bees to be considered a unified group (Briscoe and Chittka, 2001; de Ibarra et al., 2014). The CH model categorizes bee-perceived colors into six chromatic categories: ultraviolet (UV), UV-blue (UB), blue (B), blue-green (BG), green (G), and UV-green (UG). These category names also designate the corresponding floral color types. Photoreceptor excitation values were transformed into x/y coordinates within the CH model. The area of the minimum convex polygon (MCP) encompassing all color loci served as a quantitative measure of FCD (Tai et al., 2020). We processed the spectral reflectance data using the *procspec* function and visualized color loci in the CH model through the *plot.colspace* function from the pavo package (v2.9.0) in R (Maia et al., 2019; Shrestha et al., 2024). FCD (MCP) was calculated using the *fd_fric* function from the fundiversity package (v1.1.1) in R (Grenie and Gruson, 2023; Tai et al., 2020).

2.4. Data analysis

We examined the relationships between island-level FCD and island variables (area in hectares and isolation in meters) using simple linear regressions. Island area and isolation were log-transformed, and isolation was measured as the straight-line distance to the nearest mainland edge (Wang et al., 2010). We investigated the effects of fragmentation on bee color preferences by examining the correlation between the relative abundance of floral colors and the bee visitation frequencies. We quantified the relative abundance of floral colors by calculating the proportion of each floral color area throughout the total floral color area within the island. The bee-ultraviolet floral color was excluded due to an insufficient number of plant species exhibiting this color. We defined the visitation frequency as the number of bees observed visiting flowers per unit area of each floral color (Ellis et al., 2021; Oberrath and Böhning-Gaese, 1999). Box-Cox transformations were applied to the data of the relative abundance of floral colors and visitation frequencies by using the *boxcoxnc* function from the AID package (v3.0). Then we performed separate linear regressions of the transformed values against island area and isolation. Structural equation models (SEMs) were constructed using the *psem* function from the piecewiseSEM package (v2.3.0.1) (Lefcheck, 2015), and these served to evaluate the effects of island area, isolation, FCD, and floral resources (floral color area) on bee visitation frequency. The hypothesized model is shown in Fig. S2, and a detailed discussion of the hypothesized path can be found in Supplementary Methods. All analyses were performed in R 4.4.1.

3. Results

We identified 3131 plant-bee interactions types from 7954 visitation events, involving 90 bee species and 96 plant species visited by them (Tables S2, S3). The *t*-tests comparing the areas of the MCP of floral colors between plants visited by bees and all plants in the CH model showed no significant differences ($p > 0.05$). This indicates that the variation in floral color among plants visited by bees represents the overall floral color variation (Fig. S3). Therefore, subsequent analyses focused only on the plants visited by bees.

Some yellow flowers exhibited reflectance peaks in the UV spectrum, and white flowers lacked distinct reflectance peaks in the visible spectrum (Fig. 2a; Fig. S4). Among the six color categories in the CH model, the bee-blue-green contained the highest number of plant species (50 species, 51 %), followed by bee-blue (21 species, 21.4 %). The bee-ultraviolet category contained the fewest species (one species, 1 %) (Fig. 2b). The MCP values of all color points in the CH model was 0.300, which represents the FCD of plants visited by bees in the TIL (Fig. 2c).

The MCP values of study islands ranged from 0.033 to 0.264, compared with the mainland value of 0.287. FCD on islands exhibited a significant positive correlation with island area ($\beta = 0.036$, $p < 0.001$), but no relationships with isolation ($\beta = -0.053$, $p > 0.1$) (Fig. 3a, b; Table S4).

The relative abundance of bee-blue and bee-UV-green floral colors exhibited strong positive correlations with island area ($\beta = 0.192$ and 0.173, $p < 0.001$), whereas bee-blue-green displayed a significant negative correlation ($\beta = -0.177$, $p < 0.001$). In contrast, bee-green and bee-UV-blue floral colors exhibited no significant trends with island area ($\beta = 0.025$ and -0.046, $p > 0.05$). None of the floral color categories correlated significantly with isolation ($p > 0.05$) (Fig. 4a, b; Table S4). Bee visitation frequencies were significantly positively correlated with island area for bee-blue-green, bee-UV-blue, and bee-UV-green floral colors ($\beta = 0.171$, 0.134 and 0.178, $p < 0.01$), while bee-blue and bee-green floral colors exhibited no area-dependent patterns ($\beta = 0.046$ and -0.014, $p > 0.1$). Visitation frequencies were unrelated to isolation for all floral colors ($p > 0.05$) (Fig. 4c, d; Table S4).

Four of the eight hypothesized paths were retained in the final SEM, and the variable of isolation was removed. The total visitation frequency of bees was significantly influenced by FCD, whereas total floral resources had no significant effect ($p > 0.05$) (Fig. 5; Table S5). Bee-blue-green was the only floral color for which visitation frequency was significantly affected by the island FCD ($p < 0.01$) (Fig. 6a; Table S5), while floral resources had no significant effect on the visitation frequencies of any floral color type ($p > 0.05$) (Fig. 6a, e; Table S5).

4. Discussion

In this study, we examined floral color composition, diversity, and bee visitation frequency across 41 islands and 16 mainland sites in the TIL to investigate what extent bee color preferences shift in fragmented habitats and to identify the underlying mechanisms. The floral color composition in the TIL was predominantly bee-blue-green and bee-blue, and islands of a smaller area had a significantly reduced FCD. Bee visitation frequencies to bee-blue-green, bee-UV-blue, and bee-UV-green flowers increased as island area increased, which suggests that islands of a smaller area experience reduced visitation frequencies for specific colors. Habitat fragmentation altered bee color preferences: as island area increased, bees shifted their visitation preference from bee-blue and bee-green to the bee-blue-green floral color type. Total bee visitation frequency shows significant dependence on FCD, while floral resources exhibited no significant effect. However, among all floral color types, FCD exhibited a significant effect only on bee-blue-green flower visitation frequency, suggesting that fragmentation-induced preference shifts in bees may be primarily mediated by changes in FCD. From a conservation perspective, enhancing FCD on smaller islands and protecting the species associated with high-visitation floral color types is critical for sustaining mutualistic interactions between plants and pollinators.

4.1. FCD increases with island area

FCD correlates positively with plant species diversity (Binkenstein et al., 2013; Tai et al., 2020), while habitat fragmentation exerts significant negative effects on it (Santamaria et al., 2018; Sonnier et al., 2014). In the TIL, plant species diversity demonstrated a significant positive relationship with island area (Hu et al., 2019; Liu et al., 2019), a pattern consistent with the increase in FCD as island area increased. Smaller islands typically have relatively low plant species richness and abundance. To maximize pollinator attraction, rare species may exhibit

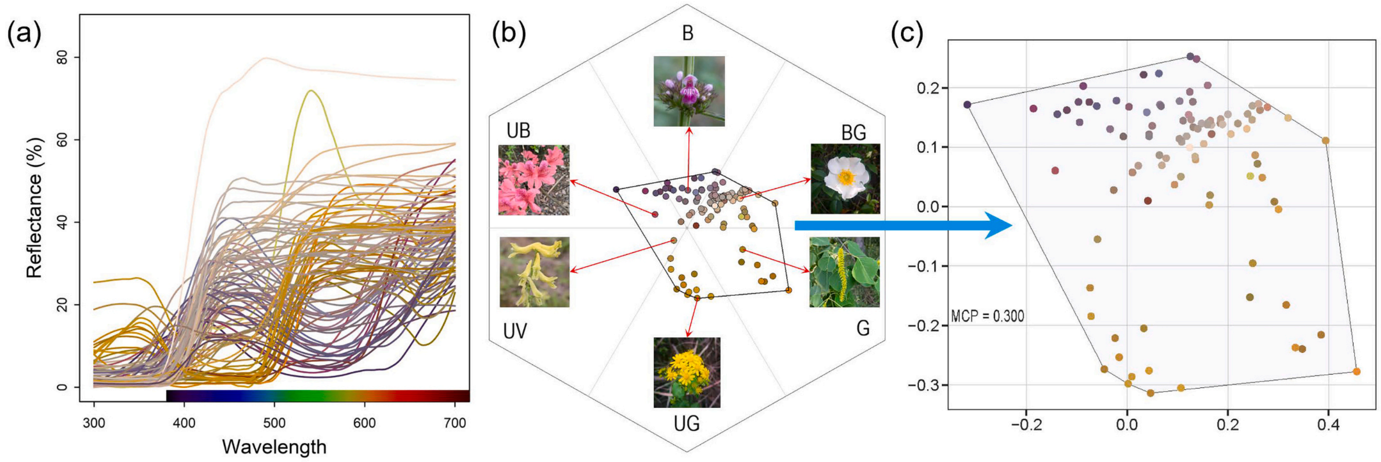

Fig. 2. Reflectance spectra of floral colors from the Thousand Island Lake, spatial distribution of floral color loci within the color hexagon model (CH model), and the minimum convex polygon (MCP) formed by these loci. Reflectance spectra of floral colors for plant species visited by bees, with the horizontal axis representing wavelengths ranging from 300 to 700 nm and the vertical axis indicating reflectance percentages of floral colors at corresponding wavelengths. Each spectral curve corresponds to a distinct plant species and its color represents the actual color of the flower (a). The distribution of floral color loci is shown in the CH model, accompanied by representative photos of plants occupying specific chromatic regions. Red arrows indicate the locations of these plants' floral color loci within the model (b). The MCP encompassing all loci in the CH model and its calculated area, which represents bee-perceived floral color diversity (c). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

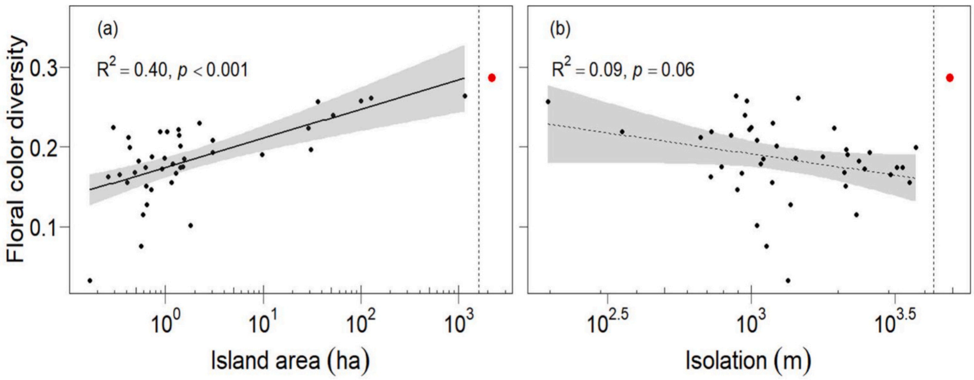

Fig. 3. Effects of habitat fragmentation on the island floral color diversity (FCD) in the Thousand Island Lake. The linear regression analyses between the FCD and island area (a) or isolation (b). Solid lines indicate significant correlations, while dashed lines denote non-significant relationships. Red dots represent the mainland. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

flower colors resembling those of more abundant or nutrient-rich species (Benitez-Vieyra et al., 2007; Johnson et al., 2003; Lunau and Wester, 2017). This adaptive strategy enhances pollinator attraction and improves the reproductive success of rare species (Bergamo et al., 2020; Camargo et al., 2023). Over time, floral color convergence within these habitats reduces overall FCD on smaller islands. Plant dispersal among islands remains effective despite isolation distances and the aquatic matrix, with seeds transported by both abiotic agents (wind, water currents) and biotic dispersers (mammals, birds) (Howe and Miriti, 2000, 2004; Zhu et al., 2025). Isolation generally exhibits no significant effect on plant species richness (Tu et al., 2019; Zhao et al., 2020) and, consequently, exerts minimal influence on FCD.

Furthermore, FCD demonstrated a strong positive correlation with bee species diversity (Fig. S5), highlighting its dual role in structuring both plant and pollinator assemblages. The decline in pollinator diversity and abundance could also increase the selective pressure on plants. Plants that adapt to these changes while maintaining reproductive success will persist. As bee diversity decreases, floral colors that effectively attract bees have the competitive advantage, leading to a convergence in floral color composition toward phenotypes favored by bees in fragmented habitats under competitive scenarios (Bergamo et al., 2020; de Jager et al., 2011; Newman et al., 2014). Consequently, this convergence will reduce the FCD of plant communities.

4.2. *Bee color preferences reflected in visitation frequencies*

With increasing island area, bee visitation frequencies rose significantly for plants with bee-blue-green flowers, despite a concurrent decline in the relative abundance of this floral color. This indicates a shift in bee color preferences toward bee-blue-green. Bee foraging strategies adaptively shift under resource constraints (Gomez-Martinez et al., 2020; Lazaro and Piazzon, 2015), reflecting trade-offs in resources (Jones et al., 1998). This preference is particularly pronounced in resource-limited habitats, where bees rely on foraging strategies to ensure stable food acquisition (Cakmak et al., 2010; Raine and Chittka, 2007; Telles et al., 2017).

The nutritional resources provided by floral rewards, primarily pollen and nectar, play a significant role in attracting pollinators. In our study region, several highly abundant species offer substantial rewards. For example, *Sinosenecio oldhamianus*, *Rosa laevigata* and *Rosa bracteata* exhibit high pollen production (Ortiz et al., 2021), *Cayratia japonica*, *Leonurus artemisia* and *Triadica sebifera* are characterized by abundant

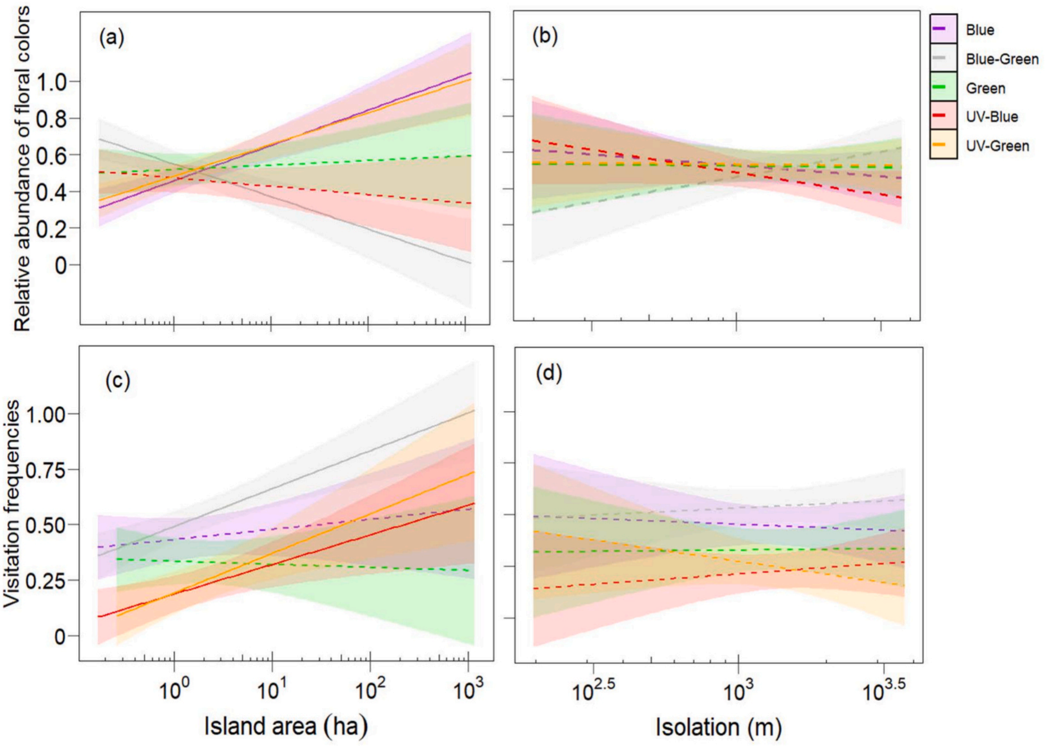

Fig. 4. Habitat fragmentation effects on the relative abundance of floral colors and bee visitation frequencies to each color in the Thousand Island Lake. Simple linear regression analyses of the relative abundance of floral colors and bee visitation frequencies to each color against island area (a, c) and isolation (b, d). Solid lines indicate significant relationships, while dashed lines denote non-significant correlations.

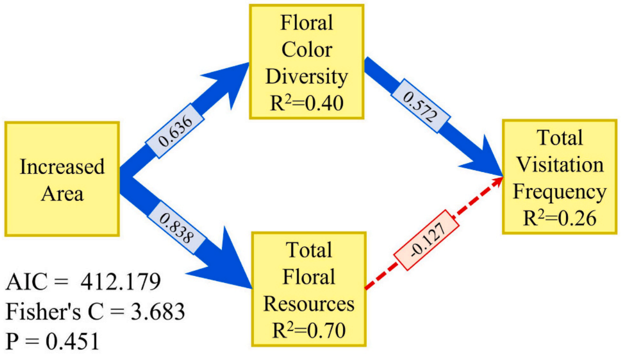

Fig. 5. The effects of island area and floral color traits on total bee visitation frequency in the Thousand Island Lake. Structural equation model (SEM) illustrates that the total bee visitation frequency was influenced by floral color diversity (FCD) and total floral resources, representing the overall pattern in our system. Blue arrows indicate positive relationships, red arrows denote negative relationships, solid lines represent significant effects, and dashed lines indicate nonsignificant pathways. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

nectar (Clark and Howard, 2019; Na et al., 2024), and *Gardenia jasminoides*, *Symplocos paniculate* and *Wisteria sinensis* serve as both nectar and pollen sources (Pinto et al., 2021; Yao et al., 2006). Plants with bee-blue and bee-green flowers include some nectar-rich species such as *Leonurus artemisia* (bee-blue) and *Triadica sebifera* (bee-green). At the same time, the reflectance spectra of bee-blue and bee-green fall within the sensitivity range of bee photoreceptors (Chittka, 1992; Peitsch et al., 1992). When bees learn to forage, they perceive these two floral colors most readily. This drives them to visit plants displaying such colors. When adopting this learned foraging strategy, bees lower their energy consumption (Internicola et al., 2009; Muth et al., 2015), which is particularly advantageous on small islands with limited resources. As floral resources become more abundant in conjunction with an increase in island area, bees develop learned preferences for alternative floral colors (Amaya-Marquez et al., 2008; Giurfa et al., 1995; Makino and Sakai, 2007), and these behavioral adaptations are transmitted across bee species (Romero-Gonzalez et al., 2020). This drives collective foraging to shift toward favoring high-reward plants (Mokkapati et al., 2024; Nityananda and Chittka, 2021), particularly those with bee-blue-green flowers. Plants with bee-blue-green flowers, like *Rosa bracteata* and *Rosa laevigata*, are associated with larger floral displays that signal greater nutritional rewards (Herrera, 2020; Lobo et al., 2016; Ortiz et al., 2021; Tavares et al., 2016), which explains their enhanced attractiveness in larger habitats.

The four major bee taxa, honeybees (Apis), carpenter bees (Xylocopa), halictid bees (Halictidae), and bumblebees (Bombus), shifted their color preferences from bee-blue and bee-green to bee-blue-green as island area increased (Fig. S6). This transition suggests that habitat fragmentation induces plasticity in pollinator behavior. Because honeybees, carpenter bees, and bumblebees exhibit pronounced competitive interactions (William and Deborah, 1979) with potential niche overlap (Goulson et al., 2002), this results in floral resource partitioning among these taxa. For instance, bumblebees employ flexible foraging strategies to adapt to resource fluctuations caused by competition. They may shift preference to plants with alternative floral colors if resources are more abundant (Inouye, 1978; Ye et al., 2024). Simultaneously, carpenter bees, which are characterized by their generalist feeding habits, utilize diverse floral resources without strict color specificity (Keasar, 2010; Raju and Rao, 2006). This behavioral divergence promotes floral resource partitioning through differential plant species selection among these taxa. With their smaller size and lower nutritional demand, halictid bees obtain nutrients from a diverse range of small-flower species such as *Mazus japonicus* (Suetsugu et al., 2016). Although halictid bees

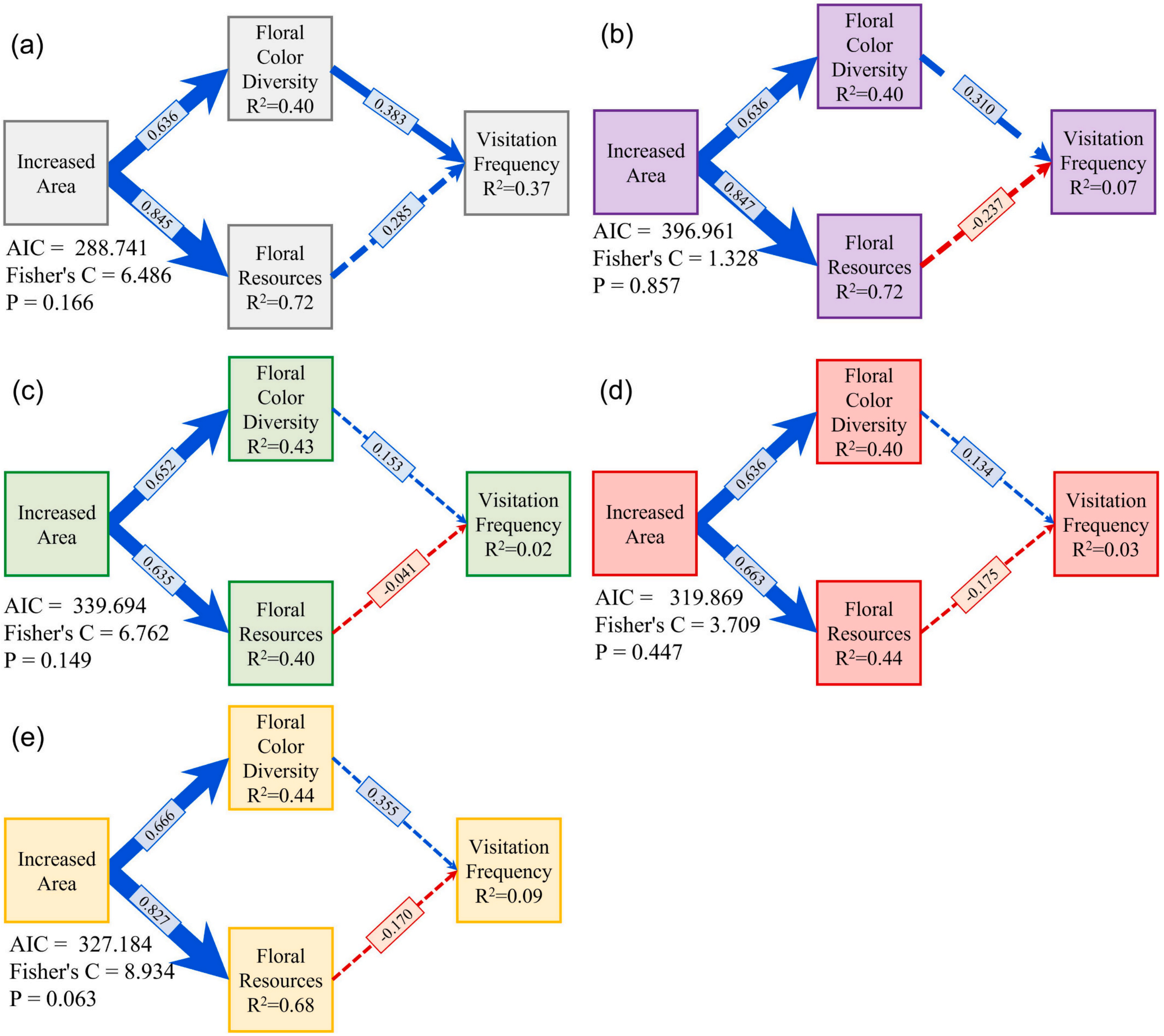

Fig. 6. The effects of island area and floral color traits on bee visitation frequencies to different floral colors in the Thousand Island Lake. The SEMs reveal that island area indirectly affects visitation patterns through its mediation of both island FCD and floral resources of specific colors. Corresponding to five flower colors types: bee-blue-green (a), bee-blue (b), bee-green (c), bee-UV-blue (d), and bee-UV-green (e). Blue arrows indicate positive relationships, red arrows denote negative relationships, solid lines represent significant effects, and dashed lines indicate nonsignificant pathways. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

exploit a broader range of floral resources and exhibit generalized color preferences, they still display a pronounced foraging bias toward bee-blue-green flowers in larger habitats (Fig. S6c).

4.3. Bee color preference shifts mediated by FCD

Island area significantly influences FCD and floral resources, and this, in turn, affects pollinator visitation frequency. Overall, FCD significantly impacted total visitation frequency, but floral resources did not. While prior studies link visitation frequency to floral abundance (Abrol, 2006; Bishop et al., 2024), our study reveals that floral resources exhibit no significant effect on bee visitation patterns within fragmented habitats. These findings indicate that FCD serves as the primary visual signal for attracting bees in fragmented environments, thereby offering a new perspective for habitat conservation efforts.

Visitation frequencies to bee-blue-green flowers increased significantly as island area increase, thus indicating a shift in bee color preference from bee-blue and bee-green to bee-blue-green. SEMs revealed that island FCD significantly enhanced visitation frequency to plants with bee-blue-green flowers, which is consistent with the overall patterns observed in the TIL. On smaller islands, plants with bee-blue-green flowers dominated. These included large-flowered shrubs (e.g., *Rosa bracteata*) and trees (e.g., *Symplocos paniculata*) with high floral density, and these species collectively occupied substantial blooming area. Consequently, bee-blue-green flowers became the predominant floral type on small islands, where this high single-color dominance corresponded with low FCD. However, an increase in island area was associated with greater plant species diversity (Hu et al., 2019; Liu et al., 2019; Santamaria et al., 2018; Sonnier et al., 2014), which consequently reduced the dominance of plants with bee-blue-green flowers. This shift generated a significant negative correlation between the relative abundance of bee-blue-green flowers and island area. The decline in bee-blue-green dominance has facilitated an increased in FCD, which has further amplified visitation frequency to plants with bee-blue-green flowers. This phenomenon reflects the intricate interaction between plants and their environment.

4.4. Conservation strategies

Based on our findings, we propose a series of conservation strategies to protect plant-pollinator interactions in fragmented habitats. In addition to preserving the existing plant species diversity on islands, enhancing FCD through strategic introductions of certain colored plants can further promote pollinator visitation and stabilize community structure, particularly on islands with limited floral color types. On smaller islands, any introduction of plant species should focus on bee-preferred plants within the CH model in the bee-blue color category, while concurrently aiming to strategically reduce the abundance and spatial dominance of plants with bee-blue-green flowers. This approach is expected to improve overall FCD and maintain baseline foraging resources. Considering that small islands may also have some rare plants, these would be part of unique plant-pollinator interaction types (Emer et al., 2018; Libran-Embid et al., 2021). Therefore, protecting rare species can also preserve distinct ecological values characterized by their specialized interactions. On larger islands, conservation efforts should prioritize protecting high-reward plants critical for bee survival, such as *Leonurus artemisia* (bee-blue), *Rosa bracteata* (bee-blue-green), and *Triadica sebifera* (bee-green). These species can provide substantial nectar or pollen resources (Clark and Howard, 2019; Na et al., 2024; Ortiz et al., 2021), further sustaining high diversity of plant-pollinator interactions at the landscape level. Lastly, to mitigate ecological risks, species introductions should be strictly limited to taxa endemic to the TIL region, thereby preventing the potential establishment of invasive species (Zhu et al., 2024).

5. Conclusions

This study examined floral color composition, diversity, and bee color preference shifts in fragmented habitats considering the visual perspective of bees. Our findings demonstrate that habitat fragmentation reduces plant species richness and consequently diminishes FCD on islands, with bee-blue-green and bee-blue floral colors becoming the dominant floral color types. A decrease in island area significantly reduces bee visitation frequencies for specific colors. In other words, fragmentation drove a preference shift: as island area increased, bees transitioned from predominantly visiting plants with bee-blue and bee-green flowers to preferentially visiting plants with bee-blue-green flowers. Overall, total bee visitation frequency was significantly influenced by island FCD. At the level of specific colors, island FCD exclusively enhanced visitation to bee-blue-green flowers, which indicates that fragmentation-driven preference shifts are mediated by changes in FCD. This study contributes to our understanding of pollinator behavior plasticity in fragmented landscapes and provides critical insights for predicting plant-pollinator interactions in fragmented habitats.

CRediT authorship contribution statement

Hongjun Xie: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Peng Ren:** Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis. **Chen Zhu:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Juan Liu:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Minghao Sun:** Writing – review & editing, Formal analysis, Conceptualization. **Xingfeng Si:** Writing – review & editing, Methodology, Funding acquisition. **Ping Ding:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

Authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111322.

Data availability

All data used in this study will be archived in Dryad upon acceptance: http://datadryad.org/share/bpt20_9wHWbEa6LohTvUCMnQ1F9_lWtxUTzsRnDdYBk.

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