



Flower specialization of butterflies and impacts of non-native flower use in a transformed tropical landscape



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ABSTRACT

Flower-feeding ecology of tropical butterflies remains poorly studied, particularly in transformed landscapes, despite that flower availability and quality affect important life-history traits and are critical to butterfly abundance. We recorded 190 butterfly species feeding on 149 flowering plant species across forests and urban parks in Singapore. Butterflies were classified as flower generalists, intermediates or specialists by fitting a power function between the number of flower species utilized and the flower visits observed for that butterfly species. Generalized least squares models were constructed between the degree of flower specialization and traits of butterfly species. Our analysis showed that more species were flower generalists than flower specialists in both habitat types. Forty-three percent of feeding observations in forested sites were on non-native flowers. Yet, flower specialists used significantly higher proportions of native flower species in their diet than flower generalists and tended to be forest dependent. Some forest butterflies were critically dependent (>70%) on single native flower species. Out of 19 butterfly species examined for response across habitats, five expanded their diet but six contracted their diet with urbanization. The regression models revealed that adult conspicuousness, habitat breadth, proboscis length, and wingspan were most strongly associated with flower specialization when accounting for phylogenetic relatedness. Our results suggest that while landscape transformation in the tropics could benefit some flower-generalist butterflies by providing extra resources, flower-specialist butterflies could further increase dependence on few native flower sources. Such butterflies may require intervention in terms of landscape management of their preferred flower resources.

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1. Introduction

Flower-feeding ecology is a critical component of butterfly life-history that affects important traits such as fecundity and longevity (Boggs and Gilbert, 1979; Schultz and Dlugosch, 1999). The distribution of nectar resources influences patterns of butterfly oviposition (Janz, 2005), dispersal, emigration and immigration rates in local populations and are partially responsible for shaping butterfly meta-population structures (Schneider et al., 2003). Furthermore, an understanding of flower use and flower preferences is required to manage habitats for butterflies (Hardy et al., 2007).

Butterfly species exhibit varying levels of flower preferences and flower specialization, defined as the utilization of fewer flower species than the average of all butterfly species scaled by the number of observations made of each butterfly species (Tudor et al., 2004). Butterflies in temperate regions are believed to be flower generalists, but some temperate butterflies have been shown to exhibit flower specialization (e.g., Stefanescu and Traveset, 2009; Tudor et al., 2004). During the flowering season when nectar resources are abundant, butterflies can be flower

specific and choose to feed only from a limited number of plant species in a habitat (Wiklund and Åhrberg, 1978; Rodriguez et al., 1994) and can sometimes be nearly absent from sites where the preferred flower resource is lacking (Severns et al., 2006). Further, preferred flowering plants can differ between time periods within sites and between sites (Wiklund and Åhrberg, 1978). Between sexes, females may visit a larger number of flowering plant species than males, presumably as a result of their higher dietary requirements (Wiklund and Åhrberg, 1978). Butterflies also have innate preferences towards certain flower characteristics – e.g., color preferences for yellow and red flowers (Weiss, 1997; Pohl et al., 2011); species with high wing loading prefer clustered or nectar-rich flowers (Corbet, 2000; Kunte, 2007). Behavioral modifications and derived proboscis morphology are also often associated with specialized feeding preferences (Bauder et al., 2013; Krenn, 2010). It is thus evident, that flower specialization of butterflies is a complex phenomenon and one that interacts with species abundance, habitat matrix, environmental conditions and species traits.

In tropical systems, some butterflies have been shown to be flower generalists (Kunte, 2007) and flower specialists (Bauder et al., 2015b) but research efforts have been minimal and largely focused only on treatments of single species or particular groups of species. An understanding of flower specialization across many butterfly species is

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necessary because butterflies are known to be important pollinators (Courtney et al., 1982), and therefore contribute to plant reproduction in tropical forests. In addition, continued deforestation and habitat degradation in tropical forests (Hansen et al., 2013) has led to changes in vegetation structure that may affect the distribution of larval host plants and also facilitate increased abundance of non-native flowering plants (Ghazoul, 2004). For example, if tropical butterflies are indeed flower generalists, then the invasion of non-native plant species that serve as novel nectar sources could alter butterfly behavior, thereby affecting reproduction of native plants. Ultimately, understanding flower use dynamics in transformed landscapes has important implications for understanding potential changes in pollination and plant reproduction in tropical forests, as well as informing management towards flowering plants for tropical butterfly conservation.

It is further necessary to assess the underlying mechanisms that drive flower specialization. Butterfly species traits may underpin their flower specialization because butterfly morphology and traits are known to influence flower choice (e.g., butterflies with short proboscis do not visit flowers with deep corollas; Corbet, 2000). Yet, research on species traits that drive flower specialization has been limited to temperate grasslands, where it has been shown that flower specialization can be best explained by habitat preference, larval host plant specialization and length of flight period of species (Tudor et al., 2004; Stefanescu and Traveset, 2009); the latter is of particular importance in highly seasonal temperate systems where butterflies and flowering plants have a limited window of opportunity and a relatively longer diapause. There are reasons to believe that different selective pressures may drive flower specialization in the tropics. For instance, vertical complexity in tropical forests may shape flower specialization, similar to how vertical stratification affects larval host plant specialization in tropical forests (Dennis et al., 2004; Basset et al., 2015). Ultimately, an analysis of species traits should help understand the underlying mechanisms that drive flower specialization.

In this study, we evaluate the degree of flower specialization in tropical butterflies and examine the interaction of habitat type with flower specialization. We identify ecological and morphological traits of butterfly species that explain the degree of flower specialization. We also evaluate the degree of native vs. non-native flower use by butterflies. Finally, we considered the potential implications of changes in flower specialization in transformed tropical landscapes.

2. Materials and methods

2.1. Study sites and data collection

The island city-state of Singapore, which lost most of its primary lowland dipterocarp forest in the 19th and early 20th century, has the core of its remaining forest reserves in primary lowland dipterocarp forest, swamp forest, young and old secondary forest in the center of the island (4.3% land area, 3043 ha, Yee et al., 2011). Degraded forest fragments and urban parks dot the rest of the island, embedded in an urban matrix. In addition, non-native plants make up nearly half of the total vascular plant flora (2032 of 4173 species, Chong et al., 2011). Singapore thus presents an ideal system to study flower specialization and the impacts of non-native plants on flower feeders in a transformed tropical landscape.

We conducted transect walks in 62 sites across Singapore (Fig. A1, Table A1) from March 2011–July 2014. When conducting transect walks, the observer walked at a standardized pace (20 m per minute) until a butterfly feeding activity was observed within 2.5 m on either side of the transect. All flower visits by butterflies at that particular plant were recorded during the observation time, which was standardized to 30 min for a tree, 10 min for a tall shrub (>2 m in height), 5 min for a short shrub or an epiphyte and 2 min for a herb. Differences in observation times on each plant form helped to account for the difficulty in observation of trees (especially in closed forest) and tall shrubs and

because they typically had larger flower loads than other life forms. After the observation time at a particular plant concluded, the observer continued the transect walk. Within a site, no particular plant was visited >3 times and the interval between repeat visits was at least 2 weeks to avoid recounting the same butterfly individuals. An average of 3 h and 1 h were spent at every visit in forested sites and urban parks, respectively.

A butterfly was recorded as feeding ('nectaring') when its proboscis was observed entering the flower. The flowering plant species was classified as native or non-native to Singapore based on the Chong et al. (2009) plant list. Observations were conducted on all flowering plants encountered, thus avoiding bias towards any particular life form or native/non-native status. We could not quantify flower resource availability (number of available flowers in the habitat) or nectar productivity, but our surveys do provide a 'snapshot' of all the flower sources utilized by butterfly species during the observation period at each visit to a site. Due to the lack of data on seasonal patterns of tropical butterflies in the region, we did not consider the effect of seasonality in our study.

2.2. Habitat classification

The study sites (Fig. A1, Table A1) were classified as forests or urban parks based on the updated vegetation map of Singapore (Yee et al., 2011). Forested sites consisted of mature forests (primary lowland dipterocarp forest, swamp forest and old secondary forest), degraded forests connected to mature forest, or forest fragments. Urban parks either adjoined forests or were isolated from forest habitat and were enriched with flower species – non-native ornamentals in most cases – that turned out to be attractive to butterflies. Two non-metric multidimensional scaling (NMDS) plots were constructed using Bray–Curtis dissimilarity ('vegan' package, Oksanen et al., 2015) to identify potential clustering of sites, classified according to habitat types. The first NMDS plot was constructed between presence and absence of flowering plant species and sites. The second NMDS plot was constructed between presence and absence of butterfly species and sites.

2.3. Degree of flower specialization

We followed the approach of Tudor et al. (2004) and Stefanescu and Traveset (2009) to classify each butterfly species as a generalist or specialist flower feeder by fitting a power function $Y = cX^z$ where Y was the number of flowering plant species visited by that species, X was the number of flower visits by that butterfly species and c and z were constants. A butterfly frequently seen feeding on flowers may be expected to use more flower species than one seen rarely. Positive deviations from this pattern would indicate flower generalization whereas negative deviations would indicate flower specialization (Tudor et al., 2004). Therefore, the degree of flower specialization was estimated as the residual from the fitted logarithmic curve between the number of flowering plant species and the number of flower visits by that butterfly species. We considered a species as a generalist feeder if the residual was >2, and as a specialist feeder if the residual less than –2 (Stefanescu and Traveset, 2009). The degree of specialization was compared across butterfly families to assess the phylogenetic basis of specialization and across habitat types to evaluate the effect of habitat on flower specialization.

2.4. Models between species traits and degree of flower specialization

Nine ecological and morphological traits were compiled for each butterfly species based on their biological relevance as potential correlates with the degree of flower specialization (Table 1). Where possible, traits were compiled using local datasets and using local expert knowledge. Proboscis length was measured on live butterflies after inserting a needle in the centre point of the coiled proboscis and straightening the proboscis out. The length was then measured as the distance between

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