

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 Ahrberg, 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 Ahrberg, 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 Ahrberg, 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; Bassett 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

Table 1

Ecological and morphological traits of butterfly species used as predictor variables in the models used to explain the degree of flower specialization.

Variables	Type	Description	Data source
Habitat breadth	Ordinal	Number of habitat types the butterfly species can be found in Singapore	A. J. unpublished data
Proboscis (mm)	Continuous	Proboscis length (mm) averaged between sexes of each species.	This study
Wingspan (mm)	Continuous	Mean forewing length (mm) averaged between sexes of each species.	Fleming (1991) and Khew (2010)
Mobility	Continuous	Relative flight mobility of each species on scale of 1–10 where '1' represents a sedentary species and '10' an extremely mobile species. Rank was averaged across 3 expert respondents.	This study
Number of larval host plant genera and families	Count	Compiled from local host plant records (published and unpublished), and verified with local butterfly experts	Khew (2010), Butterfly Circle (2015), NSS (2015) and A.J. rearing records
Global geographic range	Ordinal	Narrow (0) – restricted to Sundaland; Moderate (1) – restricted to Oriental Region; Wide (2) – Oriental Region and beyond	Corbet and Pendlebury (1992), Fleming (1991) and d'Arbera (1982, 1985, 1986)
Adult conspicuousness	Ordinal	Visually estimated (by L. P. Koh) as proportion of black, brown or grey on the upper side of both pairs of wings, where low: >70%; moderate: 30–70%, and high: <30%. The more visible sex was scored. Where a species was polymorphic, the most common form was scored.	Corbet and Pendlebury (1992), Fleming (1991) and d'Arbera (1982, 1985, 1986)
Flight height	Ordinal	Height at which species were recorded in surveys classified as 'Canopy', 'Mid-canopy' or 'Understory' species	A. J. expert classification

the base and the tip of the proboscis (same methodology as Kunte, 2007). To calculate the relative flight mobility (hereafter 'mobility') of butterflies, three butterfly experts from Singapore with >50 years of combined field experience were asked to rank butterflies on a scale of 1–10 with '1' being sedentary species and '10' being extremely mobile species. Final mobility value for each butterfly species was obtained by averaging values across expert responses.

We built generalized linear models (GLM) ('lme4' package; Bates et al., 2015) to examine the relationship between the degree of flower specialization (residuals from the power function $Y = cX^2$) and the ecological and morphological traits of butterfly species. For this analysis, 82 species with at least 10 flower visits were included. Feeding patterns of butterflies have been shown to exhibit a phylogenetic signal (Boggs and Dau, 2004; Stefanescu and Traveset, 2009), therefore, we also built generalized least squares (GLS) models to account for taxonomic relatedness of species ('APE' package; Paradis et al., 2004). Species-to-species relatedness was derived from consensus phylogeny trees that were extracted from several datasets (Braby et al., 2006; Brower and Warren, 2008; Kunte, unpublished data; Simonsen et al., 2011; Wahlberg et al., 2005, 2009; Warren et al., 2009). Phylogenetic distances for some tropical butterfly genera were not available, particularly for the family Lycaenidae; hence, branch lengths were set equal to 1 to account only for topology. All statistical analyses were performed using R software (R Core Team, 2015).

3. Results

Overall, we recorded 3092 flower visits by 190 butterfly species feeding on 149 plant species (Table A1). A higher number of butterfly species were recorded feeding in forested sites than in urban parks. However, the number of flower visits (a measure of feeding rate) and flower species utilized by butterflies was greater in urban parks than forested sites (Table 2). NMDS plot for flowering plants revealed that in general most forested sites clustered together while urban parks formed another cluster (Fig. A2a). However, NMDS plot for butterfly

species revealed an overlap of forested sites and urban parks, especially for urban park sites adjoining forests (Fig. A2b). Of the 149 flower species used by butterflies, 45 were native and 104 were non-native (Table 2). Forty percent (1240/3092) of flower visits by butterflies were to native flowers. There was a positive correlation between the number of native and non-native plant species utilized by butterflies (Pearson's $R = 0.44$, $p < 0.001$, $n = 190$).

3.1. Flower specialization across habitat types and butterfly families

Of the 190 butterfly species encountered, 58 were classified as flower generalists, 30 as flower specialists and the remaining 102 species as flower intermediates (i.e. neither generalists nor specialists) (Table 2). Each habitat type had more flower generalists than flower specialists (Table 2, Fig. 1). However, the average degree of flower specialization of butterflies was not different across habitat types (Fig. 2a). Across butterfly families, lycaenids were more flower specialized whereas papilionids were significantly more flower generalized (Fig. 2b). Of the 19 butterfly species present with at least 10 flower visits in both forests and urban parks, 11 varied in their degree of flower specialization with habitat modification towards urbanization (Table 3). Six of these species contracted their diet with urbanization i.e. became more flower specialized; five species expanded their diet and the remaining eight species had no change with urbanization (Table 3).

3.2. Correlates of flower specialization

Greater adult conspicuousness, wider habitat breadth, longer proboscis length and larger wingspan were most strongly associated with flower specialization in the GLS models that accounted for phylogenetic relatedness (Table 4). In contrast, greater mobility, wider habitat breadth, longer proboscis length and larger wingspan were most strongly associated with flower specialization in the GLM models that did not account for phylogeny. There were inconsistencies in the association of mobility and adult conspicuousness with flower specialization

Table 2

Flower generalist and specialist butterfly species by habitat types. Each flower visit by a butterfly was counted as an observation. Numbers in parentheses represent butterfly species with at least 10 flower visits. Acronyms: N = Native, NN = Non-native.

Habitat type	Number of sites	Butterfly species				Number of flower visits		Flower species used by butterflies	
		Total	Generalist species	Intermediate species	Specialist species	N	NN	N	NN
Forested habitats	28	162 (39)	36 (16)	112 (14)	14 (9)	707	543	34	38
Urban parks	34	142 (52)	38 (27)	90 (13)	14 (12)	533	1309	21	91
All habitats (combined)	62	190 (82)	58 (40)	102 (16)	30 (26)	1240	1852	45	104

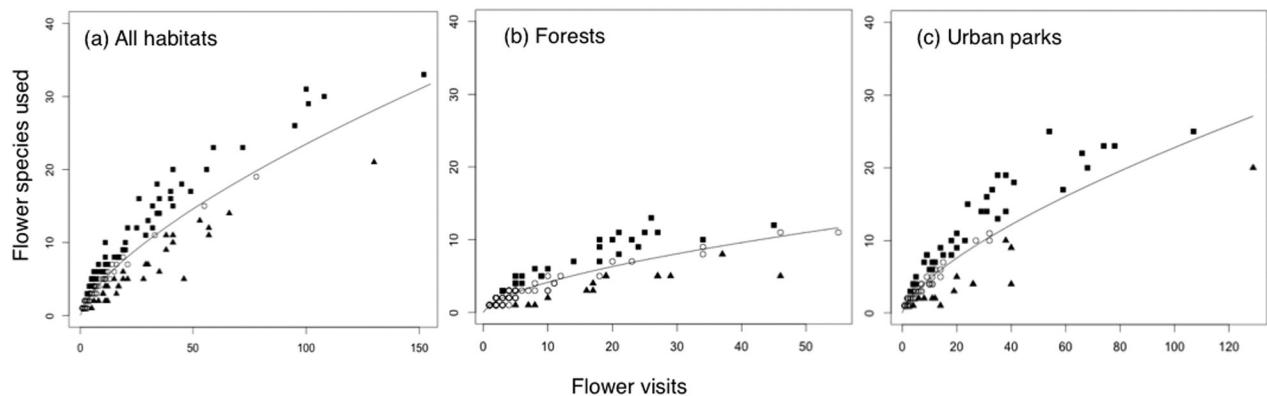


Fig. 1. Relationship between the number of flower species used and the number of flower visits by butterfly species across – (a) all habitats pooled ($p < 0.001$, $R^2 = 0.89$, $n = 190$), (b) forests ($p < 0.001$, $R^2 = 0.80$, $n = 162$), (c) urban parks ($p < 0.001$, $R^2 = 0.86$, $n = 142$). Degree of flower specialization = residuals in the above plots. Legends: Black squares = Flower generalists, open circles = flower intermediates and black triangles = flower specialists.

between GLS and GLM models. There was no association between flower specialization (i.e. residuals) and commonness (based on Singapore-wide abundance categories of Khew, 2010) for all 190 butterfly species (Pearson's $R = 0.14$, $p = 0.05$, $n = 190$) and for the 82 butterfly species with ≥ 10 flower visits (Pearson's $R = 0.09$, $p = 0.42$, $n = 82$) so there was no support for the hypothesis that common butterflies were flower generalists.

3.3. Native vs. non-native flower use

In forested sites, the average number of visits by butterflies on native flowers was similar to the average number of visits on non-native flowers; a different trend was seen in urban parks (Fig. 3a). Forty-three percent of feeding observations ($n = 162$ butterfly species) in forested sites were on non-native flowers (Table 2). In terms of the use of flower species, butterflies fed on a similar number of native and non-native flower species in forested sites (Fig. 3b). However, significantly fewer native flower species were utilized than non-native flower species in urban parks, and when both habitat types were pooled together (Fig. 3b). Specialist butterfly species used a higher proportion of native

flower species in their diet than generalist butterfly species when habitat types were pooled together, though the differences were not significant within each habitat type (Fig. 4). Flower specialists spent higher proportions of time on their preferred nectar sources and tended to be forest dependent compared with flower generalists (Table A2). Some forest butterflies were critically dependent on a few native flowers for nectar intake e.g., *Pyroneura latoia* and *Gandaca harina* fed on the native shrub *Leea indica* > 70% of the time.

4. Discussion

4.1. Evolutionary significance of flower specialization

Our finding of more species being classified as generalist feeders than specialist feeders agrees with the view that butterflies are flower generalists at the community level, and that tight plant-pollinator interactions are generally uncommon (Inouye, 1980; Kunte, 2007). Furthermore, we found that flower generalists had longer proboscis lengths than specialists. Possession of a long proboscis is beneficial to butterflies because it widens food choices available to an individual by allowing

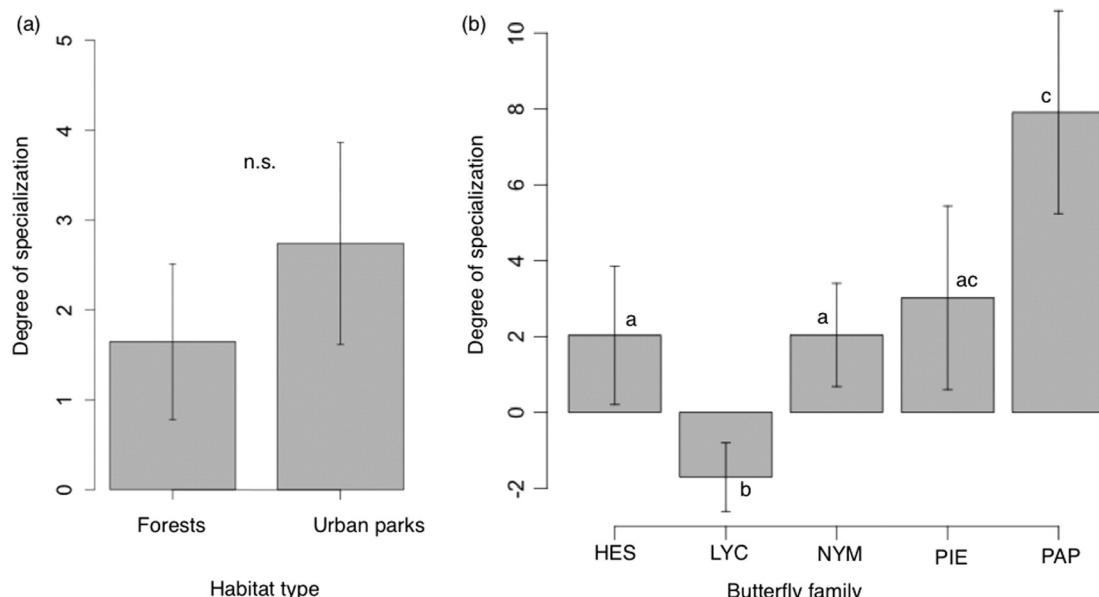


Fig. 2. Differences in the degree of flower specialization of butterflies between (a) habitat types and (b) butterfly families. $N = 82$ species with at least 10 flower visits. Bars indicate standard errors of the mean. Letters (a, b and c) besides the bars refer to statistically significant differences ($p < 0.05$, Wilcoxon signed rank test) between groups. n.s. indicates non-significance. Butterfly families: Papilionidae ('PAP'), Pieridae ('PIE'), Nymphalidae ('NYM'), Lycaenidae ('LYC') and Hesperiidae ('HES'). Positive values of degree of specialization represent flower-generalist species whereas negative values represent flower-specialist species.

Table 3

Variation in the degree of flower specialization and diet response of butterflies with urbanization in a tropical landscape. $N = 19$ butterfly species with ≥ 10 flower visits in both the habitat types.

Scientific name	Family	Forested habitats		Urban parks		Diet response
		Visits (species utilized)	Flower specialization	Visits (species utilized)	Flower specialization	
<i>Papilio iswara iswara</i>	Papilionidae	18 (10)	Generalist	14 (5)	Intermediate	Contraction
<i>Papilio polytes romulus</i>	Papilionidae	27 (11)	Generalist	68 (20)	Intermediate	Contraction
<i>Delias hyparete metarete</i>	Pieridae	45 (12)	Generalist	107 (25)	Specialist	Contraction
<i>Euploea eyndhovii gardineri</i>	Nymphalidae	21 (8)	Generalist	14 (6)	Intermediate	Contraction
<i>Cethosia hypsea hypsina</i>	Nymphalidae	34 (10)	Generalist	19 (3)	Specialist	Contraction
<i>Vindula dejone erotella</i>	Nymphalidae	26 (13)	Generalist	40 (4)	Specialist	Contraction
<i>Graphium sarpedon luctatus</i>	Papilionidae	20 (10)	Generalist	20 (9)	Generalist	No change
<i>Graphium agamemnon agamemnon</i>	Papilionidae	23 (7)	Intermediate	32 (11)	Intermediate	No change
<i>Appias libythea olfrena</i>	Pieridae	25 (11)	Generalist	31 (16)	Generalist	No change
<i>Eurema sari sodalis</i>	Pieridae	37 (8)	Specialist	20 (5)	Specialist	No change
<i>Ideopsis vulgaris macrina</i>	Nymphalidae	23 (10)	Generalist	78 (23)	Generalist	No change
<i>Doleschallia bisaltide bisaltide</i>	Nymphalidae	18 (7)	Generalist	23 (10)	Generalist	No change
<i>Junonia hedonia ida</i>	Nymphalidae	24 (9)	Generalist	35 (19)	Generalist	No change
<i>Phalanta phalantha phalantha</i>	Nymphalidae	19 (5)	Intermediate	59 (17)	Intermediate	No change
<i>Eurema hecate contubernalis</i>	Pieridae	46 (11)	Intermediate	54 (25)	Generalist	Expansion
<i>Danaus genutia genutia</i>	Nymphalidae	12 (5)	Intermediate	18 (10)	Generalist	Expansion
<i>Parantica agleoides agleoides</i>	Nymphalidae	34 (9)	Intermediate	74 (23)	Generalist	Expansion
<i>Euploea mulciber mulciber</i>	Nymphalidae	20 (7)	Intermediate	14 (9)	Generalist	Expansion
<i>Junonia almana javana</i>	Nymphalidae	11 (4)	Intermediate	38 (14)	Generalist	Expansion

access to nectar in deep flowers, which typically secrete more nectar than short flowers (Harder and Cruzan, 1990). Butterflies with longer proboscis also have a wider food canal area of the proboscis tube in accordance with the Hagen-Poiseuille law (Kingsolver and Daniel, 1995), which allows for greater quantities of nectar uptake in every visit (Bauder et al., 2015a). Long proboscis may also enable flower generalists to steal nectar from specialist flowers (Bauder et al., 2015b; Kunte, 2007). Longer proboscis, however, increase the flower manipulation time and nectar suction time of nectarivores (Bauder et al., 2015a) which can be costly in the face of competition for nectar (Kunte, 2007) and can render significant anatomical costs (Bauder et al., 2013).

Our result of conspicuous butterflies being flower specialists may indicate an important evolutionary adaptation to escape predators during feeding when butterflies tend to be particularly vulnerable to predation. Conspicuous butterflies may have evolved optimized foraging strategies or morphologies to reduce handling time on flower(s), which may reduce exposure to predators and hence, may lower predation (as shown for caterpillars – see Heinrich, 1979). The observed relationship between adult conspicuity and flower specialization also complements the potential predation risks associated with the increase in flower foraging time for butterflies with longer proboscis lengths. Inconspicuous butterflies can afford to have longer proboscis and be

flower generalists because of potentially lower predation risks. The fact that conspicuity was highly significant with the degree of flower specialization only in the model that accounted for phylogeny, suggests a phylogenetic signal in the evolution of flower specialization. However, it is unclear why this may be the case. Stefanescu and Traveset (2009) also found differing results with variables explaining the degree of flower specialization between models that accounted for phylogeny and those that did not. Patterns of allometric and functional constraints on proboscis lengths of butterflies suggest that nectar uptake morphology has evolved multiple times and phylogenetic constraints may not be strong (Kunte, 2007). Therefore, further research is needed to elucidate the role of phylogeny in the evolution of flower specialization.

Our models indicating that habitat breadth of butterflies was strongly and positively associated with the degree of flower specialization implies that habitat generalist butterflies tend to be flower generalists. Flower-generalist butterflies may have evolved strategies to thrive in conditions of wide resource availability and biotope occupancy (see Dennis et al., 2004 for life-history strategies in butterflies under gradients of r-selection, K-selection, and S-selection). In parallel, habitat specialists may have evolved or co-evolved strategies (Ehrlich and Raven, 1964) to exploit native flowers abundant in their preferred habitat to minimize effort per unit of energy intake and thus, become flower specialists.

4.2. Variability in flower specialization across habitat types

Our result of the variability of flower specialization across habitat types was likely due to vast differences in the floral assemblages of the habitat types in our study (tropical forests vs. tropical urban parks) as confirmed by the NMDS plots. This seems to suggest that flower specialization of butterflies may be a relatively flexible behaviour that is affected by the floral assemblage and relative abundance of species in a habitat. Indeed, when the floral assemblages across habitat types are relatively similar, consistency in the degree of flower specialization is observed for the majority of butterfly species across studies (Stefanescu and Traveset, 2009; Tudor et al., 2004). Even in other taxonomic groups, such as bumble bees, which are known to be typically generalist feeders, flower breadth is known to be a flexible trait resulting from behavioural adaptation to competition and resource availability (Fontaine et al., 2008). However, some unexplained variability in flower specialization across habitats may also be attributed to variations in nectar volume, concentration and contents among plant species and individual flowers during the day and season that can affect

Table 4

Results of predictor variables explaining the degree of flower specialization of butterflies. Generalized least squares (GLS) models took into account the phylogenetic relatedness of butterfly species. Generalized Linear models (GLM) did not control for phylogeny. $N = 82$ butterfly species with at least 10 flower visits.

Variables	GLS	GLM
	Coefficient (95% CI)	Coefficient (95% CI)
Habitat breadth	4.44 (1.71,7.2)**	3.36 (1.18,5.53)**
Log (proboscis)	11.2 (1.7,20.7) [#]	5.45 (1.9,8.99)**
Log (wingspan)	9.1 (0.66,17.54) [#]	4.65 (1.69,7.61)**
Mobility	-0.3 (-4.6,3.9)*	1.5 (0.73,2.22)***
Number of host plant genera	0.72 (-0.87,2.32)	0.04 (-1.2,1.27)
Number of host plant families	1.68 (-0.89,4.26)	0.27 (-1.77,2.3)
Global geographic range	0.96 (-2.3,4.2)	2.07 (-1.16,5.3)
Adult conspicuity	-4.52 (-7.1, -1.95)***	-1.1 (-3.16,1.02)
Flight height	-1.92 (-9.97,6.13)	0.42 (-1.91,2.76)

Positive coefficient values represent positive association with a butterfly species being flower generalist.

*** $p < 0.001$.

** $p < 0.01$.

* $p < 0.05$.

[#] Refers to marginally significant values with 90% CI (Confidence Interval).

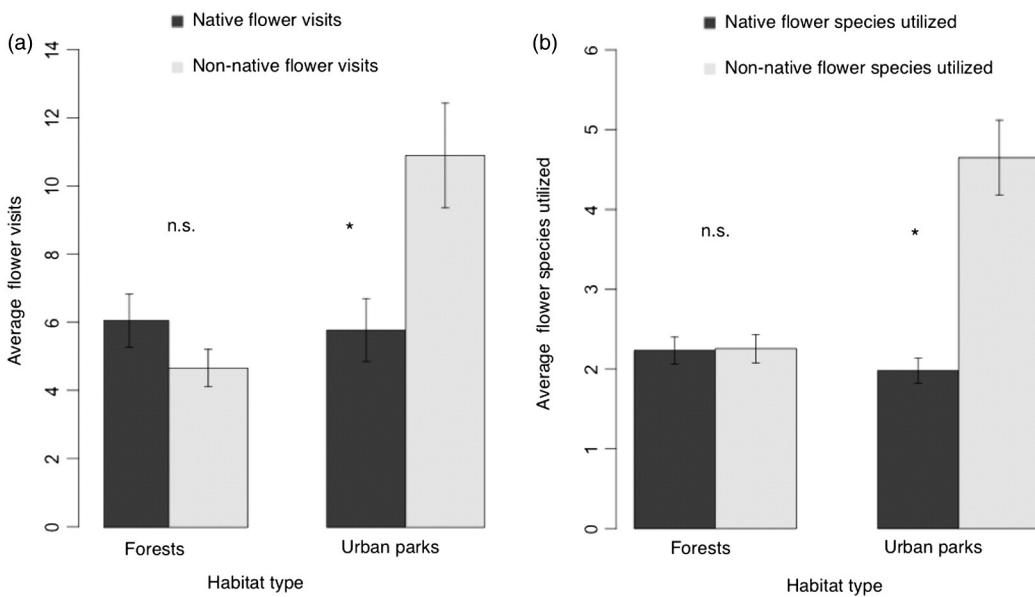


Fig. 3. a) Average flower visits and b) Average flower species utilized by each butterfly species across habitat types in the study. *Indicates statistically significant differences ($p < 0.05$, Wilcoxon signed-rank test) between the average values of native and non-native flower visits or species. n.s. indicates non-significance. Bars indicate standard errors of the mean.

preferences of flower visitors. Future studies should aim to quantify these variations to gain a fuller understanding of the variability in flower specialization at the landscape level.

4.3. Potential impacts of foraging shifts in transformed landscapes

Temperate zone studies have demonstrated reduced plant reproductive success resulting from pollinators shifting to non-native plants (e.g., Brown et al., 2002; Morales and Traveset, 2009). In the Asian dry tropics, Ghazoul (2004) showed that the introduction of the understory exotic *Chromolaena odorata* altered foraging behaviour of butterfly pollinators, which negatively affected the pollination and reproductive success of the native forest tree *Dipterocarpus obtusifolius*. In our study, 43% of feeding observations in forested sites were on non-native flowers, and 58% (11/19) of butterfly species exhibited a diet shift in urban parks, where higher abundances of non-native plants were found compared to forested sites. This suggests that butterflies spend considerable

time nectaring on non-native plants in both forests and urban parks. In addition, 48% (32 out of 67 species) of non-native flower species utilized by bees in urban parks of Singapore (Soh and Ngiam, 2013) were also utilized by butterflies in our study, suggesting that this trend of high non-native flower use may be found in other pollinator taxa as well. Foraging shifts that occur across a large proportion of butterfly species and possibly also across bee species, indicate a general trend that tropical urbanization and establishment or habitat enrichment with non-native plants may result in long-term impacts on native plant reproductive success through reduced pollinator visitation rates. Our study, however, could only quantify flower use and did not investigate the impacts of foraging shifts on seed production, dispersal and establishment of native plants.

The ecological impacts of non-native plants on butterfly ecology may be variable, and require further investigation. Five of 19 butterfly species expanded their diet by becoming less flower specialized in landscapes that had an increasing number of non-native plants, suggesting that non-native flowering plants may be benefiting some butterflies by providing extra nectar resources. Similarly, non-native flowering plants were found to provide resources to several pollinator groups by extending the flowering season in garden habitats in the UK (Salisbury et al., 2015) and in controlled laboratory experiments (Fontaine et al., 2008). Native flowering in the forests of Singapore tend to be spatially dispersed and flowering events are short, sporadic and few (except during times of mass flowering). Therefore, non-native plants which flower longer and more abundantly (A. J. pers. obs.) may make up for this shortfall in native flowering events.

To the contrary, urban parks, particularly those adjoining forests, could act as “ecological traps” for forest-dependent butterflies that get attracted by nectar availability but which may not be able to reproduce owing to the absence of specific host plants, ant associates (Pierce et al., 2002) or inappropriate microclimatic conditions. Ecological traps have been demonstrated for birds, and there is increasing evidence that such traps may be common (Battin, 2004; Schlaepfer et al., 2002). However, ecological traps can be difficult to identify because a ‘trap’ habitat can be a preferred habitat due to evolutionary responses of animals to cues that formerly correlated with habitat quality (e.g., nectar availability, Schlaepfer et al., 2002) and remain unnoticed even as they decimate animal populations until an adaptation to the novel environment occurs. This suggests that enhancing a low-quality urban habitat only with nectar resources (i.e., ornamental and butterfly-attracting flowers,

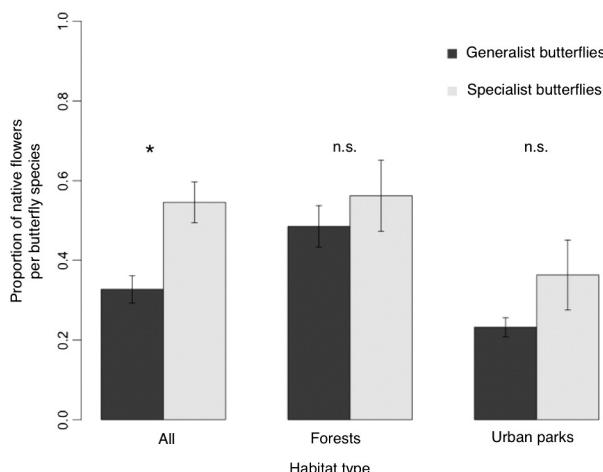


Fig. 4. Proportion of native flowers used by flower specialist and generalist butterflies across habitat types in the study. *Indicates statistically significant differences ($p < 0.05$, Wilcoxon signed-rank test) between the average values of generalist and specialist butterfly species. n.s. indicates non-significance. Bars indicate standard errors of the mean. Refer to Table 2 for the number of flower generalist and specialist species in each habitat type.

which is the typical enrichment policy in many urban settings such as Singapore) may not be enough, and may even be more worrisome because the habitat could in fact create an unintended ecological trap. Community-level experiments involving multiple plant species over the entire plant reproduction cycle may be required to get a better understanding of the true costs and benefits of non-native plant species to butterflies as well as native insect-pollinated flowering plants in tropical urban landscapes.

4.4. Applications for conservation

Our results that flower-specialist butterflies prefer native flower species over non-native flower species and that some forest dependent butterflies are critically dependent on single native flower species have important conservation implications. As tropical landscape transformation continues and native plant species decline, to be replaced by non-native plant species, flower specialists may become increasingly dependent on fewer native flower sources that can persist in the transformed landscape; an outcome considered possible for flower-feeding British butterflies (Hardy et al., 2007) and for the wetland butterfly *Lycaena xanthoides* in Oregon, USA (Severns et al., 2006). Species traits associated with flower specialization can help identify species (e.g., highly conspicuous and/or habitat-specialized, short proboscis length species) that may require intervention to maintain the availability of suitable flowering plants. Most flower-specialized butterfly families observed in this study were also found to be most extinction prone by Koh et al. (2004) and most habitat-specialized in Singapore (A. J. unpublished data). Therefore, the impacts of foraging shifts in flower specialized butterfly families may be even more critical due to their sensitivity to habitat specialization, high extinction proneness and potential synergistic interaction between these parameters. Habitat management for such butterflies would require continued persistence of their preferred native flower sources in transformed landscapes.

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Supplementary data

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