Preferences for exotic flowers do not promote urban life in butterflies

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ABSTRACT

We study whether butterfly diet predicts butterfly distribution along an urban gradient. Data come from a large scale participatory scheme involving the general public reporting butterfly abundance in their gardens (more than 6000 gardens), completed by a special survey on the relationship between butterfly species and flower species based on amateur pictures (more than 3500 pictures). Many studies show that urbanization promotes the loss of native plant species and their replacement by non-native species, so in this context we addressed the question of butterfly diet impacts provided by exotic and native plants in urban landscapes and we quantified diet diversity to identify specialist and generalist butterflies. Diet specialists had a longer proboscis and both specialization and proboscis length were positively correlated to preferences for exotic flowers. Nevertheless, diet specialist butterflies tended to avoid urban areas more strongly than diet generalists, while preference for exotic flowers was surprisingly not correlated to preferences for urban life in butterflies. All together this suggests that diet preferences do not play a strong part in determining butterfly distribution along urban gradients but also that diet specialization must be correlated to other life history traits such as dispersal ability or flexibility in habitat selection.

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1. Introduction

Flower–insect interactions have a long history that dates from the Cretaceous (Nell, 2002). The association between floral traits and pollinator specialization generates a pollination syndrome defined by Fenster et al. (2004) as a suite of floral traits, including rewards, associated with the attraction and utilization of a specific group of animals as pollinators (Waser et al., 1996). On the one hand, plants have developed a lot of devices to attract insects (Kevan and Baker, 1983; Andersson, 2003; Omura and Honda, 2005), including rewards such as nectar (Kevan and Baker, 1983), in order to get their pollen transported from flower to flower. On the other hand many insects depend on flowers being their main resource during the adult part of their life cycle (Corbet, 2000; Fenster et al., 2004; Ramirez, 2004). Insects themselves have developed very different strategies to exploit these resources leading to a continuum between the most specialized species exploiting only one plant species to the most generalist species able to exploit the full range of available flowers (Gomez and Zamora, 1999). Co-evolution between plants and pollinators (Mayfield et al., 2001; Bloch and Erhardt, 2008; Armbruster and Muchhala, 2009) involves

a lot of signals and many traits are used as cues by the pollinators, such as the color of the flower (Weiss, 1997; Reid and Culin, 2002; Li et al., 2008), the scent induced by pollen and nectar composition (Andersson and Dobson, 2003; Mevi-Schutz and Erhardt, 2005; Omura and Honda, 2005), the flower size (Bloch and Erhardt, 2008), the plant size (Dennis, 1992) and the flower pattern (Corbet, 2000). As suggested by Boggs et al. (2003), a combination of these traits is required to elicit naturally observed feeding patterns.

All together, flower dwelling insect form a vast species assemblage interacting with a vast assemblage of plant species (Burghardt et al., 2009). Importantly, these insects provide ecological services to human beings, through the pollination of cultivated flowers which could reach 35% of the worldwide crop volume (Klein et al., 2007). As any other biodiversity components, pollinating insects, their functions and associated services are impacted by human-induced global change. Here, we focused on one aspect of global change, urbanization which is one of the most dramatic land modification representing an extreme case of habitat destruction and fragmentation (Blair and Launer, 1997; McGeoch and Chown, 1997; McFrederick and LeBuhn, 2006), and on one associated perturbation, the introduction of exotic plant species. Such a large variety of ornamental flowers species affects pollinating insects by modifying the available resources (Burghardt et al., 2009). In urban areas, urban parks play a crucial part in providing a wide range of plants allowing the maintenance of pollinator communities (Hermy and Cornelis, 2000; McFrederick and LeBuhn, 2006). Private gardens may also help to support local pollinator assemblages if they offer

a rich reward to flower-visiting insects (Comba et al., 1999; Gaston et al., 2005). Although garden structure (Reid and Culin, 2002) and floral diversity (Potts et al., 2003) play an important role in pollinator attractiveness because they include a lot of flowering plants (mainly selected for ornamental criteria), both exotic and native (Burghardt et al., 2009), we do not know how they influence the presence of butterflies in urban areas.

Butterflies represent a non-negligible group of pollinators (Gregory, 1964; Pascarella et al., 2001; Kandori, 2002). The interactions between butterflies and flowers depend primarily on the reward offered by the flowers, i.e. nectar (Alonso Mejia et al., 1997; Rusterholz and Erhardt, 1997) that governs butterfly physiological processes (Baker and Baker, 1975; Moore and Singer, 1987; Hill, 1989; Mevi-Schutz and Erhardt, 2005), and on the match between flowers and butterfly eating structures (Dennis, 1992). More precisely, we studied how diet specificity predicts the distribution of butterflies along an urbanization gradient in France, where private and public gardens represent about one million ha (French Agricultural Ministry data, http://www.agreste.agriculture.gouv.fr). We hypothesized that generalist species may be more present in urban areas than specialists and we quantified how adult butterfly diet specialization and preferences for exotic flowers favor the colonization of urban areas. Eventually we studied ecological correlates associated with these diet characteristics.

The main difficulty for studying the distribution of butterflies in an urban environment is probably the data collection due to access restrictions (particularly, in private gardens). In this context, citizen science schemes offer a valuable tool to overcome this problem. Our study is based on data provided by the French Garden Butterfly Observatory. This scheme is based on butterfly observation data gathered by voluntary observers from the general public in private or public gardens from 2006 to 2008 in approximately 3500 private or public gardens each year. In addition, a special study was proposed in 2008 inviting observers to photograph butterflies feeding on flowers, providing nearly 3500 pictures.

2. Methods

2.1. Diet butterfly data

Data collection was based on pictures of feeding butterflies taken by volunteers between March and October 2008. Pictures including a butterfly/flower pair were considered only when the butterfly was seen feeding. If two or more butterflies were seen feeding on the same flower, they were considered as many butterfly/flower pairs. The only constraint was that only one picture of a given individual butterfly on a given flower species should be sent; if this individual was seen on another flower species, another picture could be taken and sent.

A total of 3942 pictures were collected all over France. Butterfly species that occurred less than 20 times were excluded from the analysis in order to allow proper estimation of diet specialization. As a result, 33 diurnal butterfly species were selected in this study. This represents 26% of the photographed species but 81% of the pictures. According to Lafranchis (2000), most of these species are widely distributed across France. In one case, two species were lumped in the analyses, due to identification difficulties: the pale clouded yellow (*Colias hyale*) and the berger's clouded yellow (*Colias alfacariensis*). Similarly, plants were identified to the genus level when species identification proved to be impossible on pictures.

2.2. Butterfly characteristics

Relationships between butterflies feeding preferences and their life history traits were studied. To achieve this, the butterflies eco-

logical (host plant family and number of host plants referenced in France, Lafranchis, 2000), physical (wingspan; proboscis length, Dennis, 1992), migratory (migratory status as two levels, migratory or no, Lafranchis, 2000) and phylogenetical features (family) were examined in order to explain butterfly diet. Phylogenetical characteristics were taken from Weller et al. (1996), and more specific information was found in Braby et al. (2006) for Pierids and in Martin et al. (2000) for Satyrids. Due to fragmentary information about butterfly phylogeny, branch lengths were not available and therefore all set equal to 1 (Appendix A).

2.3. Flower characteristics

Ten flower characteristics which could influence butterfly attractiveness were considered in this study. These were based on morphology: color (with nine classes: blue, green, purple, orange, white, brown, red, yellow and pink), symmetry (axial or radial), flower shape (with five classes: individual, capitulum, bell, lip and other), plant size (in meters with four categories: <0.5, 0.5–1.5, 1.5–3 and ≥3 m), flower size (diameter in millimeters with four categories: <15, 15–40, 40–100 and ≥100 mm); resources: nectar quality and pollen quality (with four classes: bad, medium, good and very good, using the beekeeping value defined by Royan et al., 1998); ecology: annual, persistent, other; and phylogeny (family). Even if butterflies were mainly no pollen users, several reasons led us to integrate this plant characteristic in our analysis. Indeed, some of the listed plant families did not produce nectar but butterflies were observed with proboscis extended towards such flowers. Although there is in such case no nectar reward, we could explain this behaviour by various hypotheses such as honeydew production by Homoptera on the flower or stem, but we could also suggest that various cues attracted pollinators such as scent. Indeed, pollen plays a part in pollinator attraction, particularly in the emission of scents (Dötterl et al., 2006; Waelti et al., 2009).

A correlation matrix was calculated to look for possible correlations between flower traits and identify redundant variables (Appendix B). The analysis showed a significant positive correlation between flower shape and flower symmetry and a significant positive correlation between flower shape and plant family. Significant correlations were also found between plant family and seasonal type and plant family and flower symmetry. As a result, seven flower traits were retained to develop the Butterfly Feeding Specialization Index: flower color, flower form, plant size, flower size, seasonal type, pollen quality and nectar quality.

Plants were classified as native or exotic using the French Natural Heritage Inventory website (http://inpn.mnhn.fr/). Based on the seven main flower traits selected, differences between native and exotic plant species were analyzed. We compared plant size, flower size, pollen quality and nectar with Mann–Whitney tests. The flower form, flower color and seasonality were analyzed by Chi-squared test.

2.4. Butterfly Feeding Specialization Index (BFSI)

A generalist species is a butterfly seen on different flower types with respect to their availability. Conversely, a specialist species visits only a few flower types and neglects the others. We did not have independent data on flower availability such as distribution of flower species in garden. We thus used the full range of pictures taken by amateurs as the range of flowers available to butterflies and compared, for a given flower trait, available flower category to observed flower category effectively visited by the butterfly species.

For each of the seven main flower traits selected, a specialization value was calculated following the method proposed by Julliard et

al. (2006):

$$SV = \frac{\sqrt{\mathrm{Var}(N_{i,c}/N_c)}}{\mathrm{Mean}(N_{i,c}/N_c)}$$

where SV is the specialization value for one flower characteristic, $N_{i,c}$ represents the number of pictures taken for category c for the ith butterfly species and N_c the total number of picture taken for the category c. Then, the average of these coefficients was calculated for the seven main flower traits and used as a measure of Butterfly Feeding Specialization Index (BFSI). We only used pictures of native flower species for the calculation of the BFSI, and butterfly species with at least 20 such pictures.

2.5. Native Preference Index (NPI)

This index was developed in order to calculate the proportion of native flower species in the diet of butterfly and it is based on plant species. Indeed, by counting the number of pictures where a butterfly is feeding on native plant species and comparing it to the total number of pictures taken for this butterfly, we could quantify the butterfly preferences for native flowers. This index was calculated as follow:

$$NPI = \frac{[NN_i/N_i]}{[NN - NN_i/N - N_i]}$$

where NN is the total number of pictures of butterflies taken feeding on native plants, NN_i represents the total number of pictures of the ith butterfly species taken feeding on native plants, N the total number of pictures of butterflies taken and N_i the total number of pictures of the ith butterfly species taken. Values of this index greater than 1 indicate that species have been more photographed on native than exotic plant species.

2.6. Butterfly sensitivity to urbanization

The sensitivity of butterflies to urbanization was estimated using data from the French Garden Butterfly Observatory from 2006 to 2008. Volunteers counted butterflies in their gardens (private or public and recorded environmental variables: geographical localization, garden size, floral composition of the site: with Buddleja, *Centaurea* sp. and *Scabiosa* sp., *Valeriana* sp. and *Centranthus* sp., *Geranium* sp. and *Pelargonium* sp., lavenders, crucifers, nettle, bramble, ivy, clovers or aromatic plants, surrounding landscape type and use of pesticides). No constraint on the frequency of observation was imposed, and at the end of each month (March to October), volunteers recorded online the maximum number of individuals of each butterfly species seen simultaneously in the garden during the month. Visit frequency was recorded. Volunteers recorded butterflies from a closed list of 28 common species. These data included species abundance data from 4727 municipalities spread all over France and concerned 21 species out of the 33 selected in the present study. The sensitivity to urbanization could not be calculated for twelve species, as the French Garden Butterfly Observatory lumped these with other similar species (all blue Lycaenids, all white Pierids for instance). These species are *Lycaena phlaeas*, *Lycaena tytirus*, *Polyommatus icarus*, *Celastrina argiolus*, *Plebejus agestis*, *Issoria lathonia*, *Lasiommata maera*, *Limenitis reducta*, *Pieris brassicae*, *Pieris napi*, *Pieris rapae* and *Ochlodes sylvanus*.

The measure of sensitivity was based on the abundance of butterflies in relation to the percentage of urban area in the municipality of observation, as given by the CORINE Land Cover classification (http://www.ifen.fr/). Butterfly abundance was calculated as the ratio between the total number of individuals for each species observed in a municipality between 2006 and 2008 and the number of surveyed months in this municipality. The urban-

ization gradient was strongly skewed towards low urbanization; we thus transformed percentage of urbanization into 8 classes of increasing urbanization level defined to include similar numbers of observations per categories. We calculated the parameter α of the exponential regression between the mean butterfly species abundance by municipalities classified in eight urbanization classes (<1% of urbanization: 986 municipalities, 1%: 407 municipalities, 2–3%: 688 municipalities, 4–6%: 618 municipalities, 7–10%: 503 municipalities, 11–19%: 528 municipalities, 20–40%: 470 municipalities, >40%: 527 municipalities). The lower the parameter α; the higher the species sensitivity to urbanization. A positive slope means that the species reacts positively to urbanization.

Eventually, we analyzed if the sensitivity of butterflies to urbanization was correlated to adult food preferences for exotic flowers (NPI) or to diet specialization (BFSI). We could then give a ruling on the importance of adult food resource to explain the presence of butterflies in urban areas.

2.7. Statistical analysis

Correlation tests (Pearson method) were performed to analyze relationships between (1) proboscis length and Butterfly Feeding Specialization Index, (2) proboscis length and Native Preference Index, (3) Native Preference Index and Butterfly Feeding Specialization Index and (4) Butterfly Feeding Specialization Index and sensitivity to urbanization.

Native Preference Index was analyzed with Generalized Linear Models (GLM) using wingspan, proboscis length, number of host plant species, butterfly family, host plant family and migratory status as explanatory variables. GLMs were constructed assuming Normal distribution for the NPI and a stepwise selection procedure allowed to select the best fitted model (based on the Akaike Information Criterion, AIC, Akaike, 1981). The general starting model included the Native Preference Index as a dependent variable with all the butterfly traits cited above and their possible double interactions as explanatory variables. Analyses of variance (ANOVA) of the GLMs were made using a type 3 ANOVA and associated P-values were calculated. To test for phylogenetical effects, a Generalized Least Square Model (GLS) was used to calculate corrected P-values which were compared to P-values obtained by GLM. This method allowed to test if taxonomic links between species played a role in flower selection process (Lachenbruch, 1990). This model, taking into account phylogenetic relationships between butterfly families, used the Native Preference Index as a predictive variable; host plant families, number of host plants, proboscis length and interactions between host plant families and number of host plants as explanatory variables. We assumed a Grafen correlation structure (Grafen, 1989) for the model dependence because branch lengths were not available (and therefore all set to 1).

The same method was used to test if the BFSI influenced species distribution areas along an urban gradient. Butterfly sensitivity to urbanization was used as the dependent variable, Native Preference Index and Butterfly Feeding Specialization Index and their interactions as explanatory variables.

Statistical analyses were performed with R© version 2.7.0 (2008-04-22).

3. Results

3.1. Data collection

A total of 3492 pictures of butterflies/flowers pairs were selected, including 33 butterfly species belonging to 9 families (Table 1) and 272 plant taxa belonging to 66 families (for more details on the plant species, see Appendix C). 554 municipalities

Table 1
Butterfly species list (NPI: Native Preference Index; BFSI: Butterfly Feeding Specialization Index; nc: non-calculated).

Family	Scientific name	Common name	Picture number	NPI	BFSI
Heliconiidae	*Argynnis paphia* (Linnaeus, 1758)	Silver-washed fritillary	86	0.53	1.44
	Issoria lathonia (Linnaeus, 1758)	Queen of Spain fritillary	32	0.88	nc
Hesperiidae	*Ochlodes sylvanus* (Esper, 1777)	Large skipper	34	1.07	0.93
Limenitidae	*Limenitis reducta* (Staudinger, 1901)	Southern white admiral	23	1.13	nc
Lycaenidae	*Lycaena phlaeas* (Linnaeus, 1761)	Small copper	120	1.29	0.66
	Lycaena tityrus (Poda, 1761)	Sooty copper	22	1.20	1.1
Nymphalidae	*Aglais urticae* (Linnaeus, 1758)	Small tortoiseshell	47	1.08	1.21
	Araschnia levana (Linnaeus, 1758)	Map butterfly	76	1.18	0.9
	Inachis io (Linnaeus, 1758)	Peacock butterfly	314	0.55	1.29
	Polygonia c-album (Linnaeus, 1758)	Comma butterfly	95	0.6	1.18
	Vanessa atalanta (Linnaeus, 1758)	Red admiral	196	0.7	1.31
	Vanessa cardui (Linnaeus, 1758)	Painted lady	87	0.64	1.35
Papilionidae	*Iphiclides podalirius* (Linnaeus, 1758)	Scarce swallowtail	127	0.86	1.38
	Papilio machaon (Linnaeus, 1758)	Swallowtail	106	0.73	1.61
Pieridae	*Anthocharis cardamines* (Linnaeus, 1758)	Orange tip	40	1.67	1.47
	Colias alfacariensis Ribbe, 1905; *Colias hyale* (Linnaeus, 1758)	Berger's clouded yellow; pale clouded yellow	26	0.7	nc
	Colias croceus (Fourcroy, 1785)	Clouded yellow	31	0.99	nc
	Gonepteryx rhamni (Linnaeus, 1758)	Brimstone	233	0.62	1.26
	Pieris brassicae (Linnaeus, 1758)	Large white	139	0.73	0.91
	Pieris napi (Linnaeus, 1758)	Green-veined white	132	1.37	0.79
	Pieris rapae (Linnaeus, 1758)	Small white	206	1.34	0.83
Polyommatidae	*Plebejus agestis* (Denis & Schiffermüller, 1775)	Brown argus	35	1.42	0.88
	Cacyreus marshalli (Butler, 1898)	Geranium bronze	70	1.29	0.61
	Celastrina argiolus (Linnaeus, 1758)	Holly blue	38	1.06	1.09
	Polyommatus icarus (Rottemburg, 1775)	Common blue	146	1.55	1.03
Satyridae	*Brintesia circe* (Fabricius, 1775)	Great banded grayling	35	0.15	nc
	Coenonympha pamphilus (Linnaeus, 1758)	Small health	48	1.52	1.23
	Lasiommata maera (Linnaeus, 1758)	Large wall brown	30	0.98	nc
	Lasiommata megera (Linnaeus, 1767)	Wall brown	66	0.87	1.74
	Maniola jurtina (Linnaeus, 1758)	Meadow brown	392	1.15	1.69
	Melanargia galathea (Linnaeus, 1758)	Marbled white	119	1.5	1.23
	Pararge aegeria (Linnaeus, 1758)	Speckled wood	74	0.99	0.72
	Pyronia tithonus (Linnaeus, 1767)	Gatekeeper	267	1.25	0.99

were represented all over France (Fig. 1) and more than 85% of the pictures were taken in gardens (public or private). Among the 554 municipalities referenced, 399 private gardens (72%) were followed by French Garden Butterfly Observatory volunteers. Among them, 341 gardens (85%) contained non-native and native nectar sources.
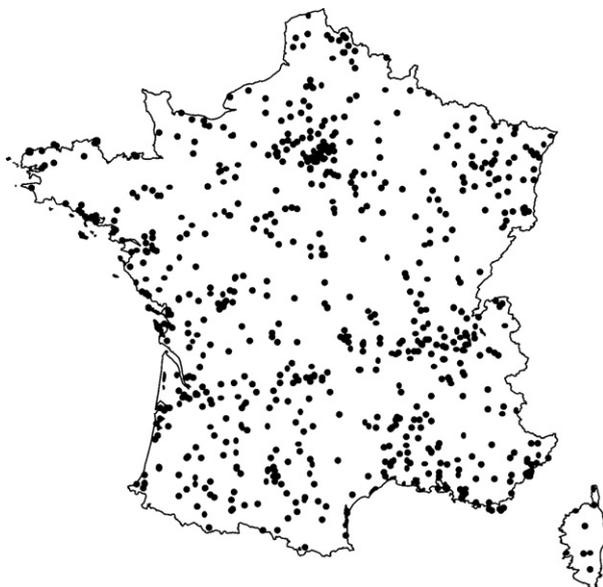
Fig. 1. Localization of the 554 French municipalities where pictures were taken.

1853 pictures represented native plant species, i.e. 53% of the total number of pictures.

3.2. Flower offer selection and comparisons between native and exotic flower characteristics

Exotic plants species were significantly (Mann–Whitney test, $P < 0.001$) higher than native plant species and their flowers were bigger (2.18 ± 0.25 m vs. 0.98 ± 0.1 m and 27.93 ± 2.39 mm vs. 19.26 ± 0.83 mm, respectively). The distribution of the pictures among different flower colors and flower patterns was different between exotic and native species (Chi-squared test, $\chi^2 = 28.83$, $P < 0.001$, df = 8; $\chi^2 = 18.93$, $P < 0.001$, df = 4, respectively).

Exotic colors and flower patterns were, respectively mainly white, pink, purple and yellow (respectively 24%, 20%, 15% and 15% of flowers) and mainly individual, capitulum and bell (respectively 31%, 23% and 20% of flowers), whereas native flower colors and patterns were, respectively mainly white, pink and yellow (respectively 23%, 23% and 20% of flowers) and mainly individual, capitulum and lip (respectively 38%, 30% and 20% of flowers).

There was no significant difference (Mann–Whitney test) between exotic and native plants for mean pollen quality (respectively 1.64 ± 0.17 and 1.47 ± 0.09, $P = 0.40$) and mean nectar quality (respectively 2.36 ± 0.17 and 2.28 ± 0.08, $P = 0.63$). The seasonality of the pictures did not differ between native and exotic species (Chi-squared test, $\chi^2 = 0.1$, $P = 0.66$, df = 1).

The Buddleja constituted undoubtedly the most attractive plant species in this study with 539 pictures. A total of 28 butterfly species (out of 33) were identified and represented 9 families. By comparison, a total of 24, 23 and 16 butterfly species (with 9 families) were

Table 2
Correlations between the Butterfly Feeding Specialization Index (BFSI) and the butterfly traits.

	Proboscis length	Wingspan	Number of host plant	Host plant family	Butterfly family
Correlation coefficient	0.43	0.32	0.17	0.09	0.01
P-value	0.03[*]	0.11	0.39	0.66	0.97

The asterisks show significant Pearson correlations coefficients (**$P < 0.01$; ***$P < 0.001$).
[*] $P < 0.05$.
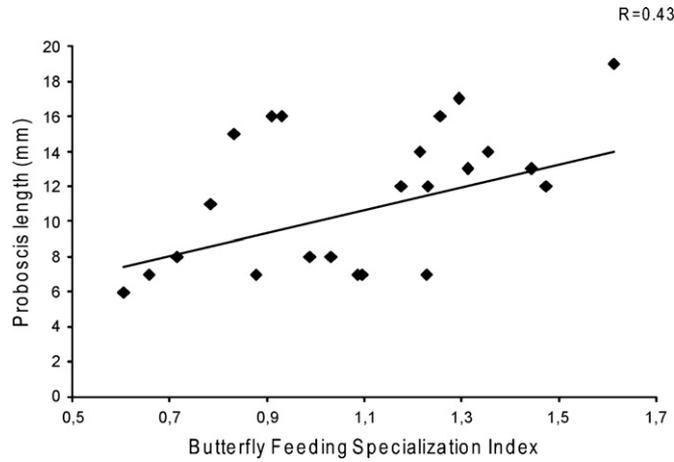
Fig. 2. Relationship between Butterfly Feeding Specialization Index and proboscis length.

Fig. 3. Relationship between Native Preference Index and proboscis length.

identified, respectively in lavenders, clovers and mints, the three most photographed plant species after Buddleja. The main families identified in Buddleja were Satyridae, Pieridae and Nymphalidae (with 7, 6 and 6 species, respectively). In terms of picture numbers, Nymphalidae represented the main family with 240 pictures (mainly represented by the peacock butterfly with 91 pictures) and Satyridae represented 87 pictures. Even if we listed only two Papilionidae species, the number of pictures was quite similar to Pieridae family (75 vs. 79, respectively).

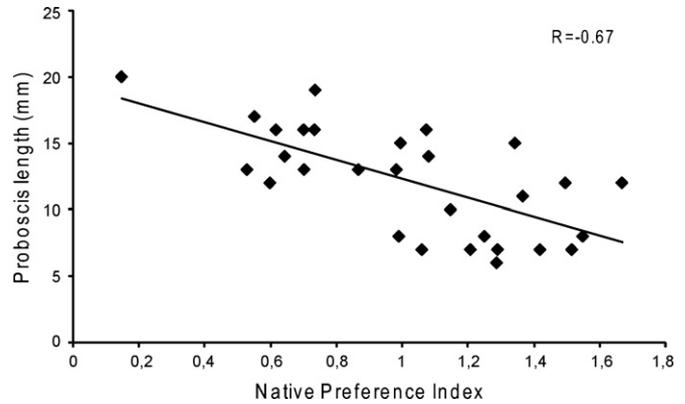### 3.3. Butterfly Feeding Specialization Index (BFSI)

Butterfly Feeding Specialization Index (compiled in Table 1) was only positively correlated with proboscis length (Table 2, Fig. 2).

3.4. Native Preference Index

The final model showed that NPI was significantly negatively related to proboscis length ($r = -0.67$, $P < 0.001$, Table 3, Fig. 3). Accounting for phylogenetical relatedness between species did not change this result ($P = 0.003$, Table 3). Thus butterflies preferences for native and exotic flowers were clearly related to the length of the proboscis (Fig. 3). Negative relationships between Native Preference Index and Butterfly Feeding Specialization Index indicated that specialist butterflies were more seen on exotic flowers than generalists ($r = -0.38$, $P = 0.04$ adjusted to proboscis length).

Table 3
Relationships between the Native Preference Index and variables included in the best fitted model using GLM (LR Chisq: Likelihood-ratio Chi square and the associated P-value) and GLS (with the corrected P-value associated) procedures.

	LR Chisq	P-value	Corrected P-value
Butterfly family	3.96	0.14	
Proboscis length	16.41	<0.001***	0.003***
Number of host plants	1.18	0.28	0.29
Host family	1.19	0.55	0.59
Number of host plants:host family	8.71	0.12	0.18

3.5. Butterfly sensitivity to urbanization

The selected model explaining butterfly sensitivity to urbanization includes Butterfly Feeding Specialization Index and Native Preference Index as explanatory variables without interactions. The sensitivity to urbanization was significantly positively related to the Butterfly Feeding Specialization Index (LR Chisq = 4.63, $P = 0.03$, Fig. 4.) and not significantly to the Native Preference Index (LR Chisq = 0.02, $P = 0.90$). While accounting for phylogenetical relatedness, sensitivity to urbanization was still significantly correlated with BFSI ($P = 0.02$) and not significantly with NPI ($P = 0.94$).

Two species, the speckled wood and the Geranium bronze, reacted positively to urbanization. All the other species reacted negatively to urbanization.
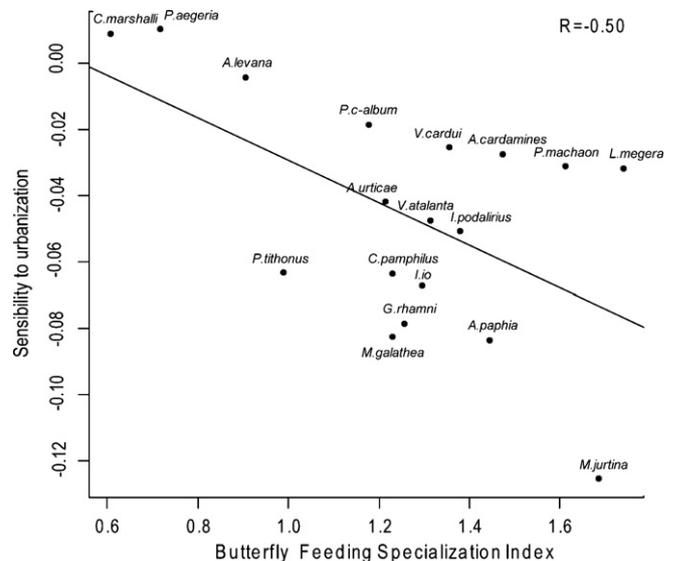
Fig. 4. Relationship between Butterfly Feeding Specialization Index and the sensitivity to urbanization.

4. Discussion and conclusion

Citizen science is characterized by volunteer involvement. Even if volunteers never detect all the butterflies in a site and species richness is often underestimated (Kery and Plattner, 2007), the bias resulting from volunteer observations is compensated by the amount of data provided by citizen science monitoring schemes. In the "flowers for butterflies" program, we compiled 3492 pictures taken in various habitat types and distributed all over France (554 municipalities). The 33 studied diurnal butterflies could be considered as representative of the common diurnal biodiversity of butterflies found in France because these species belong to nine of the major Rhopalocera butterfly families and are mostly widely distributed in France (Lafranchis, 2000).

The Buddleja welcomed a large number of butterflies. Its own characteristics explained this overwhelming attractiveness (Corbet, 2000). However, the composition of butterfly fauna visiting this plant concerned mainly large butterflies such as peacock butterfly, red admiral, painted lady, silver-washed fritillary, scarce swallowtail or painted lady. This fact could be explained by the foraging behaviour of large versus small butterflies (Corbet, 2000). Indeed compared to large butterflies which could forage easily on smallest trees such as Buddleja, smallest butterflies such as Hesperiidae, Lycaenidae and Polyommatidae species forage mainly in the herbaceous stratum.

Each species presents its own morphological features, as that give clues concerning its foraging behaviors (May, 1992; Corbet, 2000; Bloch and Erhardt, 2008). Foraging butterflies are face a wide range of flower types which differ in their structures, colors and suitability (Tiple et al., 2009). Floral geometry (symmetry and shape) also played a part in the visit of plants by pollinators. Indeed, some flowers with deep tubular corollas (such as species of Penstemon, Scrophulariaceae) are not visited by butterflies with proboscis capable of reaching nectar because there is no place to put the feet and balance to feed (Clinebell and Bernhardt, 1998; Lange et al., 2000). For example, the meadow brown was more attracted by herbaceous stratum plant species with small capitulum and lip flower shapes; white and pink flower colors. On the contrary, the scarce swallowtail was mainly attracted by shrub plants with large bell and lip flower shapes; purple and pink flower colors.

Thus we have developed the Butterfly Feeding Specialization Index which yielding a butterfly species classification along a specialist/generalist gradient with respect to their choice of flowers. Several studies on pollinators like bees reveal morphological differences between specialist and generalist (Harder, 1985) and the same findings exist for butterflies (Tudor et al., 2004; Kunte, 2007). Indeed, butterflies with long proboscis forage on deep flowers (Kunte, 2007; Tiple et al., 2009). Our results showing that specialist butterflies are mostly long proboscis species, while generalist species are mostly short proboscis species are consistent with these studies. Interestingly if a generalist butterfly species is defining as an insect visiting a lot of flowers types for dwelling nectar, the same thinking for flowers could be made. A generalist plant species could be defined if it has a broader spectrum of pollinators than their floral characters might suggest (Bloch and Erhardt, 2008).

Kunte (2007), explained these differences between specialists and generalists by competition arguing that specialist species were less competitive compared to shorter proboscis butterflies due to the higher handling time cost. Thus, for a given flower available to short and long proboscis butterflies, the latter harvest less nectar per unit of time. Indeed, the relationship between butterfly specialization and proboscis length can be interpreted as the narrowing range of flowers from which nectar can be extracted as proboscis length increases (Erhardt, 1995). Even if deeper flowers usually have higher standing nectar crops and provide higher energetic rewards (Harder, 1986), nectar access required specific adapta-

tion in butterflies for exploiting these specific and uncommon plants.

The native preference index showed that specialist butterflies (with long proboscis) were more seen on exotic flowers. Preferences for native or exotic plants were only strongly related to the proboscis length. There was no detectable influence of phylogenetical constraints. Because the length of the butterfly's proboscis is in relation to the depth of the flower corolla (Dennis, 1992; May, 1992; Kunte, 2007), we could expect that exotic flowers are deeper than native flowers. We found that exotic species were taller and had larger flower diameter than native plants. However, we did not have data referring to the corolla depth to validate the assumption that exotic flowers in the dataset were deeper than native species. Other differences between flowers were also identified. It is commonly admitted that color influences butterfly flower choice (Reid and Culin, 2002; Omura and Honda, 2005). Yet the complex mechanisms involved in color perception by insects and more particularly the role of ultra violet perception (Langanger et al., 2000; Mazza et al., 2002; Barta and Horvath, 2004) did not enable us to propose a valuable explanation to the observed differences in butterfly preferences between exotic and native flowers.

Differences in the repartition of exotic and native plant species could be noticed. Compared to more natural landscapes, in urban areas, especially in gardens, exotic flowers represent an important part of the total amount of available nectar for butterflies (Shapiro, 2002). However, even if we did not have data on the relative abundance of native and non-native nectar sources in gardens, 85% of private gardens followed by French Garden Butterfly Observatory volunteers (which represented 72% of the total sites) contained non-native and native nectar sources. These results suggest that in most cases, butterflies have choice between native and non-native nectar sources, and flower/butterfly combination should provide a good indication of the relative abundance of native and non-native nectar sources in gardens. However, in the case of an absence of more-preferred species, butterflies will visit less-preferred species by default. Without biasing our outcomes, care needs to be taken for such kind of studies.

We thus tested the hypothesis concerning the usual pattern of generalist species being commoner than specialist species in urban areas (Blair and Launer, 1997; Niell et al., 2007) and if the available adult food resources in urban areas (exotic or native flowers) could explain such pattern of distribution.

We showed that feeding specialization and not preferences for exotic or native was an important factor influencing the distribution pattern of butterflies along the urbanization gradient. There was no detectable influence of phylogenetical constraints. Our results were consistent with the literature (Dennis, 1992; Tolman and Lewington, 1997; Lafranchis, 2000) and showed that more generalist species (as the Geranium bronze, the small copper, the speckled wood or the green-veined white) occurred more in urban habitats compared to specialist butterflies (as the swallowtail or the orange tip). Thus, even if resources for specialist species were present in urban areas, they were probably not able to get there. More precisely, two generalist species reacted positively to urbanization namely the speckled wood and the Geranium bronze. Due to the dependence on cultivated *Pelargonium* species as host plants (Sarto i Monteys, 1992), we expected to find a positive response to urbanization for the Geranium bronze. For the speckled wood, the observed pattern could result from various factors. This species has several host plant such as the common couch (*Elytrigia repens*), the Cock's foot (*Dactylis glomerata*) or bromes (*Brachypodium* spp.) which are very common in urban areas. Moreover, as explained by Schweiger et al. (2006), specific adaptations could explain its presence in urbanized areas. Indeed, they suggest that some butterfly species such as the speckled wood living in landscapes undergo-

ing massive alterations may form metapopulations in response to anthropogenic habitat fragmentation (Shreeve et al., 2004).

Butterfly feeding specialization may also be correlated to other life history traits that explain the avoidance of urban life for feeding specialists. Urbanization consequences such as habitat fragmentation could constrain butterfly distribution patterns (Smallidge and Leopold, 1997; Weber et al., 2006; Bock et al., 2007). Landscape connectivity probably plays an important part in butterfly distribution and may interfere with butterfly population dynamics (Rathcke and Jules, 1993). Indeed, Corbet (2000), mentioned that body mass and wing loading affect the load-carrying (limiting distance between fueling stops and so related to the diet) and the cooling rate (limiting the distance between stops for basking or endothermic warming) of butterflies. These findings support that the persistence of common butterflies in urban areas requires connectivity between floral patches (Sutcliffe et al., 2003) including nectar sources (Baguette et al., 2000, 2003; Mennechez et al., 2003). Moreover the presence of host plants for larvae may also have an important influence on the viability of butterfly populations (Janz et al., 2001; Schultz, 2001; Dennis et al., 2004). Indeed, butterflies are highly selective in their choice of larval host plants (Dennis et al., 2004; Öckinger, 2008; Talsma et al., 2008), and Friberg et al. (2008), showed that habitat selection could precede the host plant choice. In many cases, the recognition of larval host plants involves locating the adequate habitat and urbanization could limit the abilities to locate such habitat patches due to numerous obstacles even if the larval host plants is present (Dennis, 1992).

In conclusion, our results allow us to suggest a mechanism to the usually observed pattern of generalist species being commoner than specialist species in urban areas (Blair and Launer, 1997; Niell et al., 2007) by showing that even if specialist butterflies feed on exotic flowers, they are not able to penetrate in urban areas. Butterfly distribution along urbanization gradients are more linked to butterfly feeding specialization than preferences for native or exotic species. Thus, compared to nectar availability provided by exotic or native flowers, butterfly feeding specialization appears as the main factor leading the distribution patterns of butterflies in urban areas. This study shows the importance of knowing the specific relationships between butterfly traits to understand large scale distribution patterns of common species in urbanized areas. However, comparisons with data obtained in wildland settings could be useful to have a complete overview of the functioning of butterfly communities.

Fig. A.1. .

However, despite the potential negative impacts of urbanization on insect richness (Matteson et al., 2008), urban areas seem to become pollinator reservoirs (McIntyre and Hostetler, 2001; Tommasi et al., 2004), especially when current farming methods harm pollinators such as bees or butterflies in agricultural landscapes (Kearns et al., 1998; Belfrage et al., 2005). But even if some pollinator species like bees are common in urban areas (McIntyre and Hostetler, 2001), the question of urban areas becoming refuges for specialist butterflies, because of a high availability of exotic flowers, has still to be addressed as their sensitivity to urbanization restricts the access to these high quality resources.

Acknowledgments

Appendix A.

Phylogenetical tree representing taxonomical relationships between the 33 butterfly species referenced (Fig. A.1).

Appendix B.

Correlation matrix for the nine flower traits selected. The asterisks show significant Pearson correlation coefficients (**$P < 0.01$; ***$P < 0.001$).

	Plant family	Seasonal type	Symmetry	Flower size	Plant size	Pollen quality	Nectar quality	Flower form	Color
Plant family	1	0.19*	0.23*	0.13	0.14	−0.08	−0.08	0.45	−0.14
Seasonal type		1	0.07	−0.11	−0.09	0.15	−0.04	0.09	−0.03
Symmetry			1	−0.17	−0.13	0.04	0.12	0.67	0.09
Flower size				1	−0.09	0.07	−0.10	−0.14	0.11
Plant size					1	−0.13	0.01	−0.06	−0.16
Pollen quality						1	−0.13	−0.10	0.03
Nectar quality							1	−0.05	0.16
Flower form								1	0.02
Color									1

* $P < 0.05$.

Appendix C.

Plant species list and number of pictures ordered by families.

Plant family	Picture number	Plant species
Adoxaceae	7	*Sambucus nigra, Viburnum odoratissimum*
Aizoaceae	14	*Delosperma cooperi*
Alliaceae	7	*Allium* sp., *Allium sphaerocephalon*
Apiaceae	29	*Astrantia major, Daucus carota, Fœniculum vulgare, Heracleum sphondylium, Oenanthe* sp., *Pastinaca sativa, Smyrnium perfoliatum*
Apocynaceae	4	*Nerium oleander, Vinca major*
Araliaceae	20	*Hedera helix*
Asclepiadaceae	2	*Asclepias syriaca*
Asphodelaceae	1	*Aloe lateritia*
Asteraceae	1185	*Achillea millefolium, Ageratum houstonianum, Anthemis arvensis, Arctanthemum arcticum, Arctium minus, Aster dumosus, Aster novae, Aster* sp., *Bellis perennis, Bidens tripartita, Buphthalmum salicifolium, Calendula* sp., *Callistephus chinensis, Carduus* sp., *Carlina vulgaris, Centaurea cyanus, Centaurea scabiosa., Chrysanthemum* sp., *Cichorium intybus, Cirsium arvense, Conyza canadensis, Coreopsis* sp., *Cosmos* sp., *Crepis* sp., *Dahlia* sp., *Echinacea purpurea, Echinops ritro, Erigeron annuus, Eupatorium cannabinum, Euryops chrysanthémoides, Gaillardia grandiflora, Galactites elegans, Helianthus annuus, Helianthus tuberosus, Helichrysum* sp., *Hieracium pilosella, Hypochaeris radicata, Inula* sp., *Jacobaea maritima, Leucanthemum vulgare, Liatris spicata, Ligularia* sp., *Matricaria recutita, Osteospermum* sp., *Pulicaria vulgaris, Rudbeckia* sp., *Santolina chamaecyparissus, Scabiosa colombaria, Senecio cineraria, Senecio vulgaris, Solidago virgaurea, Sonchus arvensis, Tagetes patula, Tagetes* sp., *Tanacetum vulgare, Taraxacum* sp., *Thrincia hirta, Zinnia* sp.
Balsaminaceae	1	*Impatiens walleriana*
Berberidaceae	1	*Berberis vulgaris*
Bignoniaceae	2	*Campsis radicans*
Boraginaceae	30	*Anchusa officinalis, Borago officinalis, Echium vulgare, Heliotropium europaeum, Myosotis* sp., *Symphytum officinale*
Brassicaceae	83	*Alliaria petiolata, Alyssum loiseleurii, Alyssum saxatile, Arabidopsis thaliana, Armoracia rusticana, Aubrieta deltoidea, Brassica napus, Brassica oleracea, Brassica rapa, Cardamine pratensis, Eruca sativa, Erysimum officinalis, Hesperis matronalis, Iberis sempervirens, Iberis umbellata, Lunaria annua, Raphanus raphanistrum, Raphanus sativus, Sinapis arvensis*
Campanulaceae	10	*Campanula* sp., *Jasione montana, Lobelia inflata, Phyteuma spicatum*
Caprifoliaceae	53	*Abelia* sp., *Centranthus ruber, Symphoricarpos albus*
Caryophyllaceae	69	*Agrostemma githago, Dianthus barbatus, Dianthus* sp., *Saponaria officinalis, Silene coronaria, Silene* sp.
Cleomaceae	3	*Cleome speciosa, Cleome viscosa*
Clusiaceae	5	*Hypericum perforatum*
Convolvulaceae	8	*Calystegia* sp., *Convolvulus arvensis*
Cornaceae	2	*Cornus sanguinea*
Crassulaceae	97	*Sedum* sp.
Cucurbitaceae	2	*Cucumis melo*
Dipsacaceae	25	*Dipsacus fullonum, Knautia arvensis*
Elaeagnaceae	1	*Elaeagnus angustifolia*
Ericaceae	21	*Arbutus unedo, Erica cinerea*
Fabaceae	195	*Albizia* sp., *Coronilla vaginalis, Lathyrus odoratus, Lotus corniculatus, Medicago* sp., *Phaseolus coccineus, Phaseolus vulgaris, Psoralea bituminosa, Sophora japonica, Trifolium* sp., *Vicia cracca, Vicia sativa, Wisteria floribunda*
Fumariaceae	1	*Fumaria officinalis*
Geraniaceae	30	*Geranium molle, Geranium pratense, Geranium robertianum, Geranium sanguineum, Pelargonium* sp.

Appendix C (*Continued*)

Plant family	Picture number	Plant species
Grossulariaceae	3	*Ribes nigrum, Ribes rubrum*
Hydrangeaceae	16	*Hydrangea* sp., *Philadelphus coronarius*
Hydrophyllaceae	3	*Phacelia tanacetifolia*
Lamiaceae	587	*Agastache* sp., *Ajuga reptans, Calamintha nepeta, Galeopsis angustifolia, Hyssopus officinalis, Lamium album, Lamium prupureum, Lavandula angustifolia, Manta arvensis, Melilotus* sp., *Melissa officinalis, Monarda didyma, Nepeta cataria, Nepeta* sp., *Ocimum basilicum, Origanum vulgare, Perovskia atriplifolia, Phlomis fructicosa, Physostegia virginiana, Prunella* sp., *Rosmarinus officinalis, Salvia microphylla, Salvia officinalis, Satureja hortensis, Scutellaria galericulata, Stachys officinalis, Thymus serpyllum, Thymus vulgaris, Vitex* sp.
Liliaceae	17	*Allium porrum, Allium schoenoprasum, Aphyllanthes monspeliensis, Asphodelus* sp., *Hyacinthoides non-scripta, Muscari neglectum, Narcissus pseudonarcissus*
Loganiaceae	539	*Buddleja* sp.
Lythraceae	53	*Lythrum salicaria, Syringa vulgaris*
Malvaceae	14	*Hibiscus syriacus, Lavatera arborea, Malva sylvestris*
Moraceae	1	*Morus nigra*
Nyctaginaceae	4	*Bougainvillea glabra*
Oleaceae	15	*Jasminum* sp., *Ligustrum vulgare*
Onagraceae	12	*Clarkia speciosa, Epilobium hirsutum, Epilobium montanum, Fuchsia* sp., *Gaura* sp., *Oenothera biennis*
Oxalidaceae	1	*Oxalis corniculata*
Papaveraceae	2	*Eschscholzia californica, Papaver rhoeas*
Phytolaccaceae	1	*Phytolacca acinos*
Pittosporaceae	2	*Pittosporum tobira*
Plantaginaceae	25	*Plantago* sp.
Plumbaginaceae	10	*Ceratostigma willmotianum, Limonium vulgare, Plumbago* sp.
Poaceae	2	*Elytrigia*
Polemoniaceae	20	*Phlox* sp.
Polygonaceae	2	*Polygonum bistorta, Polygonum* sp.
Primulaceae	5	*Lysimachia punctata, Primula auricula, Primula* sp.
Ranunculaceae	21	*Anemone japonica, Clematis vitalba, Delphinium* sp., *Nigella damascena, Ranunculus* sp.
Rhamnaceae	8	*Ceanothus pallidus, Ceanothus* sp., *Frangula dodonei*
Rosaceae	77	*Chaenomeles japonica, Cotoneaster integrifolius, Fragaria vesca, Kerria japonica, Photinia × fraseri, Physocarpus opulifolius, Potentilla* sp., *Prunus laurocerasus, Prunus lusitanica, Prunus* sp., *Pyracantha coccinea, Rosa* sp., *Rubus fructicosus, Rubus Idaeus, Spiraea vanhouttei, Spirea japonica*
Rubiaceae	3	*Crucianella* sp., *Galium odoratum*
Rutaceae	4	*Choisya ternata*
Saxifragaceae	5	*Astilbe* sp., *Deutzia*
Scrophulariaceae	12	*Cymbalaria muralis, Hebe* sp., *Linaria repens, Linaria vulgaris, Veronica longifolia, Veronica officinalis*
Simaroubaceae	1	*Ailanthus altissima*
Solanaceae	1	*Petunia* sp.
Tamaricaceae	1	*Tamarix ramosissima*
Tropaeolaceae	2	*Tropaeolum majus*
Urticaceae	6	*Urtica dioica, Urtica urens*
Valerianaceae	39	*Valeriana officinalis*
Verbenaceae	67	*Caryopteris* sp., *Clerodendrum* sp., *Lantana camara, Lantana* sp., *Lippia canescens, Verbena bonariensis, Verbena officinalis*
Violaceae	3	*Viola odorata, Viola tricolor*

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