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Shifting butterfly habitats and biotope affiliations accompany use of alien nectar sources after deforestation

Peter B. HARDY[1], Roger L. H. DENNIS[2, 3*]

1. 81 Winstanley Road, Sale, Cheshire, M33 2AT UK.
2. NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK
3. Institute for Environment, Sustainability and Regeneration, Mellor Building, Staffordshire University, College Road, Stoke on Trent, ST4 2DE, UK.

Abstract In the developed temperate world phytophagous insect communities are rapidly adjusting to introduced plants as larval food and nectar. In this study we investigate the readiness of butterfly species in a tropical context, experiencing relatively recent clear felling of forest, to use introduced flowering plants as nectar sources and the extent to which new butterfly-flowering plant assemblages are emerging in new biotopes. We find that introduced flowering plants are used by more species and more frequently by butterflies than native plants and that this relates to their ubiquity across sites and in biotopes and floral abundance. Moreover, distinctive assemblages of nectar-feeding butterfly species and flowering plants are associated with the emerging biotopes such as roadsides, subsistence cropland, intensive farmland, and gardens. In these new biotopes introduced plants are important in supplementing nectar resources for butterflies. We urge more intensive and detailed studies of wider resource use by native butterflies in tropical countries undergoing rapid change with deforestation to determine how butterflies are responding to emerging distinctive biotopes and the distinctive habitats, including consumer resources and utilities, these biotopes provide [*Acta Zoologica Sinica* 54 (1): - , 2008].

Key words Philippines, Habitat, Biotope, Nectar, Flowering plants, Deforestation, Resources, Butterflies, Communities

蝴蝶在生境和生物小区之间的移位伴随着对外来蜜源的利用

Peter B. HARDY[1] Roger L. H. DENNIS[2, 3*]

1. 81 Winstanley Road, Sale, Cheshire, M33 2AT UK.
2. NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK
3. Institute for Environment, Sustainability and Regeneration, Mellor Building, Staffordshire University, College Road, Stoke on Trent, ST4 2DE, UK.

摘 要 在发育成熟的温带环境中，植食性昆虫群落能迅速适应引入植物并将其作为幼虫的食物和花蜜。我们研究了经过森林砍伐的热带环境中蝴蝶对利用引入植物作为蜜源植物的适应快慢程度，并研究了蝴蝶-显花植物在新的生物小区中出现的范围，发现蝴蝶对引入显花植物的利用和探访多于本地植物，这与引入植物在调查地点、生物小区和植物丰度中的普遍性有关。此外，取食花蜜的蝴蝶和显花植物与正在形成的的生物小区有关，例如路边、农田、集约耕地以及花园。在这些新生物小区中，引入植物很重要，因为它们为蝴蝶提供了蜜源[动物学报 54 (1): - ，2008]。

关键词 菲律宾 生境 花蜜 开花植物 森林砍伐 资源 蝴蝶 群落

An inevitable consequence of deforestation and development in the tropics is that arthropods that survive the changes, particularly phytophagous insects such as butterflies, will adopt new habitats in the regions where such changes occur. They will do so whether habitat is interpreted in the traditional manner as biotope, i.e. as vegetation type or substrate, or in the resource-based view, which defines habitats on coincidence of

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* E-mail: rlhdennis@aol.com

complementary resources at sites required by different developmental stages of an organism (Dennis et al., 2003). Original forests fast disappear and in their place emerges a variety of land uses such as subsistence cropland, more intensive agriculture, urban and industrial cover, gardens, transport infrastructure. These present not just different surfaces that can be used by insects as utilities for roosting, resting, pupation, thermoregulation, mate location, and aestivating, but also new consumer resources, new flowering nectar plants and, potentially, new larval host plants (Dennis et al., 2006). The latter are occasionally accompanied by introduced insect species feeding on those plants. This process is long established in developed temperate areas such as Europe and North America where little is left of the original natural vegetation cover (Spellerberg and Sawyer, 1999). In Britain, butterflies are well known to use introduced flowering plants as nectar sources and moreover a number of alien plants are also well established as larval host plants [e.g. *Rhamus alaternus* L. (Rhamnaceae) for *Gonepteryx rhamni* L. (Pieridae); *Quercus ilex* L. (Fagaceae) for *Neozephyrus quercus* L. (Lycaenidae); Hardy et al., 2007]. In fact, in Britain, the list of introduced flowering plants is longer than that of native flowering plants as nectar sources for species (introduced plants 265 native plants 245; Hardy et al., 2007; Dennis et al., 2007; see www.geocities.com/pgll@btopenworld.com/resources/resources.htm). Moreover, one of the 265 introduced plants used as a nectar source by British butterflies [i.e. *Buddleja davidii* Franch (Buddlejaceae)] has become extremely important and has vastly more records than most indigenous plants in spreading to waste sites and cliffs.

The question is how rapidly do these changes progress and what contrasts emerge when butterfly species occupy developing biotopes associated with changing resource types? A change in resource use, for instance the adoption of a new nectar flower species, implicates a change in location and biotope occupancy to the extent that 'new' plants may be biased to places where native resources are no longer be found. To what extent have native flowering plants adjusted to the new biotopes and are being used by butterfly species within these biotopes? Thus, where tropical forests were once found, to what extent has deforestation led to the adoption of new nectar sources as opposed to the use of familiar native ones? Is the change in provenance of nectar sources progressing at the same rate as in temperate developed countries? Has it led to distinctions in occupancy among species for biotopes and characteristic plant species and life forms?

Here, to advance some appreciation of these issues, we test some hypotheses in relation to nectar flower use in a small region of the Philippines, one that was forested in the 1950s and 1960s, residual secondary forest to 1984, but which now is fast being converted into an array of biotopes associated with development. We first test whether introduced flowering plants are used more frequently as nectar sources than native flowering plants. We then test whether flowering plant use by butterflies relates to their availability and floral abundance, regardless of provenance (native or introduced). Finally, we test for the occurrence of distinct groups of nectar plant use by butterflies in relation to distinctions in life form and biotope.

1 Materials and methods

In 2007, a month long survey (July 31 – August 25) was conducted of nectar source use by butterflies in the vicinity of Binangonan, 33 km east of Manila, Philippines (Rizal Province, centred on 14°31′53.2″N, 121°11′28.5″E). Since 1984, when the district was under secondary forest, it has been extensively developed and built over; sites were selected that were native forest within the last 50 years. Seven biotopes were surveyed at 15 sites occupying a rectangle of 60 square kilometres; within this area, observations were carried out over 4 square kilometres based on standard butterfly transects (Pollard and Yates, 1993). Numbers of individuals of different butterfly species feeding at nectar flowering plants were recorded and the biotopes in which these plants occurred. Biotopes are: 1 forest, 2 stream-side with forest remnants, 3 unsurfaced road edges and tracks, 4 surfaced road edges, 5 subsistence crops and semi natural vegetation on hill sides, 6 intensive agriculture on level ground, and 7 gardens. Butterfly nomenclature follows Treadaway (1995) and plant nomenclature and provenance is taken from Madulid (1995), Sastry et al. (1980) and Moody et al. (1984). Plants were also scored for ubiquity and abundance. Ubiquity is the number of sites occupied by the nectar plants. Abundance of nectar plants is scored for flower availability on a five point scale (1 single flower, 2 flowers sparse, 3 flowers moderately common, 4 flowers abundant, 5 flowers dense).

Analyses have been undertaken to answer specific hypotheses (questions). To determine whether introduced nectar plants are used more frequently than native nectar plants, a direct comparison has been made of nectaring events and number of butterfly species exploiting nectar plants for two groups (provenance: native and introduced) regardless of plant species using a χ^2 test. For a more detailed inquiry into whether introduced nectar plant species are used more frequently than native nectar plant species, comparisons have been carried out for the same variables (nectaring events and number of butterfly species) over plant species by applying a Mann-Whitney U test. A similar comparison has been made for provenance of plant species for the number of biotopes occupied, ubiquity and abundance of flowers. For these comparisons, a hypothesis of no difference has been established between native and alien plants.

To obtain an understanding of the variables in nectar flower exploitation, nectaring events on plants and number of butterfly species exploiting nectar plants have been regressed (stepwise, backwards removal) against number of biotopes, ubiquity, abundance and provenance. Provenance was introduced as a binary variable in regressions (0 native, 1 introduced). To determine if any individual effects of provenance existed in explaining nectar flower use, provenance was entered into stepwise (backwards removal) logit regression against flowering events, number of butterfly species, biotopes, ubiquity and abundance. Principal components analysis is applied to identify patterns in the suite of variables. It is expected that numbers of nectaring events and butterfly species exploiting plants will relate in some way to plant availability, but that plant provenance affects plant use to the extent that, as distinct groups, they differ in ubiquity. A null hypothesis has been established for tests.

To determine any bias in native/introduced nectar flower exploitation, and nectar flower/biotope association, a canonical correspondence analysis (CCA) was carried out on butterfly-plant interactions (nectar events) for plants with ≥ 10 records. Significance was attained separately for butterfly/nectar flower and nectar flower biotope associations by iterative removal (species) and amalgamation (biotopes; see below) of attribute states with low frequencies until cell conditions for χ^2 tests were met (Siegel, 1956). It is expected that distinctions in nectar plant use will emerge that relate to biotope occupancy and life forms. A null hypothesis has been established for tests.

Two variables have been transformed to attain normality for regression analyses ($\log_{10}$ nectaring events; log biotopes). Analyses have been conducted in STATISTICA (Statsoft, 2001) and significance is taken to be $P < 0.05$.

2 Results

During the survey, some 62 butterfly species were observed, of which 48 species were found to use 17 plant species as nectar sources (1709 observations); 10 plants received ≥10 visits (Table 1).

Table 1 Status of flowering plants in Rizal Province, Philippines, used by butterflies as nectar sources

Plant name	Vernacular name	Family	Origin
Pseuderanthemum reticulatum (Hook f.) Radlk.	False eranthemum; Moradong dilaw	Acanthaceae	Introduced, deliberately planted, Melanesia; cultivated; ornamental shrub
Lantana camara L.	Lantana	Verbenaceae	Introduced, tropical America; invasive; shrub
Tridax procumbens L.	Tridax daisy; Coatbuttons	Asteraceae	Introduced, tropical America; invasive herb
Euphorbia heterophylla L.	Kanaka	Euphorbiaceae	Introduced, central America; herb; growing wild by roadside
Leea philippinensis Merrill	Mali-mali	Leeaceae	Native; tree
Ixora coccinea L.	Santan; Jungle Geranium	Rubiaceae	Native; deliberately planted, and cultivated; ornamental small shrub
Bougainvillaea spectabilis Willd.	Bougainvillaea	Nyctaginaceae	Introduced, deliberately planted, tropical America; ornamental shrub
Morinda citrifolia L.	Nori	Rubiaceae	Native; tree
Deeringia polysperma (Roxb.)	Bayambang	Amaranthaceae	Native; shrub
Turnera ulmifolia L.	Yellow Alder	Turneraceae	Introduced, deliberately planted, West Indies/tropical America; cultivated; ornamental shrub
Ipomoea triloba L.	Kamo-kamotehan; Littlebell; Morning-glory	Convolvulaceae	Introduced, tropical America; invasive; herb
Ruellia tuberosa L.	Meadow weed	Acanthaceae	Introduced; West Indies, Americas
Talinum paniculatum (Jacq.) Gaertn.	Jewels-of-Opar; Talinom	Portulacaceae	Introduced, central America; herb; used as vegetable
Zinnia elegans Jacq.	Zinnia	Asteraceae	Introduced, deliberately planted, tropical America; ornamental flowering herb
Bidens pilosa L.	Puriket; Beggar's Tick	Asteraceae	Native; herb
Catharanthus roseus (L.) G. Don	Chichirica; Rose Periwinkle	Apocynaceae	Introduced, deliberately planted, Madagascar; ornamental flowering herb
Muntingia calabura L.	Datiles; Jamaica cherry	Elaeocarpaceae	Introduced, Neotropics; fruit tree

A number of plant species had clearly been deliberately planted, whereas others were dispersing naturally: *Lantana camara*, *Tridax procumbens*, *Euphorbia heterophylla*, *Ipomoea triloba*, *Ruellia tuberosa*, *Talinum paniculatum* and *Stachytarpeta jamaicensis*.

Overall, there were 124 visits to native plants and 619 to introduced plants ($\chi_1^2 = 289.0$, $P < 0.0001$) based on the assumption that plants were equally accessible to butterflies. More butterfly species also visited introduced plants ($n = 45$) than native plants ($n = 24$), but this difference, based on the same equality assumptions, was not significant ($\chi_1^2 = 2.7$, $P = 0.10$).

Of the 17 nectar flowering plants, 12 are introduced and 5 native. No differences were found among the species based on provenance for nectar visits, number of species feeding on them, number of biotopes occupied, for abundance or ubiquity (Mann-Whitney U tests; $P =$ 0.23 to 0.56). Logit regression for provenance also revealed no distinctions among nectar flowering plants for these variables.

Regression analysis of nectaring events across plant species against number of biotopes, ubiquity, abundance and provenance (Table 2) indicated a sole influence on number of biotopes ($F_{1,15} = 9.95$, $P < 0.006$, standard error of estimate: 0.53, $r = 0.63$, $r^2 = 40\%$). By comparison, the sole influence on number of butterfly species feeding on plants is site ubiquity ($F_{1,15} = 12.44$ $P < 0.003$ standard error of estimate: 7.14, $r = 0.67$ $r^2 = 45\%$). A principal components analysis illustrates a very close relationship between measures of plant site ubiquity, biotope occupancy and floral abundance (Fig.1); it also shows that both number of nectaring events and numbers of butterfly species are closely related to these three plant variables but not to provenance. For this reason, relationships emerging in above regression analyses isolate the best predictors from among closely related variables.

Table 2 Basic statistics on flowering nectar plants and use by butterfly species

Plant species	Nectaring events	Number of butterfly species	Number of biotopes occupied	Provenance	Site ubiquity	Floral abundance
Pseuderanthemum reticulatum	253	27	2	2	3	2
Lantana camara	139	32	4	2	5	4
Tridax procumbens	131	24	4	2	5	5
Euphorbia heterophylla	41	10	4	2	5	3
Leea philippinensis	53	9	1	1	1	2
Ixora coccinea	26	10	3	1	4	2
Bougainvillaea spectabilis	8	5	3	2	4	2
Morinda citrifolia	14	8	1	1	1	1
Deeringia polysperma	18	6	1	1	2	2
Turnera ulmifolia	22	5	2	2	2	2
Ipomoea triloba	2	2	1	2	2	2
Ruellia tuberosa	2	2	1	2	1	2
Talinum paniculatum	2	2	1	2	1	2
Zinnia elegans	6	6	1	2	1	2
Bidens pilosa	14	6	1	1	1	3
Catharanthus roseus	3	2	1	2	2	2
Muntingia calabura	7	1	1	2	1	1

The CCA illustrates a strong set of relationships (associations) between butterfly species and nectar flowering plants, and between nectar flowering plants and biotopes (Fig.2). These groups are also shown to correspond to a bias in plant life forms, with herbs, shrubs and trees found more frequently in crop areas, gardens and forest remnants respectively. These relationships are supported by significant χ^2 tests (butterfly species and flowering plants: $\chi_{16}^2 = 281.9$, $P < 0.0001$; flowering plants and biotopes: $\chi_{18}^2 = 953.8$, $P < 0.0001$, for the latter, forests were amalgamated with stream-sides with forest remnants and surfaced road edges and intensive agriculture on level ground were amalgamated with gardens). There is taxonomic bias at family level for the number of butterflies seen in biotopes ($\chi_{24}^2 = 498.23$, $P < 0.0001$) but no bias at family level for the number of species occurring in different biotopes ($\chi_{12}^2 = 6.94$, $P \approx 0.85$).

3 Discussion

The study has several clear findings that support our expectations. First, introduced flowering nectar sources are used more frequently than native ones. Introduced flowering plants are systematically colonising new biotopes

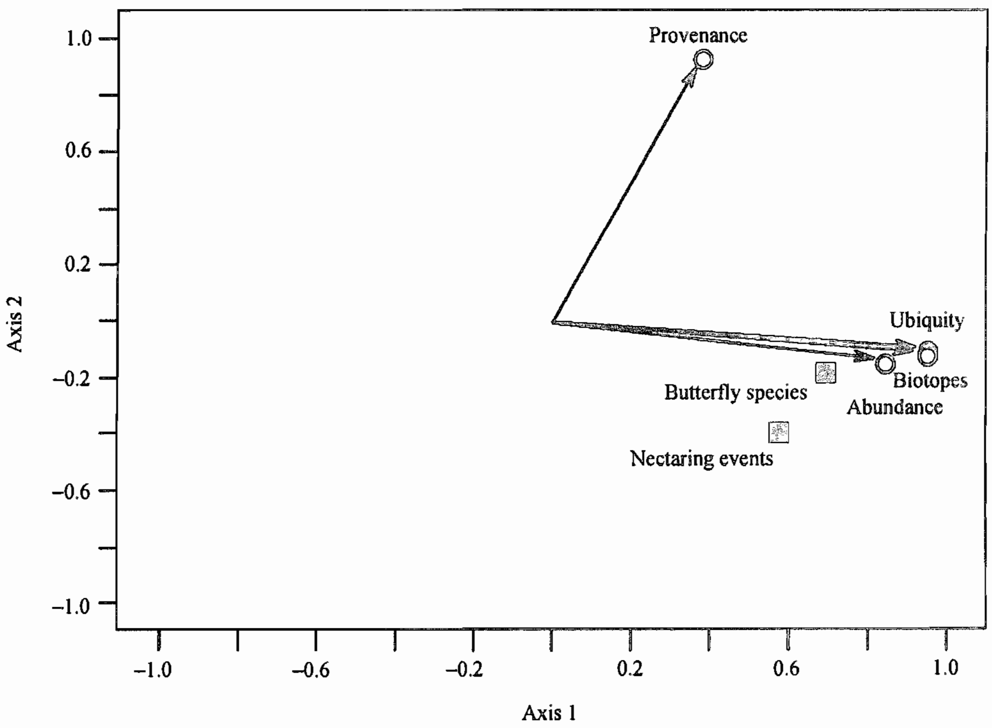

Fig.1 Principal components analysis of nectar flower use in relation to abundance

Nectaring events and number of butterfly species entered as supplementary to analysis, based on the four plant variables; see text and Table 2 for details of variables. Variance accounted: axis 1, 67%, axis 2, 23%.

emerging with forest destruction in the Philippines and are being fully exploited by native butterfly species. Although native and introduced flowering plants do not differ significantly as to the number of butterfly species using them, more butterfly species use introduced plants as nectar sources, and significantly more individual butterflies (regardless of species) use introduced plants. In fact, of those plants regularly used as nectar sources over twice as many are introduced species as are native species. Second, the use of flowering nectar sources among individuals and butterfly species corresponds to availability as is as expected. Number of nectaring events across butterfly species relates to the number of biotopes occupied by plants and the number of butterfly species using nectar plants relates to their ubiquity across sites; the principal components analysis supports the notion that nectar source use in butterflies responds much to availability. Third, there are significantly strong associations between butterfly species and flowering plants, plant life forms and biotopes they occupy. Three basic groups of plants and butterflies, distinct assemblages and potentially new communities, emerge relating to plant life forms: herbs ('weeds') in crop areas, shrubs in gardens and trees in forest remnants.

These findings suggest that much the same changes in the pattern of community ecology with development occur in the tropics as in temperate countries. Compared to use of larval host plants butterflies are generalist nectar feeders and will exploit whatever nectar sources they can access that produce sufficient energy returns; the main limits on nectar use tend to be physical, relating to proboscis length and wing loading (Corbet, 2000) whereas biochemistry plays a more fundamental part in larval host plant exploitation (Ehrlich and Raven 1965). There is a suggestion in these data that with the loss of forest, introduced flowering plants fill a gap in adult food replacing the loss of native flowering plants previously used by native butterflies. If this is the case then this begs the question of what plants are being lost with the decline in forest cover and what forest butterfly species, larval host specialists on native forest plants, are vulnerable to extinction?

An interesting feature of the butterfly-plant-biotope associations is that both introduced and native flowering plants occur in the developing biotopes (e.g. *T. ulmifolia* and *P. reticulatum* with *I. coccinea* in gardens and *T. procumbens* with *B. pilosa* in areas of subsistence crops on hillsides). There is a quantum shift in biotope associations for native plants, as well as for butterfly species depending on native plants. At the same time alien supplementary resources are accompanying the new biotopes to sustain these insect herbivores. In essence, the occurrence of butterfly species in these new, open biotopes and exploitation of introduced plants for nectaring suggests a clear shift in habitat bounds, that is, the colonisation of new landscape structures as well as reliance on new resources. That there is a substantial shift in butterfly assemblages is indicated not only in butterfly

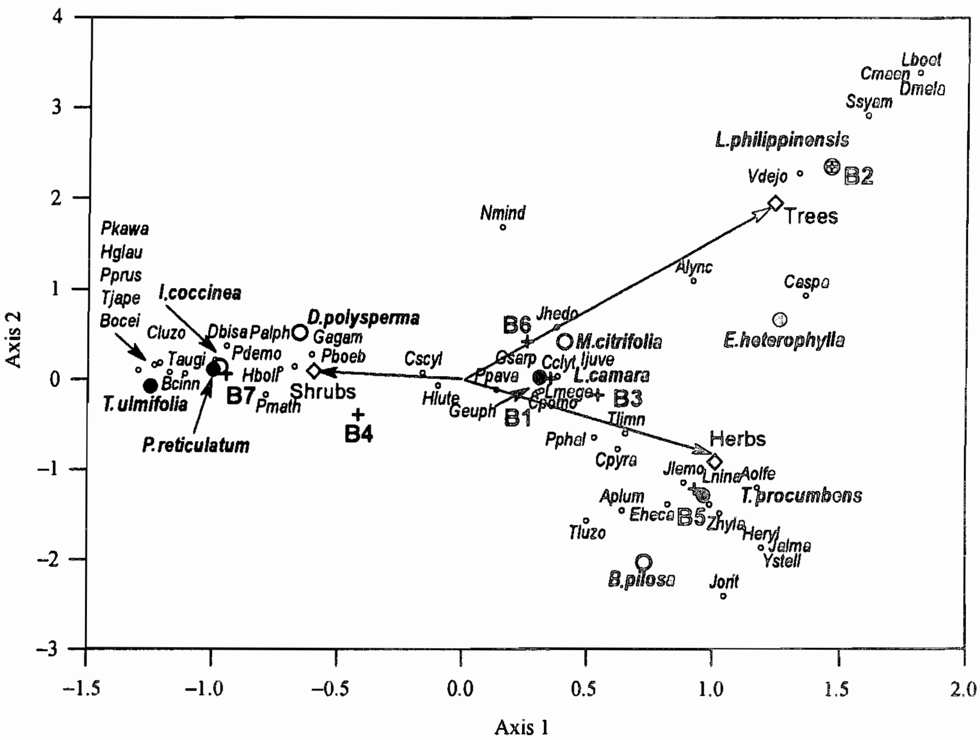

Fig.2 Canonical correspondence analysis of butterfly species, flowering plants used for nectar, biotopes and life forms

Biotopes and life forms were entered as supplementary variables and analysis was based on frequencies of nectar events on plants. % Inertia: axis 1, 27%, axis 2, 20%. Vectors shown only for life forms. Tiny circles, butterfly species represented by a generic letter and first four letters of species name; Large circles, flowering plants with open circles native plants and black circles introduced plants; crosses, biotopes (B1 to B7); diamonds, life forms. Butterfly species: Hesperiidae: *Tagiades japetus* (Stoll)[4], *Aeromachus plumbeola* (C. & R. Felder)[1,3], *Halpe luteisquama* (Mabille)[1,4], *Taractrocera luzonensis* (Staudinger)[4], *Potanthus pava* (Fruhstorfer)[3], *Telicota augias* (Linnaeus)[4], *Prusiana prusias* (C. Felder)[4], *Parnara kawazoei* (Chiba & Eliot)[4], *Borbo cinnara* (Wallace)[4], *Pelopidas mathias* (Fabricius)[4], *Baoris oceia* (Hewitson)[4]. Papilionidae: *Chilasa clytia* (Linnaeus)[3], *Papilio demoleus* Linnaeus[4], *Papilio alphenor* Cramer[4], *Graphium sarpedon* (Linnaeus)[4], *Graphium agamemnon* (Linnaeus)[4], *Graphium euphrates* (C. & R. Felder)[4], *Lamproptera meges* (Zinken)[4]. Pieridae: *Delias hyparete* (Linnaeus)[4], *Catopsilia pyranthe* (Linnaeus)[4], *Catopsilia pomona* (Fabricius)[4], *Catopsilia scylla* (Linnaeus)[4], *Eurema hecabe* (Linnaeus)[4], *Leptosia nina* (Fabricius)[4], *Cepora aspasia* (Stoll)[4], *Appias olferna* Swinhoe[4], *Appias lyncida* (Cramer)[4], *Pareronia boebera* (Eschscholtz)[1,4], *Hebomoia glaucippe* (Linnaeus)[4]. Nymphalidae: *Cethosia luzonica* C. & R. Felder[1,3], *Vindula dejone* (Erichson)[4], *Phalanta phalantha* (Drury)[4], *Junonia hedonia* (Linnaeus)[4], *Junonia almana* (Linnaeus)[4], *Junonia lemonias* (Linnaeus)[2], *Junonia orithya* (Linnaeus)[4], *Hypolimnas bolina* (Linnaeus)[4], *Doleschallia bisaltide* C. & R. Felder[4], *Cyrestis maenalis* Erichson[4], *Neptis mindorana* C. & R. Felder[1,4], *Ypthima stellera* (Eschscholtz) (Satyrinae)[1,4], *Ideopsis juventa* (Cramer) (Danainae)[4], *Tirumala limniace* (Cramer)[4], (Danainae), *Danaus melanippus* (Cramer)[4] (Danainae). Lycaenidae: *Lampides boeticus* (Linnaeus)[4], *Zizula hylax* (Fabricius)[3], *Spindasis syama* (Horsfield)[4], *Hypolycaena erylus* (Godart)[4].

Biotopes: 1 forest, 2 stream-side with forest remnants, 3 unsurfaced road edges and tracks, 4 surfaced road edges, 5 subsistence crops and semi-natural vegetation on hill sides, 6 intensive agriculture on level ground, 7 gardens. Codes from Treadaway (1995) for species: [1]endemic to Philippines, [2]rare, [3]uncommon or local, [4]common.

plant species associations at species level but also in the contrasts among taxa (families) in numbers of butterfly individuals occurring in different biotopes.

In conclusion, these findings clearly prompt further investigations and a broader view of resource use by organisms. It is particularly important for conservation to determine what other unusual resources, both utility and consumer resources, are being used by native butterfly species. A shift in one resource type can theoretically lead to shifts in use of complementary resources. Perhaps, very quickly, butterfly species in some regions of the tropics are having to adapt to changing resource types, their composition, structure and connectivity in new habitats (Dennis et al., 2006, 2007), as well as new communities of predators, parasites and competitors. This whole process raises two issues: First, there is the scientific opportunity to understand community and evolutionary changes with changing landscapes and resources; what adjustments are made in such rapidly changing environments? Secondly, following on from this, is the more important question of which species are the winners and losers with development in the tropics? How can conservation help to retain elements of the plant and insect communities? As the consequences of deforestation are largely irreversible, these are important questions. Between 1934 and 1988 the Philippines lost 9.8 million ha of forest, a descrease of 56% since 1945 (Liu et al., 1993), and despite moves towards more sustainable management, now only a fragment of the natural forest cover remains (Tumaneng-Diete et al., 2005; Verbung et al., 2006); thus, changes of habitat are inevitable and the immediate need is to understand how species are adapting to them. A key concern will be rare and endemic species. Although only 6 species observed nectaring in this study are endemic to the Philippines, and only 6 of the 48 species are rare or uncommon, today's common species may well become tomorrow's rare ones as has been witnessed for species in temperate regions (e.g. Europe, Van Swaay and Warren, 1999). As such, a multi-species vantage is essential for conservation, in the tropics as well as in temperate lands (Dennis et al., 2007), and studies of resources used by butterflies provide valuable insights for management faced with projected future environmental changes.

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