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Rapid assessment of the composition and species richness of Tobago butterfly assemblages

Erenler, Hilary E.

Environment, Earth and Ecosystem Sciences, Open University, Walton Hall, Milton Keynes, UK. MK7 6AA

hilary.erenler@open.ac.uk

ORCID: https://orcid.org/0009-0001-6478-652X

Gillman, Michael P. *

Environment, Earth and Ecosystem Sciences, Open University, Walton Hall, Milton Keynes, UK. MK7 6AA

michael.gillman@open.ac.uk

ORCID: https://orcid.org/0000-0002-1877-7745

Cock, Matthew J.W.

CABI, Bakeham Lane, Egham, Surrey TW20 9TY, UK

m.cock@cabi.org / mjwcock@btinternet.com

ORCID: https://orcid.org/0000-0003-2484-3021

*corresponding author

Abstract

The butterfly species of Tobago have been recorded for over a century but there has been no assessment of the relative abundance of species and the variation in species richness across the island. This study is a first step towards butterfly community ecology in Tobago, using timed walks and counts. Overall, 79 species comprised of over 2000 individuals were recorded from 40 hours of sampling across two years, during the transition from rainy to dry season. The species total represented about half of the known total number of species, indicating the value of this methodology for rapid sampling of the island's butterflies. Cluster analysis was used to identify four different assemblages and their constant species. Rarefaction analysis revealed a significant difference in species richness between forest, north coast and south coast. The highest richness was associated with trails near dry forest in the south-east. Lowland rainforest in the north had a distinctive fauna but low species richness. Significant change across the island is associated with large variation in climatic conditions. This study is important for understanding the biogeographic relationship with Trinidad, the Lesser Antilles and the continent. The disparity between the forest fauna of Trinidad and that of Tobago is highlighted, along with the absence of key groups in the Lesser Antilles and the highly fragmented nature of dry forest from south-east Tobago via north-west Trinidad to Venezuela.

Introduction

The island of Tobago, lying off the north-east coast of Trinidad, has a maximum extent of 41 km by 12 km (UWI 2024) and about 80% forest coverage (Global Forest Watch, 2024). The composition of its forest types was described in detail by Beard (1944) and related to landsat data by Helmer et al (2012). Forest composition ranges from lowland and xerophytic rain forest to deciduous and semi-evergreen seasonal forest. The main ridge, 29 km in length with a maximum elevation of about 600m (UWI 2024), which encompasses three rainforest communities (lower montane, lowland and xerophytic, Beard 1944, Helmer et al 2012), has been protected since 1776 (extended in 1904, Beard 1944). The main ridge provides evidence of an earlier geographical link to the South American continent, via the Northern Range of Trinidad and the Paria peninsula of Venezuela (Figure 1). The main ridge reserve is believed to be the first example of an area protected for the ecosystem services it provides (the reserve was "for the purpose of attracting frequent showers of rain upon which the fertility of lands in these climates doth entirely depend.", according to Stephen Hales in the 18th century, who considered a causal relationship between trees and rainfall – UNESCO 2024). Much of the coastal regions, and the western end of Tobago (Figure 2), have been cleared of primary forest.

Temperature is consistent through the year, with monthly averages of 26.5 to 28.5 degrees (Trinidad and Tobago meteorological data, 2024), but rainfall varies by about one metre per year across the island. Historical rainfall data provided in Beard (1944) for six stations, varied from 2327 mm and 2164 mm in Hermitage and Charlotteville in the north-east to 1820 mm at the Botanic Gardens and 1405 mm in Scarborough in the south-west. The pattern of historical data from the Government Farm in Scarborough over 31 years (early 20th century) agrees with the average 1991 to 2020 data provided by the Trinidad and Tobago meteorological service (Trinidad and Tobago meteorological data, 2024; Figure 3). A value of less than 100 mm per month for four or more months, combined with an annual rainfall of less than 2000 mm, places the Scarborough/Crown Point location in dry forest climate (Ocón et al 2021).

The butterfly fauna of the island has been studied since the early 1900s with 150 species recorded up to the mid-2010s (Cock 2017). The list of new species continues to grow, with the total currently estimated to be closer to 170 (Cock et al. 2024 gives 165 excluding new records in the current contribution). The Tobago butterfly fauna is mostly a subset of the Trinidad fauna. In Cock (2017), two species and two subspecies were highlighted as found in Tobago, but not in Trinidad. *Mysoria barcastus alta* Evans, 1951 (Hesperiidae) is a subspecies endemic to Trinidad, whereas the Venezuelan subspecies *M. barcastus venezuelae* (Scudder, 1872) is found in Tobago. *Ouleus fridericus sheldoni* Cock, 2017 is a subspecies endemic to Tobago, and differentiated from the Trinidad subspecies, *O. fridericus sinepunctis* (Kaye, 1904). *Phoebis agarithe agarithe* (Boisduval, 1836) has since been reported from Trinidad based on historical specimens (Cock and Alston-Smith 2017), but *Callimormus juventus* Scudder, 1872 (Hesperiidae) is still known from Tobago but not Trinidad. *Strymon astiocha* (Prittwitz, 1865) (Lycaenidae) has been reported from Tobago, but not Trinidad, although it is found on Chacachacare Island between Trinidad and the Paria Peninsula of Venezuela (Cock and Robbins 2016). Cock (2020) noted that *Heliconius erato* (Linnaeus, 1758) occurs in Trinidad as ssp. *adana* J.R.G. Turner, 1967 and in Tobago as ssp. *tobagoensis* Barcant, 1982, and similarly, *H. melpomene* (Linnaeus, 1758) occurs in Trinidad as ssp. *flagrans* Stichel, 1919 and in Tobago as ssp. *tessa* Barcant, 1982, but the differences are slight.

To date, there has been no description of the relative abundance of butterfly species of Tobago and their relationship to different habitats and locations. The current work aims to begin the process of filling that gap, allowing more detailed biogeographic comparisons with Trinidad, the continent and the Lesser Antilles. It also provides an opportunity to assess the suitability of walk-and-count methods (Wood and Gillman 1998, Caldas and Robbins 2003, Attiwilli et al 2024) for rapid sampling of the island's butterflies.

Methods

Nomenclature

The nomenclature used is based on the most recent checklist of Tobago butterflies (Cock 2017), but updated to reflect subsequent changes, mostly involving new generic combinations based on whole genome analysis (e.g. Zhang et al 2022).

Transects and identification

Pollard walk-and-count transects were undertaken in various habitats and locations across Tobago in January 2023 and January 2024, during the transition from rainy to dry season. In the first year, transects were restricted to locations within 6 km of Parlatuvier on the eastern part of the north coast (Figure 2). In the second year, transects covered a broader area. Butterflies were recorded within approximately 3 m of the observer during a timed walk.

Transects were divided into five different habitat/landscape categories, namely: open grassland areas (O), roadside (RS) with mixtures of grass and scrub, trails off road (T), some with adjacent forest or through forest (F), and lastly forest gap (FG). The habitats encompassed the main ridge within lower montane/lowland forest, lowland forest on the north side (Pine Hill Trace, Bloody Bay), deciduous seasonal forest (especially Blue Waters Bay on the southern part of the east coast) and coastal roads and trails up to 100 m elevation (transect detail in Appendices). The aim of the sampling was to cover a range of locations and habitats but also to include some repeated walks (both within the year and between years) to evaluate the method.

Photographs were taken of selected individuals at rest, especially those where identification was likely to be difficult, e.g., many of the Hesperiinae, or where a 'voucher' specimen was needed (photographs are available on request to the corresponding author). Identification was based primarily on Butterflies of America (Warren et al 2024) and the collection and knowledge of the third author. Identification and methods in the field were supported by the experience of the first two authors in the Caribbean, Central and South America. Initial observations around Parlatuvier were used for familiarization with the commoner species, and were not included in the data analysis.

Four species pairs were lumped as they were not possible to distinguish on the wing. *Heliconius erato* and *H. melpomene* along with *Junonia genoveva* (Cramer, 1780) and *J. zonalis* C. Felder and R. Felder, 1867 can be distinguished at rest from photographs (Cock 2019, 2020), and all four species were present in the samples. Cock and Alston Smith (2017) indicated that *Phoebis argante* (Fabricius, 1775) comprises at least two similar species in Trinidad and Tobago, but the taxonomy to apply has yet to be established, so we treat them together as *P. argante*. A further species pair (*Calycopis bactra* (Hewitson, 1877) and *C. origo* (Godman and Salvin, 1887)) is grouped as *Calycopis* sp(p.) as photographs could not provide definitive separation between the two. *Calycopis origo* is the commoner species in Trinidad and Tobago (MJWC collection).

Transects were recorded with an average start time of 10:25 a.m. and average duration of 1.7 hours (ranging from 0.75 to 3.3 hours). The durations of breaks were noted and removed from the total time, allowing a calculation of encounter rate per hour for each species.

Data analysis

The numbers of individuals per transect were normalized and then clustered using the Ward cluster method (Borcard et al 2011; vegan R package for normalizing data, Oksanen et al 2022; cluster analysis, R core team 2023). Clusters were examined for composition of transects and underlying species composition, noting any constant species in the clusters. Cluster analysis gives the same result if encounter rate is used. The latter is summarized in the results to allow assessment and comparison of relative abundance.

Rarefaction was used to compare species richness across different locations (vegan R package, Oksanen et al 2022). Initially all transects were included in the analysis with rarefaction of 20 individuals per transect. This was investigated further by combining transects from the same locations (to avoid including beta diversity) and recalculating with a higher number of individuals (120).

Results

Seventy-nine species across 2056 individuals were recorded from 24 transects over 40.5 hours. The number of individuals and species per transect ranged from 21 to 140 individuals and 6 to 33 species. Four new records for Tobago (Table 1, Figures 4-7) were all in the Hesperiinae. Three additional species had not been recorded on the island since the 1930s, with one representing only the second record since that period (Table 1, Figures 8-12).

The transects were split into four clusters (Figure 13). Repeat samples clustered closely (e.g., three forest transects from Pine Hill Trace in 2023 and 2024, two Blue Waters Bay trails in 2024 and two Castara to Englishman's Bay roadside walks in 2023). The first of the four clusters (top of diagram) included all five forest transects (located in the north). This cluster has three constant species, all of which are in the Nymphalidae, Satyrinae (*Hermeuptychia canthe* (Hübner, [1811]), *Modica myncea* (Cramer, 1780) and *Pareuptychia ocirrhoe* (Fabricius, 1776), Table 2). *Anartia amathea* (Linnaeus, 1758) (Nymphalidae) was seen in four of the five transects. The forest cluster included the only occurrences of *Morpho helenor insularis* Fruhstorfer, 1912, *Taygetis echo* (Cramer, 1775) (Nymphalidae) and *Mesosemia tullius* (Fabricius, 1787) (Riodinidae) and the new island record of *Carystus ploetzi* Mielke and Casagrande, 2002 (Hesperiidae).

The second cluster includes five samples from the South-east (Figure 2) and one north(-east) coast sample. The five constant species are drawn from three families (Hesperiidae, *Hedone praeceps* (Scudder, 1872) and *Burnsius orcus* (Stoll, 1780); Nymphalidae, *Junonia* sp(p)., and Pieridae, *Abaeis albula marginella* (C. Felder and R. Felder, 1861) and *Phoebis sennae marcellina* (Cramer, 1777)).

The third cluster is composed of north coastal roadside (Northside Road) samples from Castara Bay to Bloody Bay (a distance of about 8 km). The three pairs of transects were all repeat samples on different days within 2023 (treated here as independent although there is the possibility of observing the same individual). This cluster shares three common species with cluster 2 (*Burnsius orcus*, *Abaeis albula* and *Phoebis sennae*), one species with cluster 1 (*Hermeuptychia canthe*) and two new constants (*Anartia amathea* and the only papilionid observed, *Battus polydamas* (Linnaeus, 1758)).

The fourth cluster comprises a mixture of northern sites (including a 2023-2024 repeat between Parlatuvier and Englishman's Bay), two southern sites (Speyside lookout trail and Kings Bay trail, both with some shade – more than the southern samples in the second cluster) and a forest gap in the main ridge. In this case, the constant species are all nymphalids (*Anartia amathea*, *Junonia* sp(p). and *Hermeuptychia canthe*).

The rarefaction analysis with samples of 20 individuals from all transects identifies forest and forest gap as the least species-rich (with the exception of one northern roadside site) and suggests the southern transects have higher richness (Figure 14). Using transects from the same location with 120 individuals (Figure 15), the samples split into three different groups (standard errors not overlapping), with the least species-rich being the Pine Hill trace forest and Parlatuvier to Bloody Bay 2023, followed by an intermediate group of Parlatuvier and east to Englishman's Bay and then Castara Bay (highlighted in Figure). The most species-rich transects were the two from Blue Waters Bay in the south-east.

Discussion

The walk-and-count sampling emerges as an effective rapid technique, assessing approximately half the butterfly fauna of Tobago in only 40 hours of sampling. The clustering of repeat samples suggests that the method is robust with respect to composition. The walk-and-count method does, however, pose difficulties with some species, e.g. the numbers of often fast-flying pierids (*Eurema*, *Phoebis* and *Pyrisitia* species) can be difficult to assess, and some of the grass skippers (Hesperiinae) may be difficult to distinguish, even with very good photographs. That said, some grass skippers, such as *Troyus fantasos* (Cramer, 1780), are very distinctive and exclusion of the Hesperiinae would have removed four new records for the island. Despite some limitations, photographs are valuable for butterfly identification in even the most species-rich regions of the Neotropics (e.g., as discussed for the Cristalino Lodge reserve in Amazonia, with more than 1000 species, Mota et al 2022). Apart from an underestimate of species richness, the lumping of species might lead to misleading habitat associations (e.g. *Junonia* spp – both were present in the samples). As with *Junonia*, the lumping of *Calycopis* species might obscure habitat preferences. Based on general collecting in Trinidad and Tobago, *C. bactra* is normally found in forested areas, whereas *C. origo* is more widespread and can be common in gardens as well as dry areas (e.g. Crown Point, M.J.W. Cock unpublished). The other species pair of *Heliconius erato* and *H. melpomene* are co-mimics, with similar habitat and behaviour (Mallet and Gilbert 1995).

The large differences in rainfall and topography across Tobago, resulting in major differences in the climax forest assemblages, combined with variation in human disturbance, suggest the possibility of systematic changes in the butterfly fauna across the island (Cómbita et al 2022, Checa et al 2014, Whitworth et al 2016). This is supported by the cluster and species richness results presented here. The effect of human disturbance is seen in the low species richness of the Parlatuvier to Bloody Bay road (about six species less per 120 individuals than the westward section from Parlatuvier to Castara Bay). The eastward section of roadside from Parlatuvier to Bloody Bay is flatter, heavily strimmed and grazed, resulting in wide (greater than 10 m) sections of homogeneous grassland. In contrast, the westward sections include forest edges within 10 m and high rocky sections with good coverage of vegetation and consistent nectar sources such as *Chromolaena odorata* (L.) R.M. King & H. Rob. and *Bidens alba* (L.) DC. (Asteraceae). The south-east trail above Blue Waters Bay has similar topography, along a narrow ungrazed track rather than a surfaced road, but here the adjacent vegetation is dry forest with the understory dominated by *Anthurium* Schott (Araceae) (as noted by Beard 1944, and on the nearby island of Little Tobago, Oatham and Boodram 2006). This section was richer by six species than the westward road from Parlatuvier (120 individual rarefaction). Overall, with rarefaction of 20 individuals, the southern roadside and trail sections had an average of two more species compared to the northern roadside and trails.

The forest transects had a comparable species richness to the lowest roadside areas (e.g., an average of 6.3 species per 20 individuals for the five forest transects in the first cluster, against 6.7 species for the Parlatuvier to Bloody Bay roadside transects in the third cluster). The main ridge forests were not sampled (apart from one forest gap), however, some sections were inspected and there was no evidence of butterflies being present apart from *Hermeuptychia canthe*. Temperatures at the top of the ridge were typically lower by about five degrees than at Parlatuvier or Roxborough on any given day. Interpretation of some of the results may be affected by the restricted sampling period and the strong seasonality of many Neotropical butterflies (Castro and Espinosa 2015).

The northern lowland forest transects provide an opportunity to compare with the southern lowland forest in Trinidad (Victoria Mayaro reserve, Wood and Gillman 1998). Inspection of their walk and count results for two different forest types, and two different levels of disturbance, reveals large gaps in the Tobago forest fauna. The three constant species in the Tobago forest samples (*Hermeuptychia canthe*, *Modica myncea*, *Pareuptychia ocirrhoe*, previously *Cissia hermes*, *C. myncea* and *C. hesione*) were present in the semi-evergreen forest (most similar to the lowland forest in Tobago – both with *Carapa guianensis* Aubl. (Meliaceae) as dominant). *Magneuptychia libye* (Linnaeus, 1767) (= *Cissia libye*) was found in both the Tobago and Trinidad forest. There were a further four 'Cissia' species in the Trinidad semi-evergreen (*C. penelope* (Fabricius, 1775), *Amiga arnaca* (Fabricius, 1776) (= *C. arnaea*), *Cisandina lea* (Cramer, 1777) (= *Cissia junia*) and *Cepheuptychia cephus* (Fabricius, 1777) – with *Paryphthimoides terrestris terrestris* (Butler, 1867) also caught in fruit traps). Other Satyrinae were represented by four *Taygetis* species including *T. echo* (one individual was found in the Tobago samples), *Caligo* species, *Eryphanis automedon automedon* (Cramer, 1775) and *Catoblepia berecynthia berecynthia* (Cramer, 1777). There is one *Morpho* species seen in both islands. Most striking was the difference in Ithomiini, of which there were seven species in Trinidad and none seen in Tobago. The most abundant of these in Trinidad was *Tithorea harmonia megara* (Godart, 1819), with a high encounter rate of 7.6 per hour in the disturbed semi-evergreen forest. Three species of Ithomiini are known from Tobago, of which only one has been recorded in the last 80 years (*Ithomia agnosia pellucida* Weymer, 1875), also recorded from the semi-evergreen Trinidad forest. The other two species may have been recorded in error or be extinct in Tobago - *Pteronymia alissa amandes* Kaye, 1921 – only one record from Tobago about 1906 and *Greta andromica trifenestra* R.M. Fox, 1941, unknown since the 1930s (Cock 2017).

Four new Tobago records of Hesperiinae were documented by photographs during this study (Table 1, Figure 4-7). The arrangement of forewing white hyaline spots and the pale ventral hindwing served to recognize the female photographed in Tobago as *Carystus ploetzi* (Figure 4). Cock (2005) considered *Carystus ploetzi* to be a rare species in Trinidad, but widespread in forested areas. He reported that the caterpillars feed on palms (Arecaceae) including *Bactris major* Jacq. which is widespread in lowland Trinidad but absent from Tobago, although nine other palm species do occur in Tobago (Comeau et al. 2003).

Gallio garima garima (Schaus, 1902) was described from Trinidad and until recently was treated as *Tigasis garima garima* (Cock 2012). Based on whole genome comparisons, Zhang et al (2022) transferred it to *Gallio* Evans, 1955. Both sexes have two white hyaline spots in the forewing cell, and the male is distinctive by virtue of the narrow, oblique spot at the base of forewing space 2 (CU_1-CU_2), which is narrowed in the middle. The Tobago photograph (Figure 5) shows this feature, except the spot in space 2 is narrowed to the extent it is divided into two. This is a rare species in Trinidad, with no clear habitat association, and the life history is unknown, although it is expected to be a grass-feeder (Cock 2012).

Lerema compta (Butler, 1877) (=*Morys compta*) is a common species in Trinidad, particularly in the north of the island, and is associated with forested areas, secondary forest and suburban areas (Cock 2012). Amongst diagnostic characters, the ventral hindwing (Figure 6) is brown with an unusual chestnut tint and diffuse paler spots variably in spaces 1C to 7 (Cu_2-2A to SC+R_1-Rs). This chestnut tint has not been noted in other Trinidad species and is key to our identification of this species from Tobago. Trinidad records are year-round, although most frequent in the early dry season (January-February). Cock (2012) describes the caterpillar and pupa which he reared from *Paspalum virgatum* L. (Poaceae), although other grasses are expected to be suitable food plants.

Lerema etelka (Schaus, 1902) was described from Trinidad. It was treated as a synonym of *Morys geisa* (Möschler, 1879) for many years (e.g. Cock 2012), until Zhang et al. (2022) made *Morys* Godman, 1900 a subgenus of *Lerema* Scudder, 1872, and recognized *Lerema etelka* as a valid species separate from *E. geisa* (=*Morys geisa*). This is a moderately common and widespread species in Trinidad, mostly from forested areas and mostly recorded between October and March (Cock 2012). In this species, diagnostic features include the apex of the ventral forewing and the ventral hindwing apart from spaces 1A-1C (3A to CuA_2-1A+2A) dark brown with a purple sheen, and the ventral hindwing with pale blue-grey spots in spaces 1C-7 (CuA_2-A_1+2A to SC+R_1-Rs), that in space 4 (M_2-M_3) being elongate and displaced basally compared to the others. Based on these characters we have identified the Tobago photograph in Figure 7. Cock (2012) has reared this species from caterpillars found on *Orthoclada laxa* (Rich.) P. Beauv. and *Setaria barbata* (Lam.) Kunth (Poaceae) in Trinidad, so it will probably use a variety of soft grasses as food plants.

All four new records are identified with reasonable confidence based on the diagnostic features mentioned, but it would be desirable to confirm all with voucher specimens, especially males that have diagnostic secondary sexual characters and distinctive genitalia when dissected (Cock 2005, 2012). There have never been any resident butterfly collectors or photographers working on the island of Tobago, so that all records are the result of short-term visits. Hence it is not surprising that a few new records of butterflies continue to accumulate (e.g. Cock et al. 2024, this study), and this is likely to continue.

Comparisons with the Lesser Antilles reveal interesting patterns with distance from Tobago and the mainland. The nearest of the Lesser Antilles is the island of Grenada, 140 km north-west of Tobago. There are just 44 butterfly species recorded from Grenada (Schwarz et al. 1999), compared to more than 165 from Tobago. Many of these occur as different subspecies to those found in Trinidad and Tobago, but at the species level, 77% of the Grenada species occur on Tobago, and 86% on Trinidad. The butterfly fauna of St. Vincent and the Grenadines is slightly richer (52 species, de Silva and Horrocks 2022), but the pattern is similar. A list of 61 species from the more distant ten islands in the north-eastern Lesser Antilles (Debrot et al 2020) reveals 20 species in common with the 79 species in the Tobago transects. Notable gaps in the Lesser Antilles' fauna include Satyrinae and Riodinidae.

The rediscovery of *Strymon astiocha* (Figure 12), one of two species in Tobago not found on the island of Trinidad, illustrates the precarious, fragmented nature of butterfly populations and the ecological insights to be gained from their study. One individual was recorded near the entrance of the Blue Waters Bay hotel, on a steep rock face in full sun, nectaring on *Bidens.* Previously one individual had been recorded from Speyside by Arthur Hall in the early 1930s (Sheldon 1936), placing it close to the observed 2024 record. The adjacent dry forest agrees with a record from Chacachacare Island (Figure 1), also with dry forest. This type of forest occurs only on the extreme north-west peninsula of Trinidad (Helmer et al 2012) which is not normally accessible to the public (perhaps suggesting that *Strymon astiocha* might exist on the Trinidad mainland). Deciduous seasonal forest is highly fragmented (running from the east coast of Tobago to the north-west of Trinidad and nearby islands), increasing the chances of local extinction for species dependent on that habitat. Of the Bocas Islands between north-west Trinidad and the Paria Peninsula of Venezuela, only Chacachacare Island has been surveyed for butterflies (and that only based on a few hours collecting on a handful of days). On the continent the species is reported from Mexico to (south) Brazil (Warren et al 2024). In Brazil, *Strymon astiocha* is found in the semi-arid Catimbau National Park (Nobre et al 2008) with annual average temperatures and average precipitation rates of 700 to 1100 mm, below the lowest values for Tobago.

Future work would focus on further evaluating the spatial distribution of butterflies across the island and understanding its causes. This will contribute to better insights into the biogeography of the region. Such data and interpretation aids both conservation efforts and helps strengthen and test theories of island colonization and extinction. More specific targeting of two taxa would be beneficial. First, the grass skippers (Hesperiinae) which account for all the new species recorded in this study. Second, the Ithomiini, which are weak fliers normally associated with shady forests and forest edges and assumed to be poor dispersers, e.g. the only Ithomiini found in the Greater Antilles are endemic relic species. What is striking is that Ithomiini were so rarely observed (i.e., none) compared to Trinidad where some species are common. However, this comes down to one species. One would not expect to see *Pteronymia alissa* and *Greta andromica* on transects in Trinidad, but why is *Ithomia agnosia pellucida* much less frequently seen in Tobago? It would be interesting to do some targeted baiting, e.g., with drying *Heliotropium* in Tobago, to see how common and widespread *I. agnosia pellucida* is and whether the other two species can be detected.

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Table 1. List of new and notable species records for Tobago. Locations shown in Figure 2 with species images in Figures 4-12.

Taxon	New and notable records	Locations of 2023/4 records
Family Hesperiidae		
Ectomis octomaculata (Sepp, [1844])	1930s Roxburgh, Speyside	Richmond Orchard Road nr Glamorgan (also seen in north-east overlooking Charlotteville)
Carystus ploetzi Mielke and Casagrande, 2002	New island record	Forest trail, Bloody Bay
Gallio garima garima (Schaus, 1902)	New island record	Kings Bay trail
Lerema compta (Butler, 1877)	New island record	Castara to Englishman's Bay
Lerema etelka Schaus, 1902	New island record	Speyside lookout trail
Naevolus orius orius (Mabille, 1883)	2nd record (new 2023)	Speyside lookout trail
Rhinthon osca (Plötz, 1882)	1930s Speyside	Kings Bay trail
Family Lycaenidae		
Strymon astiocha (Prittwitz, 1865)	1930s, one specimen Speyside	Blue Waters Bay

Table 2. Species composition by cluster. Species are listed alphabetically within family. *n*, number of transects per cluster (maximum of 5,6,6,7 per cluster), mean encounter rate per hour (*m*) and standard deviation of encounter rate (*s*). Bold indicates constant species within a given cluster.

	Cluster 1			Cluster 2			Cluster 3			Cluster 4		
Taxon	n	m	s	n	m	s	n	m	s	n	m	s
Family Hesperiidae												
Anthoptus insignis (Plötz, 1882)	2	0.27	0.37	3	0.32	0.36	3	0.24	0.28	1	0.15	0.39
Antigonus erosus (Hübner, [1812])	0			1	0.15	0.38	0			3	0.16	0.21
Burnsius orcus (Stoll, 1780)	0			**6**	**5.24**	**4.95**	**6**	**1.31**	**1.38**	6	1.6	1.91
Callimormus juventus Scudder, 1872	0			0			1	0.05	0.12	2	0.18	0.32
Callimormus saturnus (Herrich-Schäffer, 1869)	0			2	0.26	0.42	4	0.27	0.25	4	0.4	0.44
Carystus ploetzi Mielke and Casagrande, 2002	1	0.27	0.6	0			0			0		
Cecropterus dorantes dorantes (Stoll, 1790)	0			2	0.28	0.45	4	0.31	0.29	2	0.16	0.27
Chioides catillus catillus (Cramer, 1779)	0			3	0.56	0.77	0			2	0.23	0.41
Cogia calchas (Herrich-Schäffer, 1869)	0			4	0.45	0.41	0			2	0.12	0.21
Corticea corticea (Plötz, 1882)	0			1	0.25	0.61	1	0.11	0.27	2	0.19	0.33
Cymaenes tripunctus theogenis (Capronnier, 1874)	1	0.13	0.3	0			1	0.11	0.27	1	0.07	0.18
Ectomis octomaculata (Sepp, [1844])	0			1	0.52	1.27	0			0		
Gallio garima garima (Schaus, 1902)	0			0			0			1	0.11	0.28
Gesta gesta (Herrich-Schäffer, 1863)	0			1	0.07	0.16	0			0		
Hedone praeceps (Scudder, 1872)	0			**6**	**2.63**	**1.61**	4	0.54	0.47	5	0.93	0.95
Lerema ancillaris (Butler, 1877)	0			3	0.39	0.48	0			1	0.08	0.2
Lerema compta (Butler, 1877)	0			0			1	0.06	0.15	0		
Lerema etelka Schaus, 1902	0			0			0			1	0.07	0.19
Mucia zygia (Plötz, 1886)	0			1	0.25	0.61	2	0.17	0.28	1	0.07	0.18
Mysoria barcastus venezuelae (Scudder, 1872)	0			2	0.23	0.36	0			1	0.07	0.19
Naevolus orius orius (Mabille, 1883)	0			0			0			1	0.07	0.19
Niconiades xanthaphes Hübner, [1821]	0			0			2	0.13	0.21	0		
Nyctelius nyctelius nyctelius (Latreille, [1824])	0			0			1	0.11	0.27	1	0.05	0.13
Ouleus fridericus sheldoni Cock, 2017	2	0.4	0.6	0			1	0.05	0.12	2	0.16	0.27

Panoquina lucas lucas (Fabricius, 1793)	0			1	0.34	0.84	0			1	0.05	0.13
Pellicia dimidiata dimidiata Herrich-Schäffer, 1870	0			0			1	0.07	0.18	1	0.07	0.19
Rhinthon osca (Plötz, 1882)	0			0			0			1	0.11	0.28
Saturnus saturnus saturnus (Fabricius, 1787)	0			0			1	0.06	0.15	0		
Spicauda simplicius (Stoll, 1790)	0			5	0.78	0.7	0			4	0.54	0.64
Spicauda tanna (Evans, 1952)	0			1	0.52	1.27	3	0.38	0.52	4	0.38	0.4
Synapte malitiosa pericles (Möschler, 1879)	0			2	0.23	0.37	1	0.07	0.17	1	0.09	0.23
Troyus fantasos (Cramer, 1780)	1	0.06	0.13	1	0.13	0.31	0			1	0.09	0.23
Urbanus esmeraldus (Butler, 1877)	0			0			1	0.06	0.15	0		
Family Lycaenidae												
Allosmaitia strophius (Godart, [1824])	0			1	0.11	0.27	0			0		
Calycopis origo (Godman and Salvin, 1887)	2	0.33	0.58	4	0.53	0.45	1	0.06	0.15	1	0.08	0.2
Chlorostrymon telea (Hewitson, 1868)	0			0			1	0.06	0.15	0		
Cyanophrys herodotus (Fabricius, 1793)	0			0			1	0.07	0.17	1	0.07	0.19
Electrostrymon joya (Dognin, 1895)	0			2	0.18	0.29	2	0.14	0.22	3	0.21	0.27
Hemiargus hanno hanno (Stoll, 1790)	0			3	1.24	2.06	1	0.15	0.36	2	0.24	0.46
Leptotes cassius cassius (Cramer, 1775)	0			4	0.97	1.14	0			0		
Ministrymon azia (Hewitson, 1873)	0			2	0.21	0.33	5	1.89	1.47	4	2.79	3.15
Pseudolycaena marsyas (Linnaeus, 1758)	0			5	1.46	1.23	1	0.06	0.14	3	0.23	0.28
Rekoa palegon (Cramer, 1780)	0			3	0.65	0.74	4	0.31	0.29	3	0.25	0.32
Strymon astiocha (Prittwitz, 1865)	0			1	0.12	0.3	0			0		
Strymon bubastus (Stoll, 1780)	0			3	0.59	0.69	0			2	0.14	0.24
Tmolus echion (Linnaeus, 1767)	0			2	0.28	0.45	0			2	0.14	0.24
Family Nymphalidae												
Anartia amathea (Linnaeus, 1758)	4	1.53	1.06	4	6.02	7.85	**6**	**19.73**	**15.08**	**7**	**7.51**	**5.74**
Anartia jatrophae (Linnaeus, 1763)	0			1	2.93	7.18	3	0.31	0.35	1	0.21	0.57
Biblis hyperia hyperia (Cramer, 1779)	0			1	0.46	1.13	1	0.07	0.17	1	0.15	0.4
Danaus plexippus nigrippus (Haensch, 1909)	0			1	0.34	0.84	0			0		
Dione vanillae (Linnaeus, 1758)	0			5	3.15	1.88	3	0.28	0.36	5	1.92	1.71
Dryas alcionea alcionea (Cramer, 1779)	0			2	0.63	1.12	0			0		

Dynamine postverta (Cramer, 1779)	0			2	0.39	0.74	0			1	0.15	0.39
Dynamine theseus (C. Felder and R. Felder, 1861)	0			4	2.76	3.15	4	1.63	1.42	5	4.46	6.06
Eueides aliphera aliphera (Godart, 1819)	0			0			1	0.07	0.17	0		
Heliconius erato/melpomene	2	0.2	0.3	2	1.86	3.1	1	0.12	0.3	4	2.33	3.1
Hermeuptychia canthe (Hübner, [1811])	**5**	**13**	**4.36**	4	1.88	2.15	**6**	**5.22**	**1.83**	**7**	**10.51**	**6.74**
Historis odius dious Lamas, 1995	0			1	0.15	0.38	0			2	0.13	0.23
Junonia genoveva/zonalis	2	0.5	0.73	**6**	**5.16**	**3.18**	3	0.51	0.88	**7**	**3.41**	**2.43**
Magneuptychia libye (Linnaeus, 1758)	3	0.46	0.56	1	0.13	0.31	0			1	0.08	0.22
Mestra hersilia hersilia (Fabricius, 1776)	0			5	4.92	3.82	4	1.41	1.23	4	3.95	4.93
Modica myncea (Cramer, 1780)	**5**	**1.16**	**0.64**	0			1	0.07	0.17	1	0.07	0.19
Morpho helenor insularis Fruhstorfer, 1912	1	0.16	0.36	0			0			0		
Pareuptychia ocirrhoe (Fabricius, 1776)	**5**	**4.13**	**4.13**	0			1	0.05	0.12	3	0.48	0.82
Taygetis echo (Cramer, 1775)	1	0.06	0.13	0			0			0		
Vareuptychia themis (Butler, 1867)	1	0.16	0.36	2	0.25	0.38	1	0.05	0.12	3	0.24	0.3
Family Papilionidae												
Battus polydamas polydamas (Linnaeus, 1758)	0			5	3.42	3.27	**6**	**1.6**	**0.85**	5	2.6	2.67
Family Pieridae												
Abaeis albula marginella (C. Felder and R. Felder, 1861)	0			**6**	**15.05**	**8.79**	**6**	**5.01**	**3.07**	6	2.53	2.19
Ascia monuste monuste (Linnaeus, 1764)	0			1	0.11	0.27	1	0.12	0.3	0		
Phoebis argante[1]	0			2	0.91	1.61	0			0		
Phoebis sennae marcellina (Cramer, 1777)	0			**6**	**5.35**	**2.84**	6	4.56	1.58	5	3.69	3.15
Phoebis statira statira (Cramer, 1777)	0			1	0.77	1.88	0			2	0.12	0.2
Pyrisitia leuce athalia (C. Felder and R. Felder, 1865)	1	0.06	0.13	2	0.84	1.5	2	0.14	0.22	4	1.25	1.8
Pyrisitia venusta venusta (Boisduval, 1836)	0			0			1	0.07	0.18	0		
Family Riodinidae												
Calephelis laverna trinidadensis McAlpine, 1971	0			5	1.46	1.4	1	0.14	0.35	1	0.11	0.28
Juditha molpe (Hübner, [1808])	0			0			0			2	0.15	0.26
Melanis electron electron (Fabricius, 1793)	2	0.24	0.33	0			1	0.05	0.12	1	0.21	0.57
Mesosemia (Perophthalma) tullius (Fabricius, 1787)	1	0.1	0.22	0			0			0		
Synargis calyce (C. Felder & R. Felder, 1862)	0			5	0.86	0.65	0			5	0.58	0.56

[1] At least two species present under this name in Trinidad and Tobago (Cock and Alston-Smith 2017).

Figure legends

Figure 1. Map of Trinidad and Tobago region. Credit: OpenStreetMap (2024).

Figure 2. Map of sampling locations in Tobago. Credit: OpenStreetMap (2024).

Figure 3. Rainfall patterns in Tobago. Historical data from Beard (1944); Scarborough (Government Farm, 31 years of data), North-east (Hermitage Estate, 31 years, highest annual total of six stations) and South-east (Kings Bay, 31 years). Months below dashed line (100 mm) defined as dry season. Months run from January (1) to December (12).

Figure 4. *Carystus ploetzi*. 26 January 2023. Bloody bay forest trail. (Image credit: H Erenler)

Figure 5. *Gallio garima*. 23 January 2024. Kings Bay trail. (Image credit: H Erenler)

Figure 6. *Lerema compta*. 25 January 2023. Castara to Englishman's Bay. (Image credit: H Erenler)

Figure 7. Lerema etelka. 25 January 2024. Trail from Speyside lookout. (Image credit: H Erenler)

Figure 8. Naevolus orius. 25 January 2024. Trail from Speyside lookout. (Image credit: H Erenler)

Figure 9. Naevolus orius, second view of individual in Figure 8. 25 January 2024. Trail from Speyside lookout. (Image credit: H Erenler)

Figure 10. Ectomis octomaculata. Richmond Orchard Road near Glamorgan. 18 January 2024. (Image credit: H Erenler)

Figure 11. Rhinthon osca. 23 January 2024. Kings Bay trail. (Image credit: H Erenler)

Figure 12. *Strymon astiocha*. (Image credit: H Erenler) Originally seen 22 January 2024 at start of Blue Waters Bay trail and then again on 24 January 2024 in the same location on the way to a different transect.

Figure 13. Cluster analysis. Details of transects in Appendices.

Figure 14. Estimates of species richness with rarefaction. All transects (list of samples 1 to 24 in Appendices).

Figure 15. Estimates of species richness with rarefaction. Sites with two or three repeat transects using rarefaction of 120 individuals. Transects/Sites are shown in rank order of species richness. The highlighted region picks out one of the three groups discussed in the text.

Appendices

Details of transects numbered 1 to 24 in order of species richness (Figure 14). See also labels on cluster diagram. S 20 are species richness estimates from 20 individuals with associated standard errors (se). Locations are shown in Figure 2 and abbreviations detailed below.

Site code	S 20	se 20	Location	Habitat	Species richness rank
FG_MainRidgegap_2024	5.14	0.74	Central	FG	1
F_Bbay_2023a	5.33	0.94	N	F	2
RS_Bbay_Parlat_2023	5.77	1.33	N	RS	3
F_PineHillTrace_2023a	6.02	1.27	N	F	4
F_PineHillTrace_2023b	6.22	0.99	N	F	5
F_Bbay_2023b	6.76	0.43	N	F	6
F_PineHillTrace_2024	6.95	1.04	N	F	7
RS_Parlat_Bbay_2023	7.57	1.40	N	RS	8
RS_Castara_Ebay_2023b	8.75	1.36	N	RS	9
RS_Parlat_BambooHillT_2023	9.05	1.42	N	RS	10
T_KingsBay_2024	9.23	1.58	S	T	11
RS_Castara_Ebay_2023a	9.23	1.57	N	RS	12
RS_Ebay_Parlat_2023	9.75	1.43	N	RS	13
RS_Parlat_Ebay_2023a	9.75	1.56	N	RS	14
RS_Parlat_Ebay_2023b	9.90	1.57	N	RS	15
RS_Parlatuvier_2024	10.42	1.43	N	RS	16
RS_Parlat_Ebay_2024	10.86	1.51	N	RS	17
T_F_MissMillsTrace_2024	10.91	1.66	N	T,F	18
T_BelmontBay_2024	10.93	1.74	S	T	19
RS_RichmondOrchardRd_2024	11.03	1.62	S	RS	20
T_Speyside_lookout_2024	11.32	1.71	S	T	21
T_BlueWatersBay_2024b	11.45	1.62	S	T	22
O_Corbingarden_2024	12.12	1.50	S	O	23
T_BlueWatersBay_2024a	12.67	1.57	S	T	24

Abbreviations

BambooHillT, Bamboo Hill Trace (Parlatuvier)

Bbay, Bloody Bay

Ebay, Englishman's Bay

F, forest

FG, forest gap

N north coast

O, open

Parlat, Parlatuvier

RS, road-side

S south coast

T, trail (off-road)