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Results and discussion

Patterns of biodiversity

Four key questions we sought to answer relating to biodiversity were: 1) How many species occur in the study region (i.e. what is the overall species richness)? 2) What kinds of species occur in the region (i.e. what is the composition)? 3) What proportion of and which taxa are restricted to the region (i.e. what is the level of endemism)? 4) How are those species distributed spatially?

Species richness

For the first question, our investigations have revealed that 163 species (132 butterflies and 31 diurnal moths), representing 166 taxa, have been recorded from the study region. Three species are each represented by two subspecies within the region: *Suniana lascivia* (with *S. lascivia larrakia* and *S. lascivia lasus*), *Appias albina* (with *A. albina albina* and *A. albina infuscata*) and *Agarista agricola* (with *A. agricola agricola* and *A. agricola biformis*). In terms of their representation within each of the four subregions, 150 species (122 butterflies and 28 diurnal moths) have been recorded from the Top End, 105 species (88 butterflies and 17 diurnal moths) from the Kimberley, 82 species (74 butterflies and eight diurnal

moths) from the western Gulf Country and 53 species (45 butterflies and eight diurnal moths) from the Northern Deserts. Thus, the Top End is substantially more diverse than the other subregions and almost three times richer than the semi-arid and arid zones of the Northern Deserts.

Interestingly, a substantial number of the species known from the study region have only been detected during the past four decades. Thirty-seven taxa (22 per cent) have been discovered or recorded for the first time since 1970 (Table 4). Of these, 11 species represent their first recording for Australia. Some of these newly recorded species concern intrusions from South-East Asia (e.g. *Appias albina infuscata*, *Danaus chrysippus cratippus*, *Acraea terpsicore* and *Junonia erigone*), while others are species entirely new to science (e.g. *Taractrocera psammopetra*, *Acrodipsas decima* and *Nesolycaena caesia*) or new taxa that have not yet been formally described (e.g. *Leptosia nina* ssp. 'Kimberley', *Synemon* sp. 'Kimberley', *Idalima* sp. 'Arnhem Land', *Hecatesia* sp. 'Arnhem Land' and *Radinocera* sp. 'Sandstone'). Notably, during the course of this study, two taxa not recorded for more than 100 years were rediscovered: an extant breeding population of *Ogyris iphis doddi* was found in

Table 4 Records of 'new' species from the study region during the past four decades (since 1970)

Species	Year	Comments	Reference
<i>Zizula hylax attenuata</i>	1971	First record for study region	Le Souëf (1971)
<i>Alcides metaurus</i>	1972	First record for study region	Braby (2014a)
<i>Idalina</i> sp. 'Arnhem Land'	1972	First record for Australia	This volume
<i>Candalides geminus gagadju</i>	1972	First record of species for study region; first record of subspecies for Australia	Braby (2017)
<i>Hecatesia</i> sp. 'Arnhem Land'	1973	First record for Australia	This volume
<i>Hypochrysops apelles</i> ssp. 'Top End'	1973	First record of species for study region; first record of subspecies for Australia	This volume (see also Common and Waterhouse 1981)
<i>Yoma sabina sabina</i>	1976	First record for study region	This volume (see also Common and Waterhouse 1981)
<i>Eurema brigitta australis</i>	1977	First record for study region	Braby (2014a)
<i>Danaus chrysippus cratippus</i>	1977	First record for Australia	Common and Waterhouse (1981); Braby (2014a)
<i>Junonia erigone</i>	1977	First record for Australia	Edwards (1977)
<i>Petrelaea tombugensis</i>	1977	First record for study region	Common and Waterhouse (1981); Braby (2015b)
<i>Danaus plexippus</i>	1979	First record for study region	Dunn (1980)
<i>Leptosia nina</i> ssp. 'Kimberley'	1980	First record for Australia	Common and Waterhouse (1981); Naumann et al. (1991)
<i>Acrodipsas myrmecophila</i>	1981	First record for study region	Dunn and Dunn (1991)
<i>Euploea alcathoe enastri</i>	1988	First record of species for study region; first record of subspecies for Australia	Fenner (1991)
<i>Hesperilla crypsigramma</i> ssp. 'Top End'	1989	First record of species for study region; first record of subspecies for Australia	Field (1990a)
<i>Nesolycaena caesia</i>	1990	First record for Australia	d'Apice and Miller (1992)
<i>Papilio anactus</i>	1991	First record for study region	Puccetti (1991)
<i>Cephereus augiades</i> ssp. 'Top End'	1991	First record of species for study region; first record of subspecies for Australia	Braby (2000)
<i>Vanessa kershawi</i>	1991	First record for study region	Puccetti (1991)
<i>Acrodipsas decima</i>	1991	First record for Australia	Miller and Lane (2004)
<i>Theclines thes sulpitius</i>	1991	First record for study region	Meyer and Wilson (1995)
<i>Euchromia creusa</i>	1993	First record for study region	Braby (2014a)
<i>Jalmenus icilius</i>	1995	First record for study region	Braby (2000)
<i>Eurema alitha novaguineensis</i>	1997*	First record for study region	Braby (1997)
<i>Theclines thes albocinctus</i>	1997	First record for study region	Grund (1998)
<i>Synemon</i> sp. 'Kimberley'	2000	First record for Australia	This volume (see also Williams et al. 2016)
<i>Agarista agricola agricola</i>	2005	First record of subspecies for study region	This volume
<i>Mimeusemia centralis</i>	2007	First record for study region	Braby (2014a)
<i>Comocrus behri</i>	2008	First record for study region	Braby (2011a)
<i>Bindahara phocides</i>	2009	First record for study region	This volume
<i>Radnocera</i> sp. 'Sandstone'	2009	First record for Australia	Braby (2015e)
<i>Appias albina infuscata</i>	2010	First record of subspecies for Australia	Braby et al. (2010b)
<i>Taractroceras psammopetra</i>	2010	First record for Australia	Braby and Zwick (2015)
<i>Ogyris barnardi barnardi</i>	2011	First record for study region	Dunn (2013)
<i>Acraea terpsicore</i>	2012	First record for Australia	Braby et al. (2014a, 2014b)
<i>Mimeusemia econia</i>	2017	First record for study region	This volume

* The earliest specimens of this species date back to 1909; however, it was previously confused with *Eurema hecabe* such that *E. alitha* was not formally recognised in the fauna until 1997.

Note: Taxa are listed in chronological order according to the year they were first discovered or detected, not necessarily the year they were first reported in the literature.

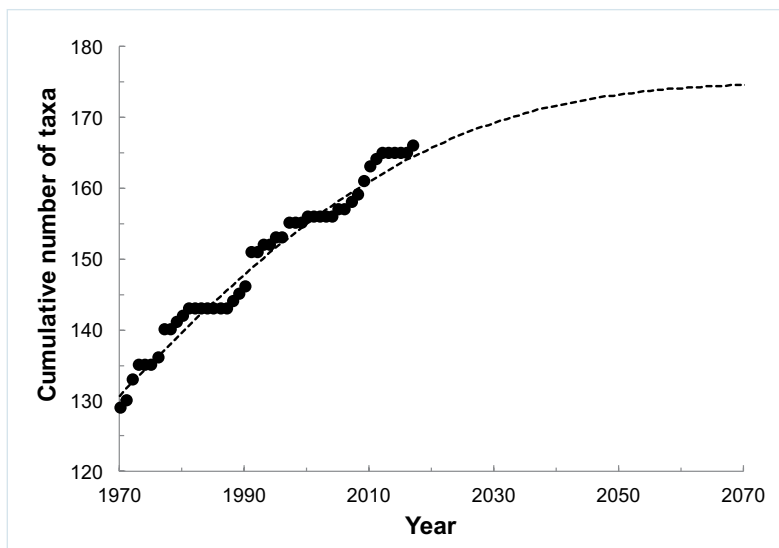


Figure 3 A species accumulation curve fitted to the number of new taxa discovered since 1970

Note: The curve is a cumulative extreme-value function (see Williams et al. 2009): $\log(-\log(1 - y/174.91)) = 0.01524 + 0.30394 * (x - 1969)$ ($r^2 = 0.975$), where y = total taxa known and x = year. The rate of species accumulation since 1970 suggests a predicted total richness of 175 taxa, which, at the current discovery rate, will be discovered progressively up to the year 2068.

Source: Prepared by the authors.

the Top End in 2014, 105 years after it was last recorded breeding, in 1908–09, by F. P. Dodd (Braby 2015a); and an extant breeding population of *Hecatesia* sp. 'Amata' was found in 2008, 121 years after it was last recorded. The latter species was previously known only from a single specimen collected in the Kimberley in 1887 by W. W. Froggatt (M. F. Braby, unpublished data). Also, the subspecies *Suniana lascivia lasus* was rediscovered on Bathurst Island in 2009, more than 70 years after it was last recorded on the island; it was previously known only from three specimens collected in 1933 by T. G. Campbell (Waterhouse 1937a). These rediscoveries and the large number of recent additions to the fauna highlight how poorly known the region is in terms of its butterfly and diurnal moth biodiversity, but also the substantial field effort undertaken during the past 45 years; northern Australia has clearly been a frontier for field discovery.

An obvious question, then, is how many species remain to be discovered? Modelling the rate of species accumulation since 1970 suggests a predicted total richness of 175 taxa, which will be discovered progressively up to the year 2068 (Figure 3). The uncertainty of this estimate (95 per cent confidence interval) is ± 9 species. Thus, it is estimated that approximately 10 ± 9 more taxa remain to be found, which at the current discovery rate may take another 50 years. In other words, the modelling suggests the inventory is close to completion, with an estimated 94 per cent of the species recorded.

Composition

In terms of composition, the fauna comprises seven taxa of Papilionidae (4 per cent), 31 HesperIIDae (19 per cent), 20 Pieridae (12 per cent), 33 Nymphalidae (20 per cent), 43 Lycaenidae (26 per cent) and 32 diurnal moths (19 per cent) representing nine different families. Thus, the lycaenids, nymphalids and hesperiids are the dominant components in the fauna. For the butterflies, these proportions compare well nationally at the species level, although the HesperIIDae (30 species, or 23 per cent) are underrepresented (hesperiids comprise 29 per cent of the Australian fauna), whereas the Nymphalidae (33 species, or 25 per cent) and Pieridae (19 species, or 14 per cent) are slightly overrepresented (nymphalids and pierids comprise 21 per cent and 9 per cent of the Australian fauna, respectively) (Braby 2016a).

Endemism

Our third question was to ascertain which species are found only within the study region. Although no genera are endemic to the study region, 17 species (including seven undescribed diurnal moths) and 35 subspecies (including five undescribed butterflies) are endemic to the region (Table 5). The poorer taxonomic resolution among the moths, with a high proportion of undescribed taxa (seven of 31 species, or 23 per cent), reflects the greater level of taxonomic interest and attention given to the butterflies. This level of endemism is relatively low at the species level (10 per cent), but rises to 31 per cent if all taxa (i.e. species and subspecies) are considered. Thus, endemism is more pronounced below the level of species, suggesting that differentiation of the fauna has been relatively recent. In addition, six species (*Leptosia nina*, *Appias albina*, *Danaus genutia*, *Cethosia penthesilea*, *Phalanta phalantha* and *Deudorix smilis*) have—within Australian limits—their geographic ranges restricted or largely restricted to the study region. That is, these species do not occur elsewhere on the Australian continent, but do occur more widely in South-East Asia.

Most of the endemic species and subspecies have narrow ranges and are restricted to the Top End or to the Top End and Kimberley subregions. Indeed, of the 52 taxa endemic to the study region, 49 (15 species and 34 subspecies, or 96 per cent) occur in the Top End and, of these, 28 taxa (10 species and 18 subspecies, or 55 per cent) are found only in the Top End (Table 5). The three remaining endemic taxa that do not occur in the Top End are *Leptosia nina* ssp. ‘Kimberley’, *Nesolycaena caesia* and *Synemon* sp. ‘Kimberley’—all of which are restricted to the Kimberley. No taxa are endemic to the western Gulf Country or the semi-arid and arid areas of the Northern Deserts. Despite the high variation in collecting effort between the subregions, available data indicate that the Top End has been important in the evolution of the butterfly and diurnal moth fauna, which supports the conclusion of Cracraft (1991) and Bowman et al. (2010) that the Top End is an area of endemism.

At the species level, all the endemics with one exception are restricted to woodland or open woodland habitats, especially those associated with sandstone or sandy soils derived from sandstone. The single exception is the diurnal moth *Ctimene* sp. ‘Top End’, which is restricted to monsoon forest. Braby (2008a) first noted this striking association between endemism and broad habitat type for butterflies across the AMT as a whole. He suggested this pattern may reflect differences in the origin and historical assembly of the biome, with the savannah fauna possibly comprising an older autochthonous element compared with those taxa associated with monsoon forest, which may be a more recent element from South-East Asia.

Table 5 Taxa (species and subspecies, including undescribed taxa) endemic to the study region and their occurrence within the four major subregions

Taxon	Distribution			
	Kimberley	Top End	Northern Deserts	Western Gulf Country
Endemic species				
<i>Mesodina gracillima</i> E. D. Edwards, 1987		++		
<i>Taractrocera ilia</i> Waterhouse, 1932		++		
<i>Taractrocera psammopetra</i> Braby, 2015	+	+		
<i>Acrodipsas decima</i> Miller & Lane, 2004		++		
<i>Nesolycaena urumelia</i> (Tindale, 1922)		+		+
<i>Nesolycaena caesia</i> d'Apice & Miller, 1992	++			
<i>Pseudosesia oberthuri</i> (Le Cerf, 1916)		++		
<i>Synemon</i> sp. 'Kimberley'	++			
<i>Synemon</i> sp. 'Roper River'	+	+	+	+
<i>Pollanisus</i> sp. 7		++		
<i>Ctimene</i> sp. 'Top End'		++		
<i>Radinocera</i> sp. 'Sandstone'	+	+		
<i>Idalima metasticta</i> Hampson, 1910		++		
<i>Idalima leonora</i> (Doubleday, 1846)	+	+		
<i>Idalima</i> sp. 'Arnhem Land'		++		
<i>Hecatesia</i> sp. 'Arnhem Land'		++		
<i>Cruria darwiniensis</i> (Butler, 1884)		++		
Endemic subspecies				
<i>Protographium leosthenes geimbia</i> (Tindale, 1927)		++		
<i>Graphium eury pylus nyctimus</i> (Waterhouse & Lyell, 1914)	+	+		+
<i>Papilio fuscus canopus</i> Westwood, 1842	+	+		
<i>Hasora hurama territorialis</i> Meyer et al., 2015		++		
<i>Hesperilla crypsigramma</i> (Meyrick & Lower, 1902) ssp. 'Top End'		++		
<i>Borbo impar lavinia</i> (Waterhouse, 1932)		++		
<i>Taractrocera dolon diomedes</i> Waterhouse, 1933	+	+		+
<i>Ocybadistes flavovittatus vesta</i> (Waterhouse, 1932)	+	+		+
<i>Ocybadistes walkeri olivia</i> Waterhouse, 1933	+	+		
<i>Ocybadistes hypomeloma vaga</i> (Waterhouse, 1932)	+	+		+
<i>Suniana sunias sauda</i> Waterhouse, 1937		++		
<i>Suniana lascivia lasus</i> Waterhouse, 1937		++		
<i>Suniana lascivia larrakia</i> L. E. Couchman, 1951	+	+		+
<i>Cephrenes augiades</i> (C. Felder, 1860) ssp. 'Top End'		++		
<i>Leptosia nina</i> (Fabricius, 1793) ssp. 'Kimberley'	++			
<i>Delias aestiva aestiva</i> Butler, 1897		++		
<i>Delias argenthona fragalactea</i> (Butler, 1869)	+	+		+
<i>Libythea geoffroyi genia</i> Waterhouse, 1938	+	+		
<i>Danaus genutia alexis</i> (Waterhouse & Lyell, 1914)	+	+		
<i>Euploea sylvester pelor</i> Doubleday, 1847	+	+		+
<i>Euploea darchia darchia</i> W. S. Macleay, 1826	+	+		

Taxon	Distribution			
	Kimberley	Top End	Northern Deserts	Western Gulf Country
<i>Euploea alcatheae enastri</i> Fenner, 1991		++		
<i>Phalanta phalantha araca</i> (Waterhouse & Lyell, 1914)		++		
<i>Hypolimnna alimena darwinensis</i> Waterhouse & Lyell, 1914		++		
<i>Hypocysta adiante antirius</i> Butler, 1868	+	+	+	
<i>Hypochrysops apelles</i> (Fabricius, 1775) ssp. 'Top End'		++		
<i>Hypochrysops ignitus erythrina</i> (Waterhouse & Lyell, 1909)	+	+		+
<i>Arhopala eupolis asopus</i> Waterhouse & Lyell, 1914	+	+		
<i>Arhopala micale</i> Boisduval, 1853 ssp. 'Top End'		++		
<i>Ogyris iphis doddi</i> (Waterhouse & Lyell, 1914)		++		
<i>Deudorix smilis dalyensis</i> (Le Souëf & Tindale, 1970)		++		
<i>Candalides margarita gilberti</i> Waterhouse, 1903	+	+		+
<i>Candalides geminus gagadju</i> Braby, 2017		++		
<i>Nacaduba kurava felsina</i> Waterhouse & Lyell, 1914		++		
<i>Agarista agricola biformis</i> Butler, 1884		++		
Total endemic species	6	15	1	2
Total endemic subspecies	17	34	1	9
Total endemic taxa	23	49	2	11

+ occurs in subregion

++ endemic to subregion

Distribution

The fourth question was to estimate how each species was distributed in space across the landscape and to determine whether there were congruent patterns in geographical range. The geographic range maps suggest there are at least 10 broad patterns (Maps 9a–h and 10a–h), which are briefly summarised as follows.

Very wide ranges

These species occur throughout all or most of the study region, from coastal areas of high rainfall to inland areas of low rainfall, and often extend to the arid areas of central Australia (Map 9a). They include *Papilio demoleus*, *Catopsilia pomona*, *C. scylla*, *Belenois java*, *Danaus petilia*, *Euploea corinna*, *Acraea andromacha*, *Hypolimnna bolina*, *Junonia villida*, *Ogyris zosine*, *O. amaryllis*, *Theclinessthes miskini*, *Nacaduba biocellata*, *Lampides boeticus*, *Zizina otis* and *Famegana alsulus*.

Wide ranges

These species are widely distributed throughout the Kimberley, Top End and western Gulf Country (Maps 9b and 9c). Two subgroups can be distinguished: 1) those that extend well into the semi-arid zone (< 500 mm mean annual rainfall), either permanently or on a seasonal basis (*Eurema herla*, *E. hecabe*, *Junonia orithya*, *Charaxes sempronius*, *Melanitis leda*, *Catopyrops florinda*, *Catochrysops panormus*, *Zizeeria karsandra* and *Freyeria putli*) (Map 9b); and 2) those that are restricted to the higher rainfall areas, generally above 700 mm annually (*Hesperilla sexguttata*, *Pelopidas lyelli*, *Ocybadistes flavovittatus*, *Telicota colon*, *Cephrenes trichopepla*, *Eurema laeta*, *Cepora perimale*, *Delias argenthona*, *Tirumala hamata*, *Danaus affinis*, *Euploea sylvester*, *Acraea terpsicore*, *Junonia hedonia*, *Ypthima arctous*, *Candalides margarita*, *Jamides phaseli*, *Euchrysops cnejus* and *Zizula hylax*) (Map 9c).

Kimberley and Top End

These species are restricted to the Kimberley and Top End and fall into three subgroups (Maps 9d–f): 1) those that are distributed continuously between the two areas across the Ord Arid Intrusion and Victoria River Drainage Basin barrier (*Graphium eurypylus*, *Papilio fuscus*, *Telicota augias*, *Elodina walkeri*, *Hypocysta adiante*, *Arhopala eupolis*, *Anthene lycaenoides*, *Prosotas dubiosa* and *Comocrus behri*) (Map 9d); 2) those that have disjunct populations on either side of the barrier (*Cressida cressida*, *Chaetocneme denitza*, *Taractrocera dolon*, *Eurema alitha*, *Appias paulina*, *Euploea darchia*, *Liphyra brassolis*, *Hypolycaena phorbas*, *Everes lacturnus*, *Birrhana cleis*, *Dysphania numana* and *Idalima leonora*) (Map 9e); and 3) those that have patchy and highly disjunct ranges in the two areas (*Petrelaea tombugensis*, *Taractrocera psammopetra* and *Radinocera* sp. ‘Sandstone’) (Map 9f).

Top End and western Gulf Country

These species are restricted to the Top End and western Gulf Country and include *Neohesperilla xiphiphora*, *Mycalesis perseus* and *Nesolycaena urumelia* (Map 9g).

Top End (broad ranges)

These species are restricted to the Top End, but have relatively wide ranges throughout all or most of the subregion and include *Neohesperilla crocea*, *Ocybadistes walkeri*, *Cethosia penthesilea*, *Hypolimnas alimena*, *Mydosama sirius*, *Arhopala micale*, *Deudorix smilis*, *Anthene seltuttus*, *Idalima metasticta* and *Cruria darwiniensis* (Map 9h).

Top End (narrow ranges)

These species are restricted to the Top End, but have fairly narrow ranges within the subregion. At least four subsets can be distinguished (Maps 10a–d): 1) those restricted to the northern half of the Top End (*Mesodina gracillima*, *Cephrenes augiades*, *Appias albina*, *Sabulana scintillata* and *Ctimene* sp. ‘Top End’) (Map 10a); 2) those restricted to the higher

rainfall areas of the north-western corner of the Top End (*Hesperilla crypsigramma*, *Parnara amalia*, *Phalanta phalantha*, *Acrodipsas decima*, *Ogyris iphis*, *Nacaduba kurava*, *Idalima aethrias* and *Agarista agricola biformis*) (Map 10b); 3) those restricted to the Arnhem Land Plateau (*Protographium leosthenes*, *Taractrocera ilia*, *Candalides geminus*, *Idalima* sp. ‘Arnhem Land’ and *Hecatesia* sp. ‘Arnhem Land’) (Map 10c); and 4) those restricted to Gove Peninsula and adjacent islands (*Euploea alcatheae*, *Yoma sabina* and *Agarista agricola agricola*) (Map 10d).

Kimberley

These species are restricted to the Kimberley and include *Leptosia nina*, *Nesolycaena caesia*, *Synemon* sp. ‘Kimberley’ and *Mimeusemia econia* (Map 10e).

Low rainfall areas

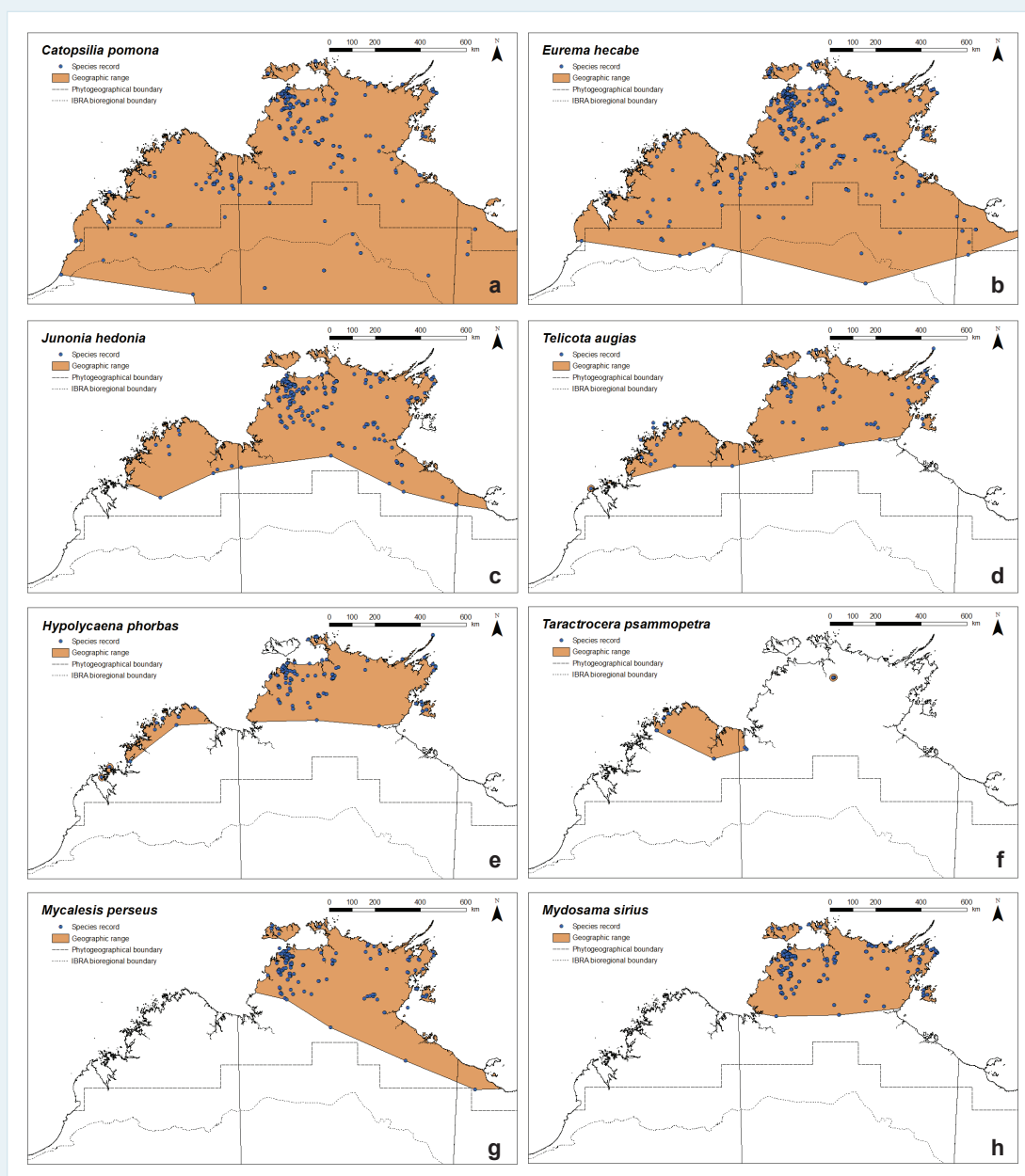
These species breed in areas with below 900 mm mean annual rainfall and occur predominantly in the Northern Deserts of the semi-arid zone (< 700 mm) (Maps 10f and 10g). They include species that are very widespread (*Catopsilia pyranthe*, *Eurema smilax*, *Elodina padusa*, *Candalides delospila* and *Synemon wulwulam*) (Map 10f) and those that apparently have more restricted ranges (*Ogyris barnardi*, *Jalmenus icilius*, *Synemon* sp. ‘Roper River’ and *Hecatesia* sp. ‘Amata’) (Map 10g).

Coastal/estuarine areas

These species are restricted to coastal/estuarine areas and include *Hasora hurama*, *Delias aestiva*, *Hypochrysops apelles* and *Theclinessthes sulphitius* (Map 10h).

Idiosyncratic ranges

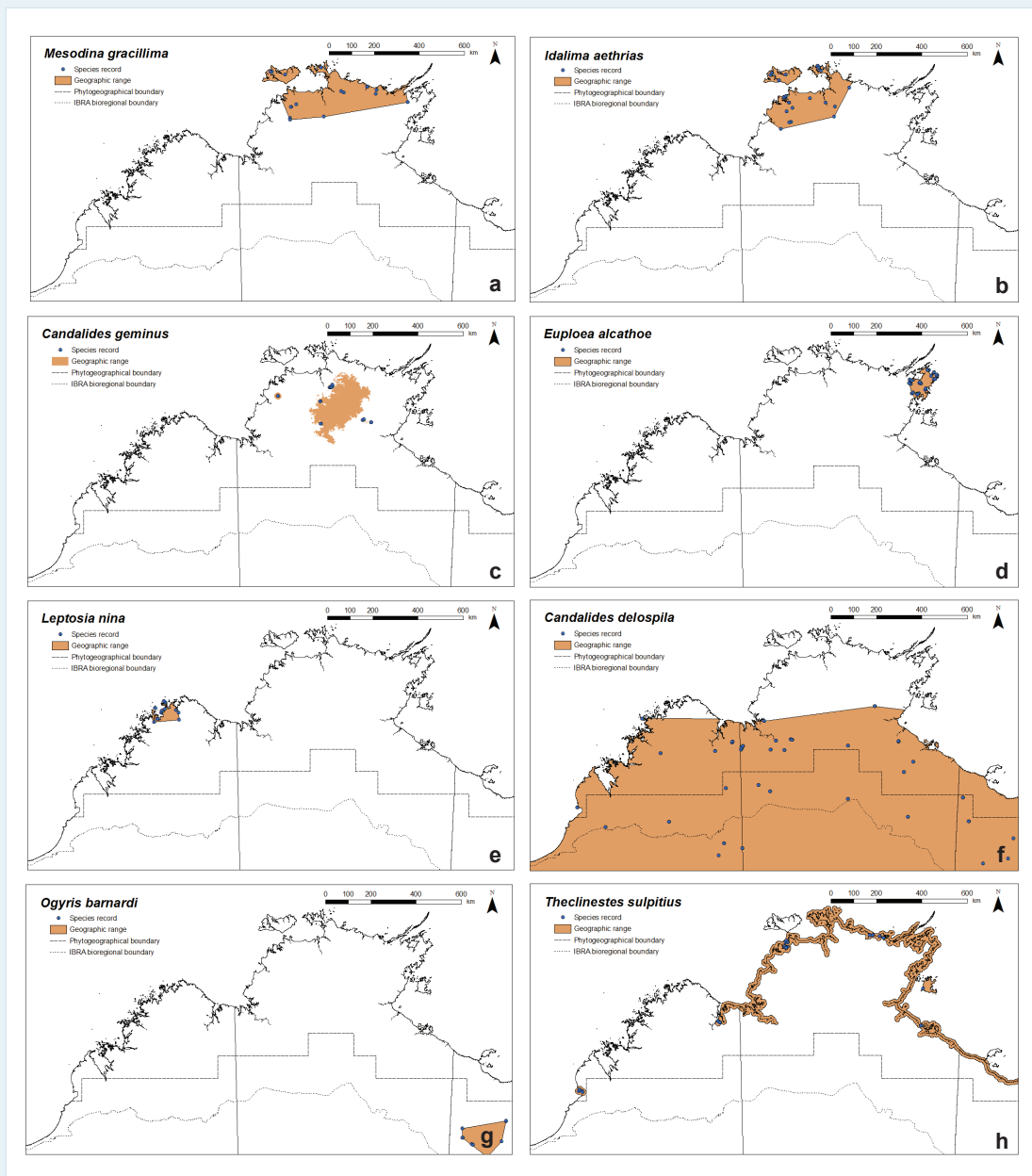
These species show no apparent pattern, and include *Papilio aegeus*, *Libythea geoffroyi*, *Danaus genutia* and Genus 1 sp. ‘Sandstone’.



Map 9 Geographic ranges of butterflies and diurnal moths in the study region, showing examples of species

(a) very widely distributed (*Catopsilia pomona*); (b) widely distributed across the Kimberley, Top End and western Gulf Country, but also extending well into lower rainfall areas of the semi-arid zone (< 700 mm mean annual rainfall) (*Eurema hecabe*); (c) widely distributed across the Kimberley, Top End and western Gulf Country, but restricted to higher rainfall areas (> 700 mm) (*Junonia hedonia*); (d) restricted to the Kimberley and Top End, but distributed continuously between the two areas (*Telicota augias*); (e) restricted to the Kimberley and Top End, but with a disjunct distribution (*Hypolycaena phorbas*); (f) restricted to the Kimberley and Top End, but with a highly disjunct and limited range (*Taractrocer a psammopetra*); (g) restricted to the Top End and western Gulf Country (*Mycalesis perseus*); (h) restricted to the Top End, but widespread in area (*Mydosama sirius*).

Source: Prepared by the authors.



Map 10 Geographic ranges of butterflies and diurnal moths in the study region, showing examples of species

(a) restricted to the Top End, but limited to the northern half (*Mesodina gracillima*); (b) restricted to the Top End, but limited to the north-western corner (*Idalima aethrias*); (c) restricted to the Top End, but mainly limited to the Arnhem Land Plateau (*Candalides geminus*); (d) restricted to the Top End, but limited to Gove Peninsula (*Euploea alcathoe*); (e) restricted to the Kimberley (*Leptosia nina*); (f) restricted to low rainfall areas (< 900 mm mean annual rainfall), but widespread in area (*Candalides delospila*); (g) restricted to low rainfall areas of the semi-arid zone, but limited in range (*Ogyris barnardi*); (h) restricted to coastal/estuarine areas (*Theclinesthes sulpitius*).

Source: Prepared by the authors.

Critical habitats and larval food plants

Of the 163 species recorded in the study region, 152 are resident or immigrant (see 'Breeding status' below). Of these resident and immigrant species, breeding habitats or suspected breeding habitats have been recorded for 141 (93 per cent). The 11 resident species for which the natural breeding habitat has not been recorded are: *Papilio aegaeus*, *Acrodipsas myrmecophila*, *A. decima*, *Bindahara phocides*, *Sahulana scintillata*, *Synemon* sp. 'Kimberley', *Pollaninus* sp. 7, *Hestiochora xanthocoma*, *Euchromia creusa*, *Leucogonia cosmopsis* and *Ipanica cornigera*. Some species breed in only one type of habitat, particularly those with very specialised ecological requirements in which the larvae feed on just one plant species or genus, whereas others breed in several different types of habitat and may utilise many different kinds of plants.

Monsoon forest

More than 50 (31 per cent) species depend on various types of monsoon forest, of which 34 (21 per cent) are obligatorily restricted to these habitats in that they do not breed in other habitats. Among these monsoon forest specialists, at least one (*Cephrenes augiades*) is restricted to the wetter monsoon forests (i.e. evergreen monsoon vine forest) associated with permanent springs, creeks and other riparian areas, whereas 12 others occur only in drier monsoon forests (i.e. semi-deciduous monsoon vine thicket) on rocky outcrops, along seasonal gullies or on coastal laterite cliffs or dunes adjacent to the beach (*Protographium leosthenes*, *Graphium eurypylus*, *Papilio fuscus*, *Badamia exclamatoris*, *Hasora chromus*, *Leptosia nina*, *Elodina walkeri*, *Appias albina*, *Libythea geoffroyi*, *Hypolycaena phorbas*, *Mimeusemia econia* and *M. centralis*). At least 14 species occur in both wet and dry monsoon forest (*Telicota augias*, *Appias paulina*, *Tirumala hamata*, *Phalanta phalantha*, *Euploea sylvester*, *E. darchia*, *Cethosia penthesilea*, *Arhopala micale*, *Deudorix similis*, *Anthene lycaenoides*, *Petrelaea tombuensis*, *Nacaduba kurava*, *Ctimene* sp. 'Top End' and

Dysphania numana), although in the wetter monsoon forests they usually breed only along the drier edges of the forest. Seven species breed only in light gaps within, or along the edge of, the rainforest, especially in the ecotone between monsoon forest and woodland (*Suniana sunias*, *Euploea alcatheae*, *Yoma sabina*, *Hypolimnas alimena*, *Anthene seltuttus*, *Everes lacturnus* and *Agarista agricola*). These last mentioned species often also occur in mixed open forest with rainforest elements in the understorey, particularly in riparian areas.

Sixteen (10 per cent) species use monsoon forest facultatively—that is, they breed equally in both monsoon forest or mixed monsoon forest and savannah woodland (*Neohesperilla crocea*, *Pelopidas lyelli*, *Taractrocera ina*, *Cephrenes trichopepla*, *Catopsilia scylla*, *Eurema alitha*, *E. hecabe*, *Elodina padusa*, *Belenois java*, *Cepora perimale*, *Acraea andromacha*, *Charaxes sempronius*, *Melanitis leda*, *Candalides margarita*, *Prosotas dubiosa* and *Catopyrops florinda*). A further nine that are more typical of savannah woodland also breed along the edges of monsoon forest (*Telicota colon*, *Euploea corinna*, *Hypocysta adiante*, *Ypthima arctous*, *Arhopala eupolis*, *Candalides erinus*, *Jamides phaseli*, *Pseudosesia oberthuri* and *Radinocera vagata*).

Monsoon forests make up only a relatively small area (less than 1 per cent) of the landscape in the study region (Russell-Smith 1991; Russell-Smith and Bowman 1992; Russell-Smith et al. 1992), yet they support a disproportionately high number of butterfly and diurnal moth species (21–31 per cent), highlighting the high biodiversity value of this habitat type. These findings parallel similar trends for plants (Woinarski et al. 2005), but contrast markedly with those for ants (Andersen and Reichel 1994; Reichel and Andersen 1996; Andersen et al. 2006, 2007b). Interestingly, despite the high proportion of rainforest specialists, few taxa appear to be endemic to monsoon forests—a pattern also evident in ants (Reichel and Andersen 1996). Of the 34 taxa obligatorily associated with monsoon forest, only one species (*Ctimene* sp. 'Top End') and 16 subspecies (*Protographium leosthenes geimbia*, *Graphium eurypylus nyctimus*, *Papilio*

fuscus canopus, *Suniana sunias sauda*, *Cephrenes augiades* ssp. ‘Top End’, *Leptosia nina* ssp. ‘Kimberley’, *Libythea geoffroyi genia*, *Euploea sylvester pelor*, *E. darchia darchia*, *E. alcathoe enastri*, *Phalanta phalantha araca*, *Hypolimnasia alimena darwinensis*, *Arhopala micale* ssp. ‘Top End’, *Deudorix smilis dalyensis*, *Nacaduba kurava felsina* and *Agarista agricola biformis*) are endemic to monsoon forests within the study region. Four monsoon forest specialists (*Leptosia nina*, *Cethosia penthesilea*, *Phalanta phalantha* and *Deudorix smilis*) represent the only known Australian occurrences of predominantly South-East Asian species. A fifth monsoon specialist, the predominantly South-East Asian pierid *Appias albina*, also has its main occurrence within Australia in the study region.

Savannah woodland

At least 88 (54 per cent) species occur in savannah woodland, but a number of these breed in other habitats. About 60 (37 per cent) species are found only in savannah woodland in the broad sense—that is, eucalypt heathy woodland, open woodland, *Acacia* woodland, riparian woodland and tropical grassland. Some of these species favour open disturbed areas for breeding (*Papilio demoleus*, *Acraea terpsicore*, *Hypolimnasia bolina*, *H. misippus*, *Theclines thes miskini*, *Lampides boeticus*, *Zizeeria karsandra*, *Euchrysops cnejus*, *Freyeria putli* and *Perioptera diversa*). Eleven of these savannah species are restricted to habitats associated with laterite or sandstone outcrops or sandy soils derived from sandstone/laterite, often with a heathy understorey or a hummock (spinifex) grass understorey (*Hesperilla crypsigramma*, *Mesodina gracillima*, *Proeidosia polysema*, *Candalides geminus*, *C. delospila*, *Nesolycaena urumelia*, *N. caesia*, Genus 1 sp. ‘Sandstone’, *Idalima* sp. ‘Arnhem Land’, *Hecatesia* sp. ‘Arnhem Land’ and *Hecatesia* sp. ‘Amata’).

Other habitats

At least nine species are regularly associated with paperbark woodland, paperbark swampland or mixed paperbark–pandanus swampland and other damp areas (*Hesperilla sexguttata*, *Parnara amalia*, *Suniana lascivia*,

Danaus affinis, *D. genutia*, *Junonia hedonia*, *Mydosama sirius*, *Zizula hylax* and *Cruria darwiniensis*)—often adjacent to evergreen monsoon vine forest. Another species (*Borbo impar*) inhabits floodplain wetlands and swamps where the native larval food plant grows in standing water, and at least three others (*Papilio demoleus*, *Junonia hedonia* and *Mydosama sirius*) breed along the margins of these habitats; most of these species also breed in other habitats. Three species are restricted to the taller closed forest mangrove communities in the Top End (*Hasora hurama*, *Delias aestiva* and *Hypochrysops apelles*). Interestingly, on Cape York Peninsula, these species (or their nearest relatives) are typically associated with tropical forest, and Braby (2012c) hypothesised that historical contraction of rainforest habitat in the Top End during periods of aridification in the Miocene–Pleistocene may have led to pronounced habitat/food plant shifts, ultimately contributing to the evolution and adaptation of these insects to nonrainforest habitats, such as mangroves.

Other species occur in very specialised habitats. For example, *Radinocera* sp. ‘Sandstone’ breeds only on its food plant growing among foot-slope boulders at the base of sandstone escarpments. Open sandstone pavements, rock ledges and the base of rock overhangs are interesting habitats because they support ‘resurrection’ grasses (*Micraria* spp.), the only plant genus that has adapted and radiated to any extent in this very specialised habitat (Lazarides 2005); in turn, these grasses support two ecologically specialised butterflies endemic to the study region (*Taractrocera ilia* and *T. psammopetra*) (Braby and Zwick 2015). *Theclines thes sulphitius* is the only species that breeds in coastal saltmarsh—a specialised habitat that is highly saline and periodically inundated by incoming tides.

Larval food plants

A complete list of known and putative larval food plants is provided in Appendix I. A total of 373 known butterfly/diurnal moth–plant associations, and a further 55 putative associations that require confirmation, have been recorded from the study region.

The putative associations are based on records from adjacent areas (e.g. Queensland), on the spatial distribution of the relevant species or on other evidence (e.g. female pre-oviposition behaviour) within the study region.

While larval food plants have been recorded for most species in the study region, data are still lacking for 26 species, and for nine species only fragmentary information, such as associations with introduced weedy taxa, is available. Notable taxa for which there are currently no published native food plant associations are the grass-feeding hesperiids, satyrines and sun-moths (*Neohesperilla senta*, *N. crocea*, *N. xanthomera*, *Parnara amalia*, *Borbo cinnara*, *Taractrocera dolon*, *Ocybadistes flavovittata*, *O. walkeri*, *O. hypomeloma*, *Suniana sunias*, *Mycalesis perseus*, *Ypthima arctous* and *Synemon* sp. 'Kimberley'), the legume-feeding pierids and lycaenids (*Catopsilia pyranthe*, *C. pomona*, *Eurema laeta*, *E. smilax*, *Zizina otis*, *Zizula hylax* and *Everes lacturnus*), three nymphalids (*Danaus chrysippus*, *Junonia villida* and *Hypolimnas bolina*), several other lycaenids (*Bindahara phocides*, *Petrelaea tombugensis* and *Sahulana scintillata*) and a number of diurnal moths (*Pollanisia* sp. 7, *Hestiochora xanthocoma*, *Ctimene* sp. 'Top End', *Euchromia creusa*, Genus 1 sp. 'Sandstone', *Leucogonia cosmopsis*, *Ipanica cornigera*, *Mimeusemia econia* and *M. centralis*).

Patterns of breeding and seasonal abundance

Breeding status

Of the 166 taxa, 151 (91 per cent) are resident within the study region (i.e. breeding regularly, with permanently established populations), three (2 per cent) are immigrant (i.e. breeding irregularly, with temporary populations) and 12 (7 per cent) are vagrant or infrequent visitors (i.e. not breeding, with non-resident populations). The three immigrants are *Badamia exclamationis*, *Nacaduba biocellata* and *Lampides boeticus*, and these species appear to enter and vacate the study region on a seasonal basis. The 12 vagrant or infrequent visitor taxa are listed in Table 6. These species rarely enter the study region—and usually in very small numbers—or they may enter on a more regular basis. Two of these species (*Borbo cinnara* and *Danaus chrysippus*) may actually be rare immigrants in that breeding possibly occurs, but the colonising populations are temporary and they fail to establish permanently; however, only circumstantial evidence is currently available on the breeding status of these species. The majority of the vagrant or infrequent visitor species belong to the family Nymphalidae (Table 6).

Table 6 List of taxa that are vagrants and/or infrequent visitors

Scientific name	Common name	Family
<i>Borbo cinnara</i> (Wallace, 1866)	Rice Swift	Hesperiidae
<i>Eurema brigitta australis</i> (Wallace, 1867)	No-brand Grass-yellow	Pieridae
<i>Appias albina infuscata</i> Fruhstorfer, 1910	White Albatross	Pieridae
<i>Delias mysis mysis</i> (Fabricius, 1775)	Red-banded Jezebel	Pieridae
<i>Danaus chrysippus cratippus</i> (C. Felder, 1860)	Plain Tiger	Nymphalidae
<i>Danaus plexippus</i> (Linnaeus, 1758)	Monarch	Nymphalidae
<i>Euploea climenae macleari</i> Butler, 1887	Climena Crow	Nymphalidae
<i>Vanessa kershawi</i> (McCoy, 1868)	Australian Painted Lady	Nymphalidae
<i>Vanessa itea</i> (Fabricius, 1775)	Yellow Admiral	Nymphalidae
<i>Junonia erigone</i> (Cramer, [1775])	Northern Argus	Nymphalidae
<i>Hypolimnas anomala albula</i> (Wallace, 1869)	Crow Eggfly	Nymphalidae
<i>Alcides metaurus</i> (Hopffer, 1856)	Zodiac Moth	Uraniidae

Note: These taxa probably do not breed in the study region (i.e. are non-resident).

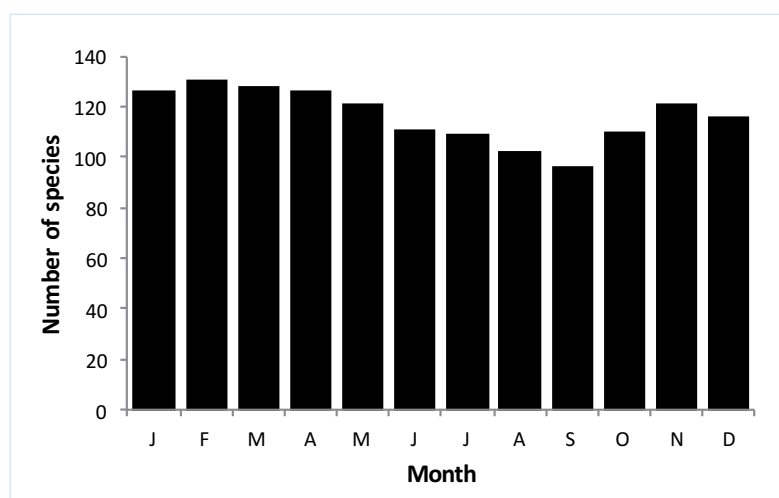


Figure 4 Temporal distribution of species richness in the study region

Note: Data are based on monthly flight period records for each of the 152 resident and immigrant species (i.e. those that breed in the region).

Source: Prepared by the authors.

Seasonality

A summary of the monthly incidence of the resident and immigrant species in the study region is shown in Figure 4. Although the phenology data for some species are incomplete or based on limited sampling, available records suggest a seasonal component in species richness. Species richness is apparently highest during the mid to late wet season (January–April), with a peak in February, steadily declining as the dry season progresses and is lowest in the late dry season (September), before increasing slightly during the ‘build-up’ (October–December). Although many species (at least 64) have been recorded in every month of the year, some are strictly seasonal and appear for just a few months (see below). For example, many species of Hesperidae and most Agaristinae fly mainly during the wet season, but a few Lycaenidae and Castniidae occur predominantly during the dry season (*Acrodipsas myrmecophila*, *Ogyris barnardi*, *Sahulana scintillata*, *Theclines thes albocinctus*, *Synemon wulwulam* and *Synemon* sp. ‘Roper River’).

Available data on the breeding phenology (i.e. temporal incidence of the immature stages) and seasonal abundance of adults indicate that about half of the region’s species breed, or are suspected to breed, continuously throughout the year, whereas the other half breed seasonally. The continuous breeders have multiple generations during the year and

they achieve this in one of several ways. First, some species specialise on larval food plants that are perennial and thus available all year round (e.g. non-deciduous vines, mistletoes, palms or grasses that grow where conditions are permanently moist and buffered from climatic extremes). Second, other species (e.g. some lycaenids) feed on a range of plants, but switch their food plants on a seasonal basis according to the availability of new leaf shoots, flowers or fruits. Some ecologically specialised species (e.g. *Hasora hurama*, *H. chromus* and *Deudorix smilis*) that feed only on a single plant species have a similar strategy but appear to switch between individual plants that are seasonally available. Third, a strategy adopted by some species (e.g. several satyrines and *Acraea* spp.) is to breed throughout the year, but as the dry season progresses their reproductive activity declines and/or they contract to moist refuges. Fourth, at least four species (*Eurema smilax*, *E. hecabe*, *Belenois java* and *Zizeeria karsandra*) are highly nomadic and/or migratory, with populations shifting across a wide area within the study region, presumably tracking resources that are ephemeral or unpredictable in space and time. Several other highly mobile species (e.g. *Papilio demoleus* and *Catopsilia* spp.) may adopt this strategy, but it is not clear whether they breed all year round. Another—and perhaps the most bizarre—tactic of a continuous breeder is displayed by *Taractrocera ilia* (Braby and Zwick 2015). The adults emerge and fly all year round, but the larvae (all instars) enter diapause during the dry season when their food

plants (resurrection grasses) become completely desiccated. However, diapause in final instar larvae is frequently terminated before the onset of the wet season such that the larvae pupate and emerge as adults shortly afterwards in the mid to late dry season. These adults then mate and the females lay eggs on the dry plants; the eggs develop and hatch soon after, but the first instar larvae then enter diapause.

Species that breed seasonally usually have only one or a few generations annually, or one generation followed by a partial second generation. The larvae of these species generally specialise on plants that are either short-lived annuals or seasonal perennials (e.g. deciduous vines) or they exploit plant parts (e.g. new leaf shoots) that are only available for a few months of the year, typically during the wet season. These species have developed an array of life history strategies to survive the non-breeding season when the food plants are not available, which is usually during the long dry season. We identified at least four strategies. First, several grass-feeding hesperiids (e.g. *Taractrocera* spp., *Neohesperilla* spp. and *Proeidosa polysema*) and possibly a few lycaenids (e.g. *Zizula hylax*, *Everes lacturnus*, *Euchrysops cnejus* and *Freyeria putli*) remain, or are suspected to remain, in larval diapause. Second, several swallowtails (e.g. *Protographium leosthenes*, *Graphium eurypylus* and *Papilio fuscus*), at least two lycaenids (*Nesolycaena urumelia* and *N. caesia*) and most of the agaristine moths remain in pupal diapause, often for many months or even years. The agaristines typically pupate underground or deep under bark at the base of tree trunks, where they are also protected from dry season fires. Four other species (*Appias albina*, *Delias aestiva*, *Cethosia penthesilea* and *Phalanta phalantha*) are suspected to have capacity for pupal diapause during periods of food shortfall, but to our knowledge this has not been confirmed. Third, a number of pierids (e.g. *Catopsilia pomona*, *Eurema laeta* and *E. herla*) and nymphalids (most danaines, *Junonia* spp., *Yoma sabina*, *Hypolimnys* spp., *Melanitis leda* and *Mycalesis perseus*) remain, or are suspected to remain, in adult reproductive diapause. The adults of these species contract to moist refuges, where they

remain relatively inactive for many months, sometimes in immense numbers (e.g. *Euploea corinna*). Finally, three immigrant species (*Badamia exclamationis*, *Nacaduba biocellata* and *Lampides boeticus*) enter the study region on a seasonal basis and appear to breed only for a short period before vacating.

Although some caution must be exercised when interpreting patterns of seasonal changes in relative abundance based on collection and observation records, our data suggest that, where sufficient records are available, at least six broad patterns may be discerned (Figures 5a–h), as follows.

Early wet season

These species peak in adult abundance during the ‘build-up’ of the early wet season when conditions are very humid and hot—typically in November and December, but sometimes in late October or early January, depending on the arrival of the pre-monsoon storms (Figure 5a). All of these species are seasonal breeders and include three swallowtails (*Protographium leosthenes*, *Graphium eurypylus* and *Papilio fuscus*), several agaristines (*Perioptia* spp., *Radinocera* spp., *Idalina* spp. and *Cruria donowani*) and the undescribed noctuid Genus 1 sp. ‘Sandstone’.

Mid wet season

These species peak in adult abundance during the monsoon rains of the mid wet season—typically in January and February, but sometimes in late December or early March, depending on the timing of the monsoon(s) (Figures 5b and 5c). Continuous breeders that show this pattern are *Hasora chromus*, *Taractrocera ilia*, *Telicota augias*, *Appias paulina* and *Acraea terpsicore*. Seasonal breeders that show this pattern include *Badamia exclamationis*, *Taractrocera ina*, *Neohesperilla xiphiphora*, *Appias albina*, *Synemon phaeoptila* and *Ipanica cornigera*.

Late wet season – early dry season

These species peak in adult abundance during the late wet season and/or early dry season (March–May) (Figures 5d and 5e). A large number of species show this pattern,

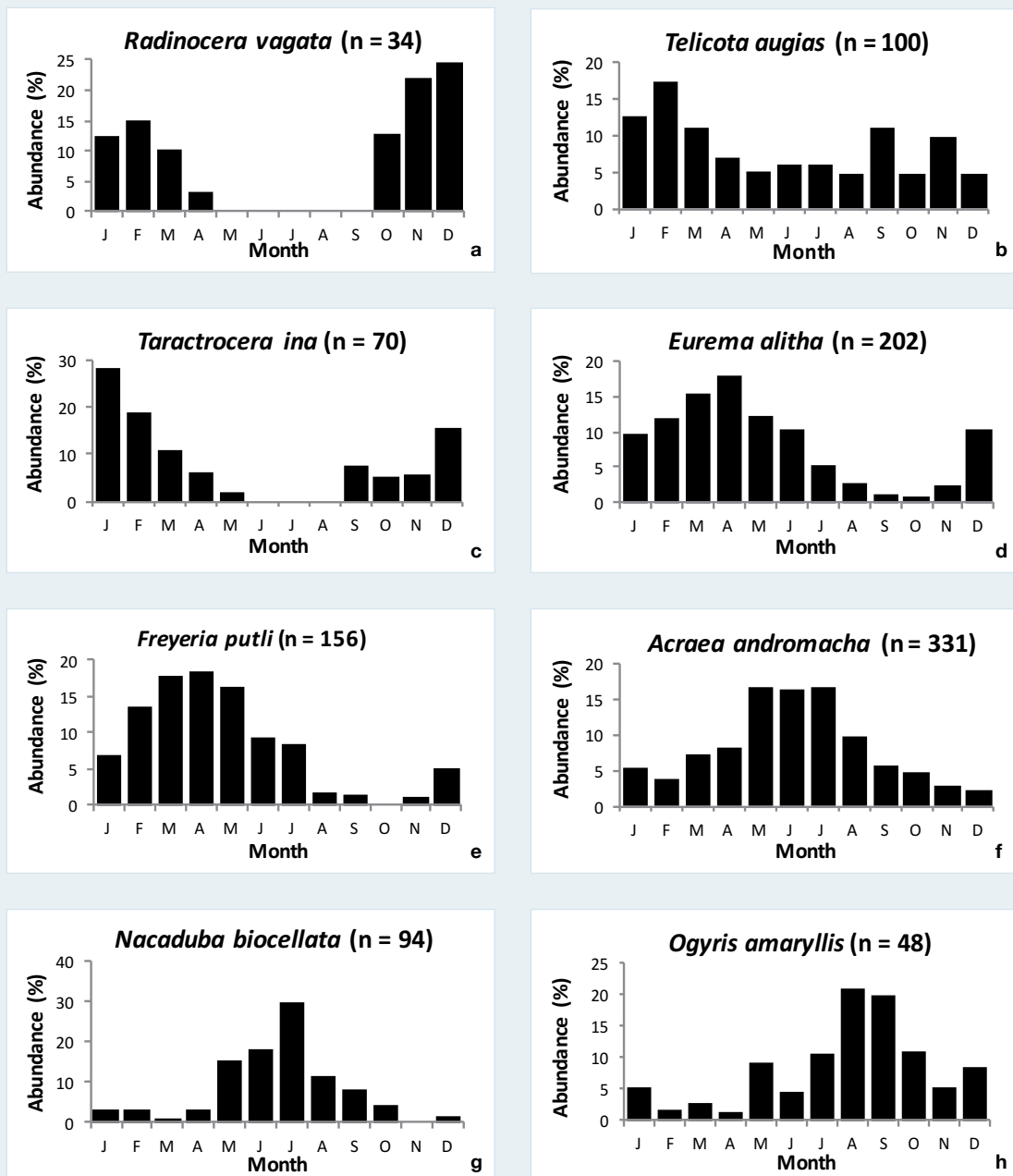


Figure 5 Seasonal variation in adult abundance of butterflies and diurnal moths in the study region, showing examples of species peaking at different times of the year

(a) early wet season (*Radinocera vagata*, a seasonal breeder); (b, c) mid wet season (*Telicota augias*, a continuous breeder, and *Taractrocera ina*, a seasonal breeder); (d, e) late wet season – early dry season (*Eurema alitha*, a continuous breeder, and *Freyeria putli*, a seasonal breeder); (f, g) mid dry season (*Acraea andromacha*, a continuous breeder, and *Nacaduba biocellata*, a seasonal breeder); (h) late dry season (*Ogyris amaryllis*, a continuous breeder).

Note: The relative abundance of each species (per cent) is based on the number of temporal records, defined as the occurrence on a particular date (time) at a given site (space), for the study region.

including both continuous breeders or likely continuous breeders (e.g. *Papilio demoleus*, *Cressida cressida*, *Borbo impar*, *Parnara amalia*, *Pelopidas lyelli*, *Ocybadistes flavovittatus*, *Telicota colon*, *Cephrenes trichopepla*, *Catopsilia pyranthe*, *C. scylla*, *Eurema alitha*, *E. hecabe*, *Cepora perimale*, *Mydosama sirius*, *Catochrysops panormus*, *Jamides phaseli*, *Famegana alsulus*, *Zizina otis* and *Zizeeria karsandra*) and seasonal or putative seasonal breeders (e.g. *Hesperilla crypsigramma*, *Taractrocera anisomorpha*, *T. dolon*, *Eurema herla*, *Libythea geoffroyi*, *Junonia villida*, *J. orithya*, *Hypolimnias misippus*, *H. bolina*, *Melanitis leda*, *Nesolycaena urumelia*, *Everes lacturnus*, *Euchrysops cnejus*, *Freyeria putli* and *Synemon wulwulam*).

Mid dry season

These species peak in adult abundance during the mid dry season (May/June and July), when conditions are dry and cool, especially at night (Figures 5f and 5g). This group includes both continuous or putative continuous breeders (e.g. *Ocybadistes walkeri*, *Suniana* spp., *Eurema smilax*, *Elodina padusa*, *Acraea andromacha*, *Ypthima arctous*, *Arhopala micale*, *Deudorix smilis*, *Candalides margarita*, *C. erinus* and *Catopyrops florinda*) and seasonal breeders (e.g. *Eurema laeta*, *Delias aestiva*, *Cethosia penthesilea*, *Junonia hedonia*, *Mycalesis perseus*, *Sahulana scintillata*, *Nacaduba biocellata*, *Zizula hylax* and *Lampides boeticus*).

Late dry season

These species peak in adult abundance during the late dry season, when conditions are dry and hot to very hot—typically during the period August–October (Figure 5h). All of these species are continuous breeders and include *Belenois java*, *Charaxes sempronius* and several taxa associated with mistletoes (*Delias argenthona*, *Ogyris* spp. and *Comocrus behri*).

Nonseasonal

These species show little seasonal variation in abundance or no clear or consistent pattern throughout the year (e.g. *Catopsilia pomona*, *Elodina walkeri*, *Tirumala hamata*, *Danaus affinis*, *Euploea sylvestris*, *E. darchia*,

Hypolimnias alimena, *Liphyra brassolis*, *Arhopala eupolis*, *Hypochrysops ignitus*, *Anthene seltuttus*, *A. lycaenoides* and *Dysphania numana*).

Conservation status

Of the 166 taxa assessed for their conservation status according to the IUCN Red List criteria, 14 were ranked as Not Applicable (NA) and therefore were not evaluated. For the remaining 152 taxa, the data for 16 were inadequate to make an evaluation on the extent of extinction risk and thus were categorised as Data Deficient (DD). For the 136 taxa for which there were adequate data, one species was ranked as Vulnerable (VU), four as Near Threatened (NT) and 131 were assessed as Least Concern (LC) (Table 7). No species from the study region are known to have become extinct since European settlement, although one species (*Pollanisus* sp. 7) has not been detected since it was first recorded 110 years ago. However, the paucity of records of *Pollanisus* sp. 7 probably reflects a combination of lack of targeted survey, seasonality, likely occurrence in remote areas and the inconspicuous nature of adults of this species. The putative larval food plant (*Pipturus argenteus*) occurs mainly in eastern Arnhem Land, with a very sporadic occurrence closer to Darwin, in the Northern Territory.

The threatened (VU), Near Threatened (NT) and DD taxa are also listed in Appendix II, which provides a summary of the criteria, justifications and actions needed. The taxa of most conservation concern are *Ogyris iphis doddi*, *Euploea alcathoe enastri*, *Hypochrysops apelles* ssp. 'Top End', *Idalima* sp. 'Arnhem Land' and *Hecatesia* sp. 'Arnhem Land'—all of which are endemic to the Top End. However, at least nine of the DD species (*Hesperilla crypsigramma* ssp. 'Top End', *Suniana lascivia lasus*, *Acrodipsas myrmecophila*, *A. decima*, *Ogyris barnardi barnardi*, *Nesolycaena caesia*, *Theclinesstes albocinctus*, *Pollanisus* sp. 7 and *Agarista agricola agricola*) are of conservation interest because they may qualify as Near Threatened (NT) once adequate data are available. That is, these taxa are possibly threatened (Appendix II).

Table 7 Summary of conservation status of taxa based on IUCN Red List categories and criteria

Red List category	Number of taxa	Taxa
Vulnerable (VU)	1	† <i>Ogyris iphis doddi</i>
Near Threatened (NT)	4	† <i>Euploea alcathe enastri</i> , † <i>Hypochrysops apelles</i> ssp. 'Top End', † <i>Idalima</i> sp. 'Arnhem Land', † <i>Hecatesia</i> sp. 'Arnhem Land'
Least Concern (LC)	131	
Data Deficient (DD)	16	<i>Badamia exclamationis</i> , † <i>Hesperilla crypsigramma</i> ssp. 'Top End', † <i>Suniana lascivia lasus</i> , <i>Acrodipsas myrmecophila</i> , † <i>A. decima</i> , <i>Ogyris barnardi barnardi</i> , <i>Bindahara phocides</i> , † <i>Nesolycaena caesia</i> , <i>Petrelaea tombugensis</i> , <i>Theclinesstes albocinctus</i> , † <i>Synemon</i> sp. 'Kimberley', † <i>Pollanisus</i> sp. 7, <i>Euchromia creusa</i> , <i>Mimeusemia econia</i> , <i>M. centralis</i> , <i>Agarista agricola agricola</i>
Not Applicable (NA)	14	<i>Papilio anactus</i> , <i>Borbo cinnara</i> , <i>Eurema brigitta australis</i> , <i>Appias albina infuscata</i> , <i>Delias mysis mysis</i> , <i>Danaus chrysippus cratippus</i> , <i>Danaus plexippus</i> , <i>Euploea climena macleari</i> , <i>Acraea terpsicore</i> , <i>Vanessa kershawi</i> , <i>Vanessa itea</i> , <i>Junonia erigone</i> , <i>Hypolimnas anomala albula</i> , <i>Alcides metaurus</i>
Total	166	

† taxa endemic to the study region

Note: See Appendix II for justifications and actions needed for threatened (VU), NT and DD taxa.

Taxa assessed as LC are not listed.

Very few species have restricted distributions (Appendix II). Of the 34 resident and immigrant taxa identified as having small geographic range sizes (< 40,000 sq km), nine (*Protographium leosthenes geimbia*, *Taractroceralia*, *Leptosia nina*, *Hypochrysops apelles*, *Ogyris barnardi barnardi*, *Euploea alcathe enastri*, *Yoma sabina*, *Nesolycaena caesia* and *Agarista agricola biformis*) had an estimated EOO of less than the threshold of 20,000 sq km to qualify for a possible Red List category under criterion B1. A further 17 taxa (*Badamia exclamationis*, *Suniana lascivia lasus*, *Acrodipsas myrmecophila*, *A. decima*, *Ogyris iphis doddi*, *Bindahara phocides*, *Petrelaea tombugensis*, *Theclinesstes albocinctus*, *Synemon* sp. 'Kimberley', *Pollanisus* sp. 7, *Euchromia creusa*, *Idalima* sp. 'Arnhem Land', *Radinocera* sp. 'Sandstone', *Hecatesia* sp. 'Arnhem Land', *Mimeusemia econia*, *M. centralis* and *Agarista agricola agricola*) are known only from one or two spatial records or breeding sites (i.e. their AOO is likely to be < 2,000 sq km) and thus they may qualify for a Red List category under criterion B2. However, most of these taxa were evaluated to be LC or DD when two of three other subcriteria were considered—specifically, the number of locations and evidence of decline (Appendix II).

In terms of representation in the NRS, most taxa are adequately represented to varying degrees. However, 14 taxa are poorly represented in the conservation reserve system: *Suniana lascivia lasus*, *Acrodipsas myrmecophila*, *A. decima*, *Ogyris barnardi barnardi*, *Jalmenus icilius* and *Theclinesstes albocinctus* are currently not known to be represented in any conservation reserve. *Ogyris oroetes oroetes*, *O. iphis doddi*, *Nesolycaena caesia*, *Petrelaea tombugensis*, *Nacaduba kurava felsina*, *Theclinesstes sulphitius*, *Synemon* sp. 'Roper River' and *Agarista agricola agricola*, which have been recorded from two or more locations, are each currently known from only a single conservation reserve. Of these 14 taxa, four (*Ogyris barnardi barnardi*, *O. oroetes oroetes*, *Jalmenus icilius* and *Synemon* sp. 'Roper River') occur predominantly in the semi-arid zone (in *Acacia* low open woodland or eucalypt open woodland habitats) of the Northern Deserts and western Gulf Country, while two (*Suniana lascivia lasus* and *Ogyris iphis doddi*) occur on the Tiwi Islands.

Overall, our assessment indicates that the fauna is in reasonably good health; no species are known to have become extinct and there are few threatened taxa. The relatively low frequency of threatened taxa in large part reflects two standout features of northern Australia: 1) the landscapes it supports are still relatively intact; and 2) many species have large geographic range sizes across the study region, particularly those associated with savannah woodland. Although the region is not immune from threats, the geographic ranges of most species are large enough to buffer against local impacts. However, as Woinarski et al. (2005) point out, having species with such widespread distributions over a relatively uniform landscape does not necessarily imply that loss of any local area/population may be inconsequential. Many of the ecological processes underpinning the health and heterogeneity of the landscape, such as fire and flooding, must also operate over vast areas, such that loss of a subset of the range and disruption of natural processes may have far-reaching (and unforeseen) consequences.

For species that have relatively small geographic range sizes, the key threatening process likely to adversely affect butterfly populations at present is decline of ecological resources (larval food plants and/or habitat) through inappropriate fire regimes, especially an increase in the frequency and extent of dry season burns. At present, the fire frequency in many tropical savannahs of northern Australia, particularly in the higher rainfall areas, is far too frequent, such that relatively long unburnt habitat (more than five years) is now rare in the landscape (less than 3 per cent of the total area) (Andersen et al. 2005, 2012; Russell-Smith and Yates 2007). Habitat loss and fragmentation are also a concern, particularly for *Ogyris iphis doddii* and *Hypochrysops apelles* ssp. 'Arnhem Land'. However, other threats may become significant in future, such as the ongoing invasion of grassy weeds—particularly gamba grass (*Andropogon gayanus*) and mission grasses (*Cenchrus pedicellatus* and *C. polystachios*)—and the concomitant grass–fire cycle (Rossiter et al. 2003; Douglas and Setterfield 2005; Setterfield et al. 2010, 2013), especially for specialist species inhabiting savannah woodland, riparian

woodland/open forest and the edges of riparian monsoon forest. The African gamba grass currently poses the greatest invasion threat due to substantial changes in community structure, fuel loads and impacts on fire regimes, and has been listed as a key threatening process under Commonwealth legislation. Habitat loss due to the expanding pastoral, agricultural/horticultural and mining industries is likely to have a detrimental effect on savannah woodland specialists in future (Garnett et al. 2010), and impacts on butterfly populations (their abundance and/or occupancy) will need to be carefully monitored. The long-term viability of patches of monsoon forest and the disproportionately rich butterfly assemblages they support may ultimately depend on reducing the frequency and intensity of fire in the surrounding matrix (Bowman 2000), as well as maintaining connectivity; any loss or decline of essential pollinators and seed dispersers or impediments that reduce their ability to move effectively between patches may have detrimental consequences (Russell-Smith and Bowman 1992).

The effects of global climate change and the response or resilience of tropical butterflies to such change are presently unclear. Predictions are that atmospheric carbon dioxide concentrations will continue to increase, leading to promotion of woody vegetation (monsoon forest) over grass (savannah woodland); sea level will rise, which will most likely impact the extent of coastal floodplains; and cyclones will become more intense, which will likely render patches of monsoon forest more susceptible to weed invasion. The impacts of increased temperature and rainfall, however, are less certain (Garnett et al. 2010). The recent catastrophic loss of large areas of mangrove communities in the Gulf of Carpentaria—due possibly to a combination of above-average temperatures and successive poor wet seasons—is indicative of the rapid and extensive environmental change that may be triggered more frequently in the future by escalating global climate change.

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