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Coasting along to a wider range: niche conservatism in the recent range expansion of the Tawny Coster, *Acraea terpsicore* (Lepidoptera: Nymphalidae)

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Abstract

Aim: The Tawny Coster *Acraea terpsicore* is a highly mobile butterfly that has recently expanded its spatial distribution from South Asia to South-East Asia and Australia. Here, we determine if the realized climatic niche has changed during the expansion and analyse the geographic pattern of spread in Australia.

Location: Asia and Australia.

Methods: We collated occurrence records, divided the geographic range into three spatio-temporal phases (pre-expansion, early-expansion and late-expansion) and then developed ecological niche models for each phase. To determine whether the realized niche has changed during the range expansion, we performed a principal component analyses and niche overlap analysis. Finally, we calculated the annual rate of range expansion to estimate the speed and pattern of geographic spread.

Results: The climatic niche of *A. terpsicore* differs only slightly in the pre-expansion and late-expansion ranges and was most distinct in the early-expansion range. The species' range in Australia expanded at an average rate of ~ 135 km/year (range: 34–359 km/year). Female-biased migration occurred in north-eastern Queensland at the leading edge of the range, the first documentation of this phenomenon in butterflies.

Main Conclusions: *Acraea terpsicore* represents one of the fastest documented geographic range expansions of any species, highlighting how rapidly butterflies can colonize new areas, even where environmental conditions are substantially different to those in their original distribution. However, we found little evidence of climatic niche shift, and only a minor niche shift is apparent in the early-expansion and late-expansion ranges. It remains unclear what triggered the sudden expansion, but it has been hypothesized that tropical deforestation provided conditions that initiated local range expansion, and further work on the possible mechanisms involved is required.

KEYWORDS

biological invasion, butterfly, climate change, ecological niche modelling, niche shift, sex-biased migration

1 | INTRODUCTION

The distribution of many species is changing, in response to climate change and habitat deterioration (Chown et al., 2007; Lenoir et al., 2010; Lenoir & Svenning, 2015; Nieto-Lugilde et al., 2015; Parmesan, 2006; Walther et al., 2009). Such changes have been observed in many taxonomic groups, including insects (Forister & Shapiro, 2003; Furlong & Zalucki, 2017; Parmesan et al., 1999), mammals (Moritz et al., 2008), birds (Maclean et al., 2008) and amphibians (Davies et al., 2019; Urban et al., 2008). The climatic niche is the range of environmental conditions in which a species can sustain itself (Broennimann et al., 2007; Guisan et al., 2014), and it can be maintained in the face of a changing climate (niche conservatism), or it might adjust to the new conditions at a location (niche shift) (Broennimann et al., 2007; Guisan et al., 2014; Peterson, 2011; Wiens et al., 2010; Wiens & Graham, 2005). Spatial models predicting species' potential range and changes in species' geographic distribution in response to climate change or habitat alteration often assume that when a species encounters suitable conditions it will be able to persist (Fleishman et al., 2001; Peterson et al., 2001; Sykes et al., 1996), although it is known that when only a small fraction of a landscape is habitable, species might colonize very slowly (Collingham & Huntley, 2000), or extinctions due to Allee effects might occur (Blackburn et al., 2015; Liebhold et al., 2016; Liebhold & Tobin, 2008; Taylor & Hastings, 2005; Tobin et al., 2011).

Many analyses assume niche conservatism when modelling range expansion, especially in the case of non-native species which can be detrimental to biodiversity, industry and human health (Kriticos et al., 2015; Pearman et al., 2008; Wiens et al., 2009; Clark et al., unpublished data). Yet, many invasive animal species are able to occupy climatic conditions in their newly invaded range that differ markedly from those in their original range (Araújo et al., 2013; Broennimann et al., 2007; Guisan et al., 2014; Hill et al., 2013; Tingley et al., 2014), although such climatic niche shifts appear to be rare among terrestrial plants (Petitpierre et al., 2012). Distinguishing niche shift from niche conservatism is an important aspect of understanding the responses that species make to changing conditions, such as climate, and can help predict future speciation and biological invasion events (Lockwood et al., 2005; Fridley et al., 2007; Sax et al., 2007; Kearney et al., 2008; van Klinken et al., 2009; McGeoch et al., 2010; Early & Sax, 2014; Ricciardi et al., 2017; Sutherland et al., 2018). In addition, invasive species are often considered habitat generalists due to their ability to thrive in a wide range of habitats (Marvier et al., 2004; Richardson et al., 2000). In that sense, habitat specialists appear more prone to extirpation, although Franco et al. (2006) showed that both specialists and generalists can be vulnerable to sudden environmental change. It is often hard to predict the future distribution of species with large geographic ranges, especially when the range is expanding. Yet, we have limited information on whether non-invasive expanding species show niche conservatism or niche shift.

Here, we investigate the climatic niche for a range-shifting species, the Tawny Coster *Acraea terpsicore* (Linnaeus), and its geographic pattern of spread, particularly in Australia. A range-shifting species is "a species tracking its environmental niche through a range expansion or relocation beyond its historical native range" (Wallingford et al., 2020). *Acraea terpsicore* was until recently considered endemic to the Indian subcontinent (India, Bangladesh and Sri Lanka – Chowdhury et al., 2017; Larsen, 2004; van der Poorten & van der Poorten, 2016; Wynter-Blyth, 1957), but during the past few decades it has naturally and rapidly expanded its geographic range, with chronological records from the following countries (years): Thailand (1984–1988: Nishimura, 1994; Takanishi, 1988; West, 1996), Nepal (<1989: Smith, 1989), Malay Peninsula (1992: Arshad et al., 1996), Vietnam (1992: Nishimura, 1994; Pierre & Bernaud, 1997), China (Hainan) (1994: Chou, 1994; Huang, 2002), Singapore (2006: Khew, 2008), Indonesia (2008–2011: Braby et al., 2014a; Matsumoto et al., 2012), Timor-Leste (2012: Braby, Bertelsmeier, et al., 2014), Australia (2012: Braby, Bertelsmeier, et al., 2014; Braby, Thistleton & Neal, 2014; Sanderson et al., 2012), Laos (2012: Nakamura & Wakahara, 2012); Pakistan (2012: Mal et al., 2014), Cambodia (2013: Braby, Thistleton, & Neal, 2014), Bhutan (2014: Nidup, 2015) and Malaysian Borneo (2016: Abang et al., 2017).

Acraea terpsicore was first recorded from Australia near Darwin in the Northern Territory in April 2012 (Braby, Bertelsmeier, et al., 2014; Sanderson et al., 2012), and the species has continued to expand its distribution across the Australian continent. After colonizing Darwin, the butterfly rapidly spread to areas to the south and east, and then to the Kimberley region in Western Australia (Braby et al., 2018; Braby, Thistleton, & Neal, 2014). In 2016, the first adults crossed the Gulf of Carpentaria and appeared on the western coast of Cape York Peninsula in northern Queensland (Wilson, 2016) and the southern Torres Strait (Ham, 2020); it then quickly spread to the eastern coast of Queensland (Dunn & Petrie, 2017; Dunn & Woodger, 2017; Field, 2017; Franklin et al., 2017; Miller, 2017). Given the abrupt shift in the direction of the colonization, and the very rapid eastward transition, Field (2017) proposed that unusual hot and strong westerly to northerly winds during Severe Tropical Cyclone Debbie propelled many butterflies in that direction and thus was responsible for the arrival of the species in the coastal areas of north-eastern Queensland. Dunn and Woodger (2017) also speculated that the arrival of the species further south in Townsville (in April–May 2017) was related to wind currents from Cyclone Debbie. However, these hypotheses have not been tested, and the timing of the two events may have simply been a coincidence.

It is not entirely clear how *A. terpsicore* became established in South-East Asia (Indo-China). Braby, Bertelsmeier, et al. (2014) outlined four main hypotheses: (a) the species naturally expanded its range out of India/Bangladesh and colonized Thailand via Myanmar (Burma); (b) the species was accidentally introduced into Thailand from the Indian subcontinent; (c) the species was intentionally introduced into Thailand for the commercial butterfly house industry from which it escaped; and (d) the species always existed in Thailand and Vietnam, but has since become

more abundant and widespread as a result of habitat modification. Given the sudden and massive range expansion in South-East Asia, we suspect the first hypothesis is more likely and this may have been facilitated by substantial habitat loss and modification in Indo-China because the butterfly exploits ephemeral or disturbed habitats. Regardless of the mechanism of initial colonization, the species is now on the move and coasting along to a wider range. We have three aims: (a) to study the range expansion of *A. terpsicore* to determine whether it is colonizing a new climatic niche space (niche shift) or maintaining the same niche (niche conservatism); (b) to describe the rate and geographic pattern of its recent spread in Australia; and (c) to establish whether migration is associated with the leading edge of the range expansion.

2 | METHODS

Australia has a highly variable and mostly semi-arid climate (Head et al., 2014), and during the past 140 years, there have been 12 incursions by nine species of butterfly, of which only two species—Monarch *Danaus plexippus* (Zalucki & Clarke, 2004) and Cabbage White *Pieris rapae* (Jones et al., 1980; Peters, 1970)—have become established (Braby, Bertelsmeier, et al., 2014). At least seven butterfly taxa from the Oriental/Pacific regions have reached the continent as rare vagrants/visitors; however, there are no breeding records of those species (Braby, Bertelsmeier, et al., 2014). *Acraea terpsicore* represents only the third butterfly species to have recently successfully colonized and become established on the Australian continent.

Acraea terpsicore is a medium-sized butterfly with a reddish-orange (males) or orange-brown (females) colouration, although occasionally females are similar in colour to males. Adults generally fly 1–3 m above the ground but are capable of higher and more powerful bouts of flight (Braby, 2016). It completes several generations annually, and in northern Australia, it is most abundant during the wet season and early-dry season (Braby et al., 2018). Larval food plants include Passifloraceae, Violaceae and Cucurbitaceae (Braby, Thistleton, & Neal, 2014; Kehimkar, 2008; Khot & Gaikwad, 2011). In Australia, the butterfly mainly utilizes *Hybanthus enneaspermus* and, in the Northern Territory, occasionally the "Top End" form of stinking passionflower, *Passiflora foetida* (Braby et al., 2018; Braby, Thistleton, & Neal, 2014). In Queensland, it has been more commonly found breeding on *Passiflora* spp., including *P. aurantia* and the Queensland form of introduced *P. foetida*.

We collated occurrence records from across the known geographic distribution of *A. terpsicore* and then developed ecological niche models for three different parts of its range: (1) pre-expansion, before 1984 (India, Bangladesh and Sri Lanka); (2) early-expansion, mainly from 1984 to 2011, but including recent records in 2012–2016 (South and South-East Asia); and (3) late-expansion, from 2012 to present (Australia). These models were then used to investigate the geographic spread into Australia, and to assess whether the species is maintaining its original realized climatic niche or is adjusting to a new niche.

2.1 | Occurrence data

Multiple sources were used to build a global database of occurrence records of *A. terpsicore* (see Supporting Information). Initially, we downloaded records from GBIF (Global Biodiversity Information Facility) and ALA (Atlas of Living Australia), and supplemented these with additional records collated from the literature. However, there were relatively few records from the pre-expansion range (India, Bangladesh and Sri Lanka), and so we sought reports from social media posts by amateur observers ("citizen scientists"). Records were excluded where a specific and identifiable locality was not mentioned. Geographic coordinates were determined by searching atlases and gazetteers, and records were discarded in cases where geographic locations could not be confidently assigned. For locations without geo-coordinates, we estimated the coordinates for the locality using Google Map with a spatial precision of up to 50 km. Finally, we included personal observations from Bangladesh (SC) and Australia (MFB), as well as those derived from correspondence with naturalists and entomologists (see Acknowledgements). Overall, the total number of spatial (i.e. unique occurrence) records for our dataset was 1,203.

To study the geographic spread of *A. terpsicore* in Australia, all occurrence records from 9 April 2012 (when the butterfly was first detected) to 31 December 2019 were collated. The data consisted of four main sources: (a) observations, (b) photographs, (c) specimens and (d) the scientific literature. The major source of data was from photographs (e.g. in iNaturalist where there is a robust community review process before a record is considered research grade). Observation records were not strictly moderated beyond the processes embedded in each of the underlying sources, so there is potential for some uncertainty in the data. However, given the distinctiveness of *A. terpsicore*, and the absence of extreme outliers in the dataset, we consider the error rate in underlying data to be very low and not significant.

2.2 | Ecological niche modelling

Ecological niche modelling is a technique that is used to analyse and predict the probable distribution of species in terms of various explanatory variables (Elith et al., 2006, 2011; Guisan & Zimmermann, 2000), and has become a key tool in macroecological studies (Araújo et al., 2019; Hanson et al., 2019; Norberg et al., 2019). Such models have been widely used to predict the distributions of widespread species, as well as species that have been accidentally or deliberately introduced into new geographic areas (Elith et al., 2006, 2011; Guisan & Zimmermann, 2000; van Klinken et al., 2009; Thuiller et al., 2005, 2006).

We used MaxEnt (Phillips et al., 2017) in R (version 3.5.3) (R Core Team, 2013) to model the global distribution of *A. terpsicore*. Prior to model fitting, records were removed from the database using the "CoordinateCleaner" package (Zizka et al., 2019) in cases where: (a) they duplicated an existing record; (b) they had imprecise or invalid

coordinates; or (c) they were assigned to a country inconsistent with the position of the coordinates. We used 19 bioclimatic variables concerning rainfall and temperature with a spatial resolution of 2.5 min (~21.63 km^2) which were downloaded from the WorldClim database (https://worldclim.org/data/worldclim21.html).

The model was tuned using three feature class combinations: "L," "LQ" and "LQP" (Phillips et al., 2017) and two regularization multipliers (1, 2) using the ENMeval package (Muscarella et al., 2014). The regularization multiplier imposes a penalty for including additional parameters, while feature classes control the response curve shape (Araújo et al., 2019). We selected the best predictive model by calculating the AUC value (area under a receiver operating characteristic—ROC—curve), which shows how well the model fits the data (Elith et al., 2011; Jiménez-Valverde, 2012; Phillips & Dudík, 2008). If the AUC value lies between 0.7 and 1.0, it indicates a well-fitted model that is substantially better than random (Phillips & Dudík, 2008). The contribution of each variable to the overall model was estimated, and the species distribution model was thresholded by maximizing the sum of the sensitivity and specificity statistics (Liu et al., 2005).

2.3 | Climatic niche overlap

As noted above, occurrence records were grouped into three phases, reflecting the major spatio-temporal stages of the range expansion: (a) pre-expansion (original range in South Asia, before 1984), (b) early-expansion (range in South and South-East Asia outside original range, mainly between 1984 and 2011) and (c) late-expansion (range in Australia, from 2012 to 2019). To identify whether *A. terpsicore* is maintaining the pre-expansion niche or colonizing new environmental conditions, we performed a principal component analysis (PCA) and calculated the niche overlap in R (version 3.5.3). We built a principal component analysis from the values of the climate variables at each cell (~22 km^2) with one or more occurrence points. We removed one variable (BIO 16: Precipitation of Wettest Quarter) from the analyses as there were no values for more than 50% of the cells.

To calculate the percentages of niche overlap between the pre-expansion, early-expansion and late-expansion ranges, we overlapped the ecological niche map from each spatio-temporal region and used the "nicheOverlap" function in the "dismo" package in R (Hijmans et al., 2017).

2.4 | Range expansion in Australia

To determine how the spatial distribution of *A. terpsicore* has changed since it was first detected in Australia near Darwin in 2012, we constructed convex hulls for each yearly accumulated distribution using ArcMap (version 10.7.1). We then calculated the spatial range by accumulating records up to and including each year—thus, the spatial map for 2013 included all the data points for 2012 and 2013; the spatial map for 2014 included all the data points for 2012, 2013 and 2014, and so forth; see Gupta et al. (2020) for the rationale. These polygons included unsuitable habitats because they encompass all the known, inferred or projected sites of present occurrence of the taxon. After developing the convex polygons for each year, we modified the convex hull boundaries using the "Editor" tool of ArcMap according to the criteria developed by Braby et al. (2018) to estimate the geographic range. Areas in the polygon were included if they were located within a specified distance or had intervening larval food plant records. Thus, the distribution was considered to be continuous when spatial records within the geographic range were up to 200 km apart, with or without intervening larval food plant records, or 200–500 km apart, but only with intervening larval food plant records. Conversely, distribution records were considered to be disjunct or isolated when the closest points were separated by 200 km or more and there were no intervening larval food plant records, or when the closest points were separated by more than 500 km and there were intervening larval food plant records. Different distance rule sets and thresholds were applied to the lower rainfall areas of the semi-arid zone (350–700 mm: 750 km) and arid zone (≤350 mm: 1,000 km) to account for the low sampling effort in these areas. Areas in the ocean were excluded, and areas near the coast (i.e. within 150 km of the coastline) and nearby small islands that fell outside the line joining two distribution records were included in the geographic range, but only if the larval food plant was present or if the butterfly would be expected to occur in the intervening area based on expert opinion.

To calculate the rate of range expansion, we used two different approaches. First, we calculated the centroid of the range polygon for each year (time slice) and then measured the distance from the first record to each successive centroid. Second, we used the accumulated records—the same procedure that we used to construct the convex hull—and then calculated the mean distance from the first record point to the convex hull edges. We then considered the average of these two methods as an estimate of the rate of expansion.

3 | RESULTS

3.1 | Climatic niche space

The ecological niche modelling of environmental suitability indicated that the extant distribution of *A. terpsicore* closely matched each of the three phases of the geographic range (Figure 1). Models had an AUC of 0.96 for the pre-expansion range, 0.95 for the pre-expansion plus early-expansion range and 0.93 for the overall distribution, indicating excellent performance with low rates of commission error. Qualitative comparison of the models indicated that the overall model (i.e. based on all occurrence records for the three geographic range phases) best fitted the observed data (Figure 1d). In contrast, the models generated using records from the pre-expansion range only (Figure 1b), or from the pre-expansion and early-expansion range combined (Figure 1c), did not predict the late-expansion distribution as accurately. However, all models (Figure 1b–d) generally under-predicted the range in South-East Asia and Australia, only

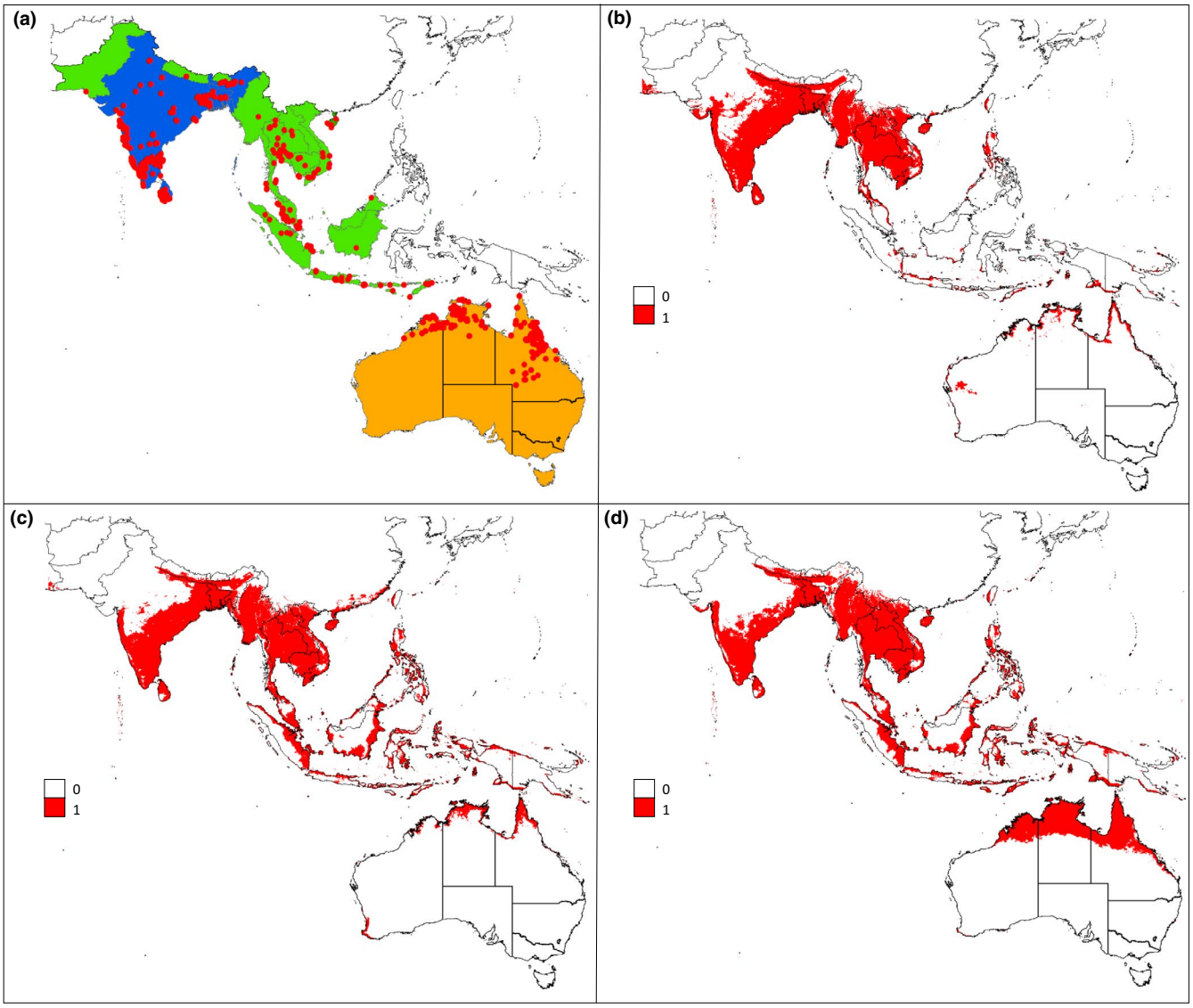

FIGURE 1 Distribution of environmental suitability for *A. terpsicore* using models constructed from (a) the three geographical regions, with blue depicting the pre-expansion range (India, Bangladesh and Sri Lanka), green the early-expansion range (South and South-East Asia), and gold the late-expansion range (Australia); (b) records from the pre-expansion range only; (c) records from the pre-expansion and early-expansion range; and (d) records from the pre-expansion, early-expansion and late-expansion range. The binary colour bar indicates environmental suitability (1 = suitable; 0 = unsuitable). Red dots show the location of each occurrence record (see Supporting Information)

partially covering the "known" distribution (Figure 1a), suggesting that the species occurs in environmental space that is partially novel in some parts of South-East Asia and Australia, at least in comparison with its pre-expansion distribution in South Asia. These results suggest that the environmental conditions occupied by *A. terpsicore* in Australia (late-expansion range) are rather similar to those in India, Bangladesh and Sri Lanka (pre-expansion range), but slightly dissimilar to those in South and South-East Asia (early-expansion range).

The principal component analysis showed that a broad range of environmental conditions was occupied across the species' geographic range (Figure 2). The environmental conditions for data points within the early-expansion and late-expansion ranges were nested within the overall conditions for the pre-expansion range. The niche overlap analysis showed that 83% of the early-expansion and late-expansion distribution fits within the pre-expansion range.

3.2 | Range expansion in Australia

Since first being discovered in Australia near Darwin in April 2012, *A. terpsicore* has expanded its range extensively (Figure 3a). Initially, the expansion in the Northern Territory was towards the east and south of the Top End, although by 2013 it had already colonized the eastern Kimberley of northern Western Australia (WA) to the south-west of Darwin. By 2014, it occupied the entire Top End, and in the following year (2015) its range included much of the Kimberly

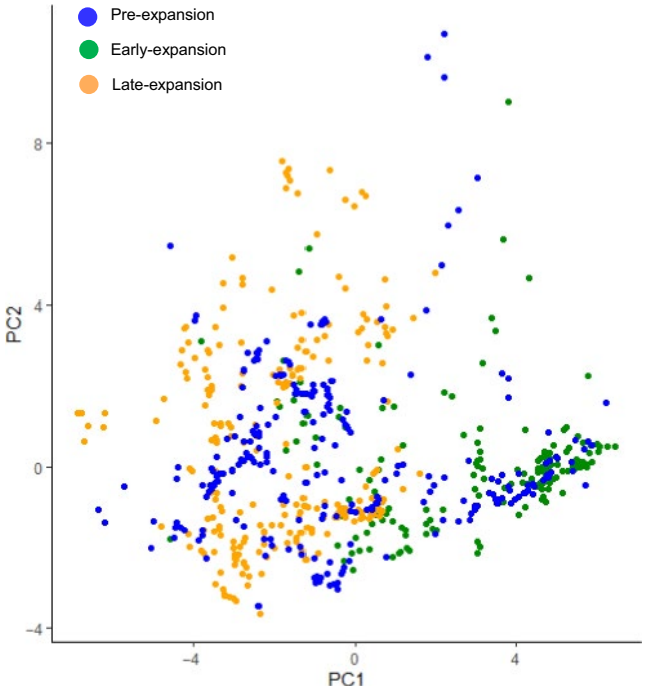

FIGURE 2 Principal component analysis representing the environmental conditions occupied by *A. terpsicore* in the pre-expansion range (India, Bangladesh and Sri Lanka), early-expansion range (South and South-East Asia) and the late-expansion range (Australia)

region. It was first detected at Broome, WA in the Kimberley on 26 September 2015 (G. Swann, personal communication), which represents the south-western-most limit of the species' range. In 2016, it spread rapidly eastwards and crossed the Gulf of Carpentaria, reaching Horn Island in the southern Torres Strait, QLD by February of that year (Ham, 2020) and western Cape York Peninsula in northern Queensland (QLD) by August (Wilson, 2016). Once it reached Queensland, the species moved with astonishing speed and colonized the entire area of northern Queensland within two years (i.e. by 2018), as well as inland areas in south-western Queensland in the semi-arid and arid zones, including the Barcoo River and Welford National Park (by March 2017, S. Bond, personal communication). By 2019, the range continued to expand into the Gulf Country and semi-arid areas of inland Queensland (Figures 3a, 4a). In Queensland, the current south-eastern-most extent of the species' range is Nebo (R. Richter, personal communication) and the south-western-most extent is Barcoo Shire (J. Beer, personal communication).

There may well have been multiple entries of the species into Australia; however, this is unlikely to have affected the overall pattern of spread across northern Australia because of the directionality. The butterfly has largely been moving south and east, and the nearest source of colonization of Australia is to the north-west of the continent (i.e. Timor and Lesser Sunda Islands). Certainly, the expansion into the Kimberley appeared to be from the Top End rather than from Indonesia based on the chronology of data points 2013–2015. However, there may well have been multiple colonizations in northern Queensland from the Northern Territory (Top End) across the Gulf of Carpentaria in 2016 (Figure 3a suggests two colonization events). Interestingly, the pattern of colonization and subsequent spread in Cape York Peninsula was via the ocean rather than via land in the Gulf of Carpentaria.

Overall, the average expansion rate in Australia was ~ 135 km/year, with the highest rate observed in 2017 (~359 km/year) (Figure 3b). Of the available breeding records (n = 38) in Australia (Figure 4a), most were from north-eastern Queensland (particularly Cairns and Townsville), but there was also evidence of breeding in the Kimberly and the Top End of the Northern Territory (mainly around Darwin).

3.3 | Migration

There were 20 records of migration (Table 1), all of which coincided with the arrival of the species in north-eastern Queensland in 2017 (Figure 4b). The first published report of directional movement was by Field (2017) who recorded large numbers moving SSE (up to 45 adults per hour across a 50 m transect) in the Cairns area on 28 March 2017, although adults were first noted migrating ENE five days earlier near Georgetown on 23 March 2017 (J. Booij, personal communication). Subsequently, numerous reports of migration were recorded over the next two weeks, but the migration continued up until at least early June (Table 1). The most spectacular movement was recorded at Greenvale on the 2 April 2017 by MF Braby and LJ Aitchison who noted large numbers of butterflies flying ESE at the rate of approximately 438 individuals per hour across a 50 m transect. At this site, it was estimated that the butterflies were flying at a velocity of approximately 10 km per hour. Around the same time, S. Bond (personal communication) observed large numbers of *A. terpsicore* at the Welford National Park (Welford Waterhole, Lochern National Park and the Barcoo River south of Longreach and Stonehenge, QLD), which are more than 500 km SSW of Greenvale. The simultaneous occurrence of mass movements of adults over such a wide area (from Cairns to Bowen, and inland to Georgetown, QLD) suggests that migration may be involved in the range expansion. Moreover, the occurrence of the butterfly in the Channel Country of inland south-western Queensland in 2017 (Figure 3a) suggests the migration had pushed the species' range far beyond its predicted climatic envelope (Figure 1d).

[Correction added on 7 December 2020, after first online publication: the figure citation has been updated.]

4 | DISCUSSION

Acraea terpsicore has rapidly expanded its range well beyond its original distribution in the Indian subcontinent to colonize South-East Asia and the Australian continent over the past four decades. Initially, we hypothesized that this butterfly may have shifted or adapted to a new distinct niche by colonizing new environments given the substantial extent of its spatial expansion, but PCA and niche overlap analyses indicate that it is largely occupying the same realized niche in different zoogeographical regions. Initially, the niche shifted slightly, reflecting the new conditions in some parts

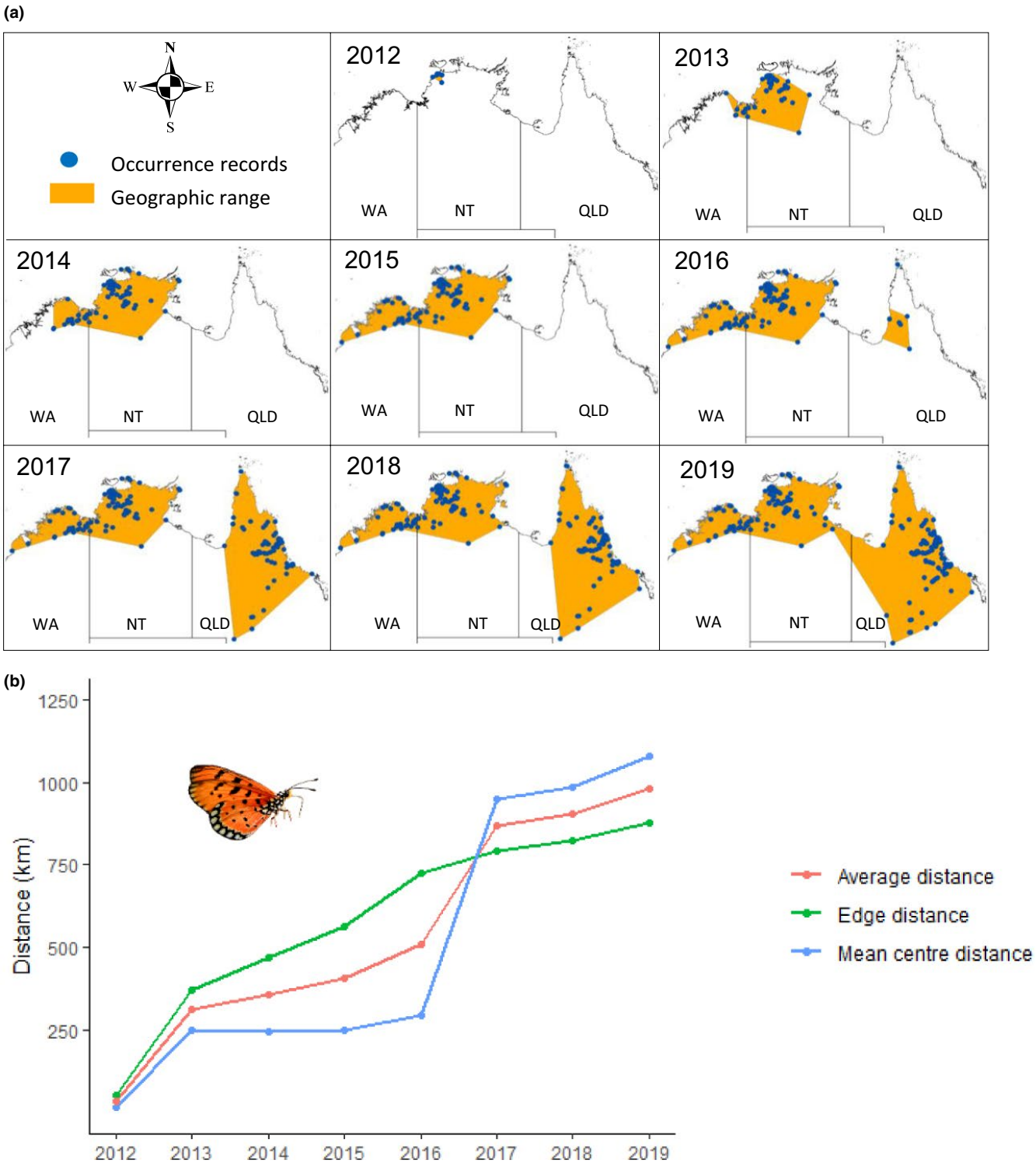

FIGURE 3 Range Expansion of *A. terpsicore* in Australia, showing: (a) temporal changes in the geographical range between 2012 and 2019. Polygons incorporating cumulative records are shown for each year. "WA" is "Western Australia," "NT" is "Northern Territory" and "QLD" is "Queensland." (b) Summary statistics of the rate of spread. "Edge distance" is the distance between first record in Australia and each edge of the convex hull, "Mean centre distance." is the distance between the first record and each year's mean centre of the polygon(s), and "Average distance" is the average of "Edge distance" and "Mean centre distance"

of South-East Asia, but it now occupies conditions in Australia that are relatively similar to those in its pre-expansion distribution in the Northern Hemisphere, suggesting niche conservatism. The only possible exception to this is in the semi-arid and arid zones of south-western Queensland (Channel Country) where the mean annual rainfall is below 400 mm. In this area, the species is largely restricted to ephemeral riparian habitats (Ham, 2020), and it remains uncertain whether it is permanently established there. It is possible

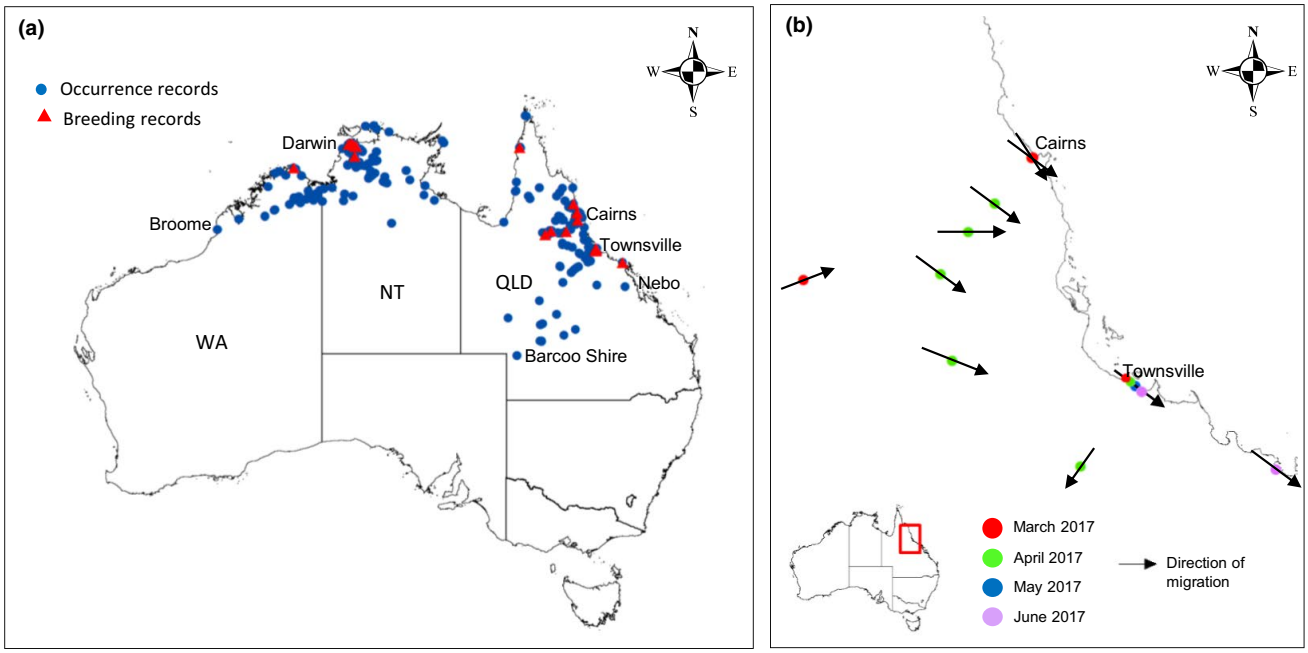

FIGURE 4 Spatial, breeding and migration records of *A. terpsicore* in Australia. (a) total occurrence records, 2012–2019, with red triangles representing confirmed breeding records (mating or immature stages), "WA" is "Western Australia," "NT" is "Northern Territory" and "QLD" is "Queensland"; and (b) migration records in 2017, with colours representing month and arrows representing the direction of migration

that *A. terpsicore* colonizes the Channel Country periodically, breeding temporarily along watercourses but only after good wet seasons.

When predicting the extent of an expansion or invasion, "climate-matching" is a common approach, which is predicated on the species maintaining its original ecological niche when colonizing a new habitat (Peterson, 2003). For example, using museum records and climate data, Peterson et al. (1999) developed climatic niche modelling for 37 sister taxon pairs of birds, butterflies and mammals and found that many species show niche conservatism. More recently, Cardador and Blackburn (2020) showed that alien birds tend to maintain their original (native) niche in their new (alien) ranges. In contrast, Fitzpatrick et al. (2007) showed that when fire ants (*Solenopsis invicta*) are first introduced and become established in a new area, they invade areas that are similar to their original niches, but then they expand into a new niche, which is colder and drier and mostly dissimilar to their original niche. These limited studies suggest that there may be differences between range-shifting species and invasive species, with niche conservatism predominating in range shifters like *A. terpsicore* and niche shifting occurring in invasive species. Note we follow the definition of Wallingford et al. (2020) for invasive species, which is "an introduced species (i.e. a non-native species transported to a new ecosystem by humans intentionally or unintentionally) that causes negative ecological, economic or environmental impacts".

From the principal component analysis, most of the bioclimatic variables were strongly correlated, but the variables with the highest correlations were bio7 (temperature annual range, $r = -0.96$) and bio-4 (temperature seasonality, $r = -0.91$) for PC1 and bio1 (annual mean temperature, $r = -0.95$) and bio-10 (mean temperature of the warmest quarter, $r = -0.85$) for PC2. Both the early-expansion range (South and South-East Asia) and late-expansion range (Australia) overlapped 83% of the pre-expansion (South Asia) climatic niche. The partial niche shift for *A. terpsicore* suggests that there might be some implications in terms of changes to ecological process (e.g. competition with *Acraea andromacha*, herbivory of the native larval food plant and possibly pollination of some plants), which could lead to changes in the realized niche over ecological and evolutionary time (Broennimann et al., 2007).

Considering the extensive logging of tropical forests in South-East Asia, Braby, Bertelsmeier, et al. (2014) hypothesized that deforestation led this species to colonize initially into new areas (disturbed habitats). In the Sundaland biodiversity hotspot (which includes the Malay Peninsula, Sumatra, and Java, as well as Borneo), more than 92% of the original extent of primary vegetation has been lost (Myers et al., 2000). Such land-use changes have led to profound losses of, and threats to, South-East Asia's unique tropical biodiversity. In contrast, for habitat generalists or pioneer species like *A. terpsicore*, extensive deforestation and agricultural expansion and to a lesser extent, urbanization, during the past few decades may have provided conditions favourable for colonization and ultimately range expansion (Braby, Bertelsmeier, et al., 2014; see also Halsch et al., 2020 regarding the Gulf Fritillary butterfly *Agraulis vanillae*). However, we cannot test this hypothesis with our data and analysis.

Breeding records in several different parts of the range in Australia (Kimberly, Top End and northern Queensland) suggests that *A. terpsicore* is not only well established, but probably breeds throughout most of its geographic range on the continent (Figure 4a) based on the co-occurrence of its major larval food plant *Hybanthus enneaspermus*. [Correction added on 7 December 2020, after first online publication:

TABLE 1 Records of migration of *Acraea terpsicore* in northern Queensland during 2017 [Correction added on 11 December 2020, after first online publication: table has been modified.]

Location	Date	Observer	Migration direction	Comments
20 km E of Georgetown (18°17'21"S, 143°42'52"E)	23 MARCH 2017	J. Booij	ENE	12 adults observed flying over 2.5 hr period
Georgetown	24 MARCH 2017	J. Booij	ENE	4 adults observed flying during the morning
Cairns Esplanade (16°55'07"S, 145°46'46"E)	28 MARCH 2017	Field (2017)	SSE	7–8 adults per 10 min/50 m transect (09:30–09:55 hr) = 45 adults per h/50 m
Smithfield, Cairns (16°49'08"S, 145°41'51"E)	28 MARCH 2017	Field (2017)	SSE	0–6 ($\bar{x} = 3.5 \pm 3.00$ *SD*) adults per 10 min/50m transect (10:30–11:25 hr) = 21 adults per h/50 m. Sex ratio (F:M) of migration was female biased at 13:5
Half-moon Creek, Cairns (16°48'02"S, 145°42'42"E)	28 MARCH 2017	Field (2017)	SSE	1–5 adults per 10 min/50 m transect (11:40–12:10 hr) = 18 adults per h/50 m
Smithfield, Cairns (16°49'08"S, 145°41'51"E)	29 MARCH 2017	Field (2017)	SSE	0–1 adults ($\bar{x} = 0.25 \pm 0.50$ *SD*) per 10 min/50 m transect (07:00–07:25 hr, 10:30–11:10 hr) = 1.5 adults per h/50 m
Smithfield, Cairns (16°49'08"S, 145°41'51"E)	29 MARCH 2017	Field (2017)	NNW	0–1 adults ($\bar{x} = 0.25 \pm 0.50$ *SD*) per 10 min/50 m transect (07:00–07:25 hr, 10:30–11:10 hr) = 1.5 adults per h/50 m
Kelso, 17 km SW of Townsville	30 MARCH–5 APRIL 2017	Dunn and Petrie (2017)	SE	Many hundreds observed passing through during the week in constant direction
Half-moon Creek, Cairns (16°48'02"S, 145°42'42"E)	31 MARCH 2017	Field (2017)	SSE	1–3 adults ($\bar{x} = 1.0 \pm 1.41$ *SD*) per 10 min/50 m transect (08:10–10:00 hr) = 6 adults per h/50 m
Half-moon Creek, Cairns (16°48'02"S, 145°42'42"E)	31 MARCH 2017	Field (2017)	NNW	0–1 adults ($\bar{x} = 0.75 \pm 0.50$ *SD*) per 10 min/50 m transect (0810–1000 hr) = 4.5 adults per h/50 m
Cairns, Grove St (Paramatta Park) (16.91991°S, 145.75682°E)	31 MARCH 2017	M.F. Braby	SE	c. 10 adults observed flying in consistent direction over 1 hr period (13:00–14:00 hr). Migration sex-biased (all female)
Herberton	1 APRIL 2017	M.F. Braby, L.J. Aitchison & D.C. Franklin	SE	Several adults observed flying in consistent direction around midday. Migration sex-biased (all female)
Forty Mile Scrub NP (18.10931°S, 144.82555°E)	2 APRIL 2017	M.F. Braby & L.J. Aitchison	SE	Many adults observed flying in consistent direction during morning. Migration sex-biased (all female)
4 km W of Greenvale (18.99705°S, 144.94604°E)	2 APRIL 2017	M.F. Braby & L.J. Aitchison	ESE	12–19 ($\bar{x} = 14.6 \pm 3.58$ *SD*) adults per 2 min/50 m transect (13:50–14:00 hr) or 73 adults per 10 min/50 m = 438 adults per h/50 m. Migration sex-biased (all female)
Charters Towers (20.076°S, 146.258°E)	3 APRIL 2017	M.F. Braby & L.J. Aitchison	SSW	Small numbers of adults flying in consistent direction over 0.5 hr period (12:00–12:30 hr). Migration sex-biased (all female)

(Continues)

TABLE 1 (Continued)

Location	Date	Observer	Migration direction	Comments
Lappa Junction Road (Chillagoe Road to Mt Garnet)	30 APRIL 2017	G. Sankowsky	E	Many adults observed flying in consistent direction in the morning (mostly males) and in the afternoon (quite a few females)
Townsville	8 MAY 2017	A. King	SE	1 adult observed flying in constant direction
Townsville	9 MAY 2017	L. Ring, J. Ring & A. King	SE	A few adults (males and females) observed flying in persistent and constant direction
16 km W of Bowen (20.0051°S, 148.0954°E)	6 JUNE 2017	Dunn and Petrie (2017)	SE	Female observed flying at steady speed in constant direction, not deviating despite a headwind (SSE)
Townsville-Bowen	6 JUNE 2017	Dunn and Petrie (2017)	SE	10–12 adults (both sexes) observed crossing the Bruce Hwy (c. 180 km) over 2 hr against the prevailing wind

the figure citation has been updated.] The disparity or unevenness in breeding records in north-eastern Queensland (e.g. Cairns, Townsville) compared with the Kimberly and Top End reflects the concentration of lepidopterists in those cities compared with the sparsely populated areas elsewhere in north-western and northern Australia. Moreover, the realized distribution in the monsoon tropics of northern Australia, as of 2019, closely matches the projected spatial distribution based on ecological niche modelling undertaken six years ago, particularly the 2050 global climate warming scenario (Braby, Bertelsmeier, et al., 2014). However, while global warming may be partly responsible for the range expansion, we suggest the wider distribution at present compared to the modelled distribution (under current climatic conditions) is probably due to two other factors: (a) the modelled range may have been slightly inaccurate based on limited data at that time (only 89 occurrence points); and (b) the leading edge (southern boundary) of the geographic range may actually be larger than the breeding range due to adults temporarily moving (migrating) into areas that are suboptimal (i.e. beyond its climatic niche). Further sampling and monitoring over time are required to provide a better picture of the precise geographic range boundary of *A. terpsicore*, especially the breeding range in the inland (marginal) areas of its distribution.

The colonization rate of *A. terpsicore* in Australia varied dramatically between years. Previously, authors divided the "area travelled" (straight line distance) by the "duration" (time elapsed between records) and thus, calculated the rate of expansion; however, there were substantial differences in these estimates. In the early-expansion range, Noor et al. (2017) estimated the expansion rate from Singapore to Kota Samarahan at 150 km/year and from Kota Samarahan to Sri Aman to be 100 km/year. In South-East Asia and Australia (i.e. from Thailand to Australia), Braby, Bertelsmeier, et al. (2014) estimated that the average expansion rate was ~200 km/year, with a possible increase in rate after the species reached the Malay Peninsula (from 170 km/year between 1984 and 1992 to 230 km/year between 1992 and 2012). However, once the species reached the Australian mainland, the expansion rate appeared to increase dramatically and was estimated to be 315 ± 56 km/year within 14 months of arrival (Braby, Thistleton, & Neal, 2014). Similarly, Field (2017) estimated the rate of expansion to be 334 km/year based on the spread from Darwin to Cairns between 2012 and 2016. However, all these estimates are based on data from different timeframes and point distances and do not consider changes in rate over time, which appears to be the case. Here, we followed two different procedures to calculate annual changes in distribution. The overall average expansion rate was estimated to be of 135 km/year. However, it is clear that when the butterfly entered northern Australia, the rate of expansion increased exponentially (from ~277 km/year in 2013 and 2016 to ~359 km/year in 2017), but then declined two years after arrival in Queensland (~34 km/year in 2018 and 76 km/year in 2019).

Acraea terpsicore is a highly mobile species, and migration has been recorded both in the pre-expansion range (India, Bangladesh and Sri Lanka) and late-expansion range (Australia) by several authors (Dunn & Petrie, 2017; Field, 2017; Larsen, 1988; Williams, 1927, 1930; Chowdhury et al. unpublished data). In Australia, available records of migration in 2017 showed that most individuals were moving in a south-easterly direction, aligning with the overall direction of the range expansion. This suggests that migration is involved in the range expansion, perhaps especially at the leading edge of the colonization front, and was not related to Tropical Cyclone Debbie, which occurred well before the migration records in April–June 2017. Most of the migration records of *A. terpsicore* were female-biased, and on many occasions, only females were observed migrating. These butterflies did not stop to refuel, search for the larval food plant or exhibit mating behaviour, thus meeting the classic criteria

of migration (Kennedy, 1985). To our knowledge, this is the first documentation of a female-biased migration in butterflies. Sex-biased dispersal is not uncommon, with many birds showing female-biased dispersal and mammals showing male-biased dispersal (Handley & Perrin, 2007; Moussy et al., 2013; Trochet et al., 2016). However, sex-biased migration is quite rare, having been recorded among some salmonids (Kitanishi et al., 2012), but not among butterflies.

In summary, we found no evidence of a niche shift in *A. terpsicore*. Although some partial niche shifting has occurred, this appears to be restricted to the early-expansion range in South-East Asia. While there is much overlap between the original and newly occupied environmental conditions, the species is traversing (and possibly breeding in) places where conditions are slightly different to those in the pre-expansion range. However, in northern Australia, except for inland south-western Queensland, the species now occupies environmental conditions that are relatively similar to those in its pre-expansion range in India, Sri Lanka and Bangladesh, indicating niche conservatism. The late-expansion range in Australia continues to expand, especially in the Gulf Country and inland areas of the Channel Country. However, the annual rate has clearly declined during the past two years (2018 and 2019), suggesting the climatic niche envelope is close to being fully realized, a niche which took only eight years to achieve since colonization and establishment in 2012. Migration at the leading edge of the range expansion appears to have contributed to an exponential expansion rate in Queensland during 2017. Ecological niche modelling suggests suitable environmental conditions are available in Taiwan, the Philippines, Sulawesi, Maluku and mainland New Guinea (Figure 1d), suggesting that further range expansion in future is more likely to occur in these areas of South-East Asia and lowland New Guinea rather than in Australia. The trigger for the range expansion remains unclear.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

We have attached all the spatial records in the Supporting Information, and all the other related datasets that we collected or generated during the analysis will be provided upon request.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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