Received: 31 August 2022 | Accepted: 19 November 2022

DOI: 10.1002/inc3.13

REVIEW ARTICLE

INTEGRATIVE CONSERVATION XTBG WILEY

Trends and progress in studying butterfly migration

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Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Numbers: DFG-FZT 118, 202548816

Abstract

Several hundred butterfly species show some form of migratory behaviour. Here we identify how the methodologies available for studying butterfly migration have changed over time, and document geographic and taxonomic foci in the study of butterfly migration. We review publications on butterfly migration published in six languages (English, Simplified Chinese, Traditional Chinese, Japanese, Korean, and Spanish), summarise how migration in butterflies has been studied, explore geographic and taxonomic patterns in the knowledge base, and outline key future research directions. Using English search keywords, we found only 58 studies from Asia; however, after searching in local languages, we found an additional 98 relevant studies. Overall, butterfly migration studies are mostly from North America and Europe. Most studies focus on three species: monarch (*Danaus plexippus*), painted lady (*Vanessa cardui*) and red admiral (*Vanessa atalanta*). About 62% of publications are focused on the monarch, with nearly 50% of migratory butterfly species mentioned in only a single paper. Several research methods have been applied to ascribe migratory status and to study the physiology, neurobiology, and ecology of migration; however, virtually all this research is on a handful of species. There remain hundreds of species for which we do not understand the comprehensive seasonal pattern of movement, flight destinations, wintering, or breeding grounds. A better understanding of movement ecology and migratory connectivity is needed to effectively conserve migratory butterflies. It is essential that research becomes more geographically and linguistically representative since migrants frequently cross political borders and international cooperation is necessary for their conservation.

KEYWORDS

geographic bias, literature trend, methodological advancement, migration ecology, monarch, taxonomic bias

1 | INTRODUCTION

Migration is a widespread phenomenon among animals, often timed to exploit seasonal resource availability, with periodic movement from a habitat that has become unsuitable (Dingle, 2014; Liedvogel et al., 2011). Migration can reduce the burden of parasitic infections and disease in a population by allowing individuals to escape from contaminated habitats and leave infected individuals behind: migratory butterflies with sublethal infections are less likely to migrate and/or complete the journey (Bartel et al., 2011). Migration has attracted a lot of attention from biologists and naturalists, yet much remains mysterious (Dingle, 2014). Many migratory species are declining, mostly due to habitat destruction, overexploitation of resources, and climate change (Chowdhury, 2023; Smith, 2014; Thogmartin et al., 2017; Wilcove & Wikelski, 2008; Zylstra et al., 2021).

Conserving migratory species is challenging because threats occurring at any location along the migratory route and at any stage of the life cycle can impact the entire population (Chester et al., 2022; Martin et al., 2007; Reynolds et al., 2017). This means that a whole series of intact habitats, perhaps in different jurisdictions, needs to be protected (Wilcove & Wikelski, 2008). Thus, understanding the patterns of spatial connectivity is central to conserving migratory species (Gao et al., 2020; Webster et al., 2002; Wilcove & Wikelski, 2008). While significant progress has been made in characterising and understanding migration in birds (Faaborg et al., 2010; Robinson et al., 2010), less is known about the ecology and conservation of migratory butterflies, except for a few well-known species (e.g., monarch, painted lady; Chowdhury, Fuller, et al., 2021). Migratory butterflies occur disproportionately in tropical rainforests (Chowdhury, Zalucki, et al., 2021), where deforestation is proceeding rapidly (Sodhi et al., 2010). More research is needed to determine if migratory butterflies are at acute conservation risk at any stage of their life cycle. Although Chowdhury, Fuller, et al. (2021) identified 13 lines of evidence (e.g., mass movement, breeding population not established) to ascribe migratory status to butterfly species, only a single line of evidence has been used for 92% of all diagnoses of migration in butterflies, so our knowledge remains superficial in many cases. Here we review the history of studying migration in butterflies, and the primary methodologies to study migration to facilitate the conservation of migratory butterflies.

Insects are the most speciose taxonomic class on earth (Gaston, 1991; Stork, 2018), and provide key ecosystem functions and services, as pollinators, herbivores, predators, and decomposers (Didham et al., 1996; López-Hoffman et al., 2017; Satterfield et al., 2020; Semmens et al., 2011; Yang & Gratton, 2014). They also occur in human-modified ecosystems, often as vectors of human, livestock, or plant diseases, or as herbivores that directly damage crops (Dingle, 2009; McGeoch, 1998; Reynolds et al., 2006; Walther et al., 2002). Every year, many trillions of insects migrate from one part of the world to another, often crossing international borders (Chapman et al., 2011). For example, nearly 3.5 trillion insects traverse the southern United Kingdom every year, transferring more than 3000 tons of biomass (Hu et al., 2016).

Although our current understanding of insect migrations is limited for most taxa, especially for pollinating insects, butterflies are, to some extent, an exception (Brower et al., 2006; Meitner et al., 2004; Pierce et al., 2014; Satterfield et al., 2020; Chowdhury, Fuller, et al., 2021; Chowdhury, Zalucki, et al., 2021). Yet existing knowledge is limited to a subset of migratory butterflies that have drawn more scientific attention, such as those that are diurnal, brightly coloured, and fly relatively close to the ground, making their migration easier to detect and observe (Dingle, 2014).

Previous reviews of insect migration have also been limited to English-language studies. For a biological phenomenon that occurs across continents and in hundreds or thousands of species, such as insect migration, a more comprehensive literature review across languages and sources is needed. Information on butterfly migration is often published in nonpeer-reviewed journals (i.e., grey literature) (Chowdhury, Fuller, et al., 2021), while up to one-third of scientific documents related to biodiversity conservation are published in languages other than English (Amano, González-Varo, et al., 2016). Ignoring non-English-language and grey literature can severely bias our understanding (Amano & Sutherland, 2013; Amano et al., 2021; Chowdhury, Gonzalez, et al., 2022; Egger et al., 1997; Konno et al., 2020; Møller & Jennions, 2001; Jennions & Møller, 2002a, 2002b). Chowdhury, Fuller, et al. (2021) reported >3% of butterfly species ($N = 568$) migrate, but this is probably an underestimate, as only papers in English were reviewed for that study. Chowdhury, Fuller, et al. (2021) also briefly described geographic and taxonomic biases in studies on butterfly migration. However, non-English-language literature is often found for species and in areas where little or even no English-language literature is available (Amano et al., 2021). To better understand geographic and taxonomic biases in studies on butterfly migration, we need to conduct literature searches in non-English languages.

Here we expand the recent global overview on butterfly migration (Chowdhury, Fuller, et al., 2021) by compiling relevant literature from multiple sources including both peer-reviewed and grey literature that are available in English or five other languages. To identify knowledge gaps and provide a pathway to advance our understanding of butterfly migration, we analyse trends in existing studies (geographic, taxonomic and temporal trends), describe the chronological development of studying butterfly migration, and point out where further research might be fruitful.

2 | METHODS

2.1 | Butterfly migration

Butterflies are small-bodied, usually living as adults for only a few weeks to a year (Oberhauser & Solensky, 2004), with the distances they travel during migrations varying greatly among species (Dingle, 2014). While many vertebrates migrate thousands of kilometres and individuals generally make the return journey, sometimes repeatedly throughout their lives, the situation is more complex for invertebrates (Chapman et al., 2015; Chowdhury, Fuller, et al., 2021; Malcolm & Slager, 2015; Malcolm et al., 1993, 2018; Menz et al., 2019; Stefanescu et al., 2013). Butterfly migration often entails multigenerational movement, with flights by each generation continuing for periods of days to weeks (Dingle, 2014; Holland et al., 2006; Malcolm et al., 1993; Nesbit et al., 2009; Talavera et al., 2018). For example, North American monarch butterflies travel 5000–7000 km per year, but it takes three–five generations to complete the full annual cycle. Each fall, the monarchs fly down to the Trans Volcanic Plateau of Mountains in Mexico from different parts of the United States and Canada and the spring migrants undertake the return journey from Mexico to the United States and Canada (Brower et al., 2006; Dingle et al., 2005; Malcolm, 2018).

It is challenging to define migration in butterflies, and several definitions have been offered (Chowdhury, Braby, et al., 2021). Migration encompasses phenomena at different levels of biological organisation (physiological, individual/behavioural, population/spatial/ecological) but is often characterised as a behaviour that has ecological consequences (Chapman et al., 2015; Dingle & Drake, 2007). Here we have used the definition provided by Kennedy (1985); "*Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses but promotes their eventual disinhibition and recurrence*."

2.2 | Literature search

For the literature search, we used (i) Google Scholar (https://scholar.google.com) with the keywords: 'Butterfly migration' and 'Migratory butterflies' and checked the first 100 pages, (ii) PubMed (https://pubmed.ncbi.nlm.nih.gov) with the same key words, (iii) Web of Science (Web of Science Core Collection; https://apps.webofknowledge.com) using the search string TS = (Butterf* AND migr*) with 1900–2020 as the year range, and (iv) Google (https://www.google.com) using the same keywords that we used for Google Scholar. When scanning relevant studies, we noticed that many authors published their work in local journals, especially the following four: *Atalanta* (Germany), *Phegea* (Belgium), *Bulletin of the Allyn Museum* (United States), and the *Journal of the Bombay Natural History Society* (India). Therefore, we further checked all the issues of these four journals to make the review more comprehensive. Similarly, Chowdhury, Fuller, et al. (2021) obtained some studies from the South-East Asia and the Neotropical regions, including publications in non-English languages. We, therefore, conducted searches in five additional languages. Using the equivalent of 'Butterfly migration' and 'Migratory butterflies' we searched in Google Scholar for papers in Simplified ('蝴蝶 迁徙', '蝶 类 迁徙', '迁徙性蝴蝶' and '迁徙性蝶类") and Traditional ('蝴蝶 遷徙', '蝶類 遷徙', '遷徙性 蝴蝶' and '遷徙性蝶類) Chinese, Japanese ('チョウ' '蝶', '渡り', '移動'), Korean ('이주' and '이주성 나비') and Spanish ('Mariposas migratorias' and 'Migración de mariposas'). Because some of the relevant Japanese literature may not be found using the keywords, '蝶, 渡り' and '移動', we made an additional search using the keywords, '昆虫' and '海上'.

Overall, we obtained 1097 studies; however, 172 of these studies were not relevant (e.g., not on migration, or on moths), which we excluded. We retained 925 studies, published between 1833 and 2020, that mentioned butterfly migration in the abstract, of which 581 are in English, 246 in Spanish, 59 in Japanese, 28 in Simplified Chinese, and 11 in Traditional Chinese. The complete bibliography is provided in the Supporting Information section (Table S1). From each study, we recorded the title and year published, the subject species, geographic location, and the techniques used to establish (or discuss) migratory behaviour, as well as any information provided on parameters such as migratory behaviour, density and distance travelled. To assess geographic and taxonomic patterns, we used the locality and species information and grouped them into six continents (North America, South America, Europe, Africa, Asia and Oceania).

To investigate whether interest in butterfly migration is increasing, we compared the number of papers specifically about butterfly migration to those on any aspect of butterfly biology between 1990 and 2019. Using Web of Science Core Collection (Advanced Search), we searched for papers using two keywords: 'TS = (Butterf* AND migr*)' for migratory butterflies, and 'TS = (Butterf*)' for butterflies. We only considered English-language papers, recognising that our results for this search might largely reflect patterns in North America or Europe where most English-language papers were located.

3 | RESULTS

3.1 | Chronological development of methods of studying butterfly migration

While lepidopterists have been recording insect movements for centuries, interest in butterfly migration only began in earnest at the beginning of the 20th century. The movement of millions of migratory butterflies at low altitude intrigued both professional lepidopterists and amateurs around the world, but it took a few more decades for researchers to start utilising formal scientific techniques to advance their research (Chowdhury, Fuller, et al., 2021; Satterfield et al., 2020). Here we summarise the development of methods of studying butterfly migration, based largely on the English-language literature, with some inputs from key non-English-language studies, to reveal how research has developed, starting with the first record of a butterfly migrant, the discovery of overwintering sites, then the various methods used to track individuals and ascertain navigation, and finally the recent development of genetic tools and analyses.

While most studies on butterfly migration are on mass movement, increasingly sophisticated methods have become available to study different aspects of butterfly migration (Figure 1). The first major work on butterfly migration was by C. B. Williams, who summarised previous records and observations up to 1930 and listed 217 migratory butterflies from around the world (Williams, 1930), of which 64 were from India and Sri Lanka (Williams, 1927, 1938, 1939a), some from the United State, Guyana, and Mexico (Williams, 1939b), and the rest from Europe, Asia and Australia (Williams et al., 1942; Williams, 1939a, 1957). Torben B. Larsen described 137 migratory butterflies from tropical Africa and Asia in a series of works published between 1975 and 2005 (Larsen et al., 2005; Larsen,1975,1977,1982,1984,1986,1987,1988a,1988b, 1992a, 1992b, 1992c, 1995, 2004). Major early works on the migratory butterflies of South America were published by William Beebe, who described migration in 68 species (Beebe, 1949a, 1949b, 1950a, 1950b, 1951). Most of these early studies diagnosed migration based on visual observations of directional movements.

3.1.1 | Tracking migratory butterflies

Tracking the migratory movements of insects is challenging but is becoming more efficient and effective. The direction of migration can be established using simple observations and/or mark-recapture. Levin et al. (1971) used only the angle of arrival at, and departure from, a point to define the flight direction of bees and butterflies. Measuring the vanishing angle is widely used to establish flight directions (i.e., the cardinal direction of the released specimen when it disappears from view) (Srygley, 2001; Srygley et al., 2006). Brussard and Ehrlich (1970) and Baker (1978) used different two-dimensional techniques to track butterfly movements, while Zalucki et al. (1980) used theodolites to identify the direction of flight in three-dimensions, although the work was limited to only 20–25 m. Nowadays, radio-tracking (Knight et al., 2019; Patterson et al., 2008), harmonic radar (Cant et al., 2005; Ovaskainen et al., 2008), and even spatial population dynamics models (Flockhart et al., 2015; Hanski & Thomas, 1994) have been used to track, record, analyse or infer movement paths. Nearly all these techniques are limited to describing short-range movement behaviours.

We examined the following types of studies on butterfly migration: mark-release-recapture, radar studies, interception traps, natural markers, isotopic analyses, and flight chambers.

Mark–release–recapture

Mark–release–recapture procedures can identify the direction and distance a butterfly has moved but they are labour-intensive, and recapture rates are typically very low. For monarch butterflies, hundreds of thousands of adults have been tagged in the summer breeding range in the last five decades, but only a few hundreds to thousands then recovered from overwintering sites in Mexico (Monarch Watch Organization, University of Kansas, https://www.monarchwatch.org/). Even so, this work has established the general direction of migratory flights, the connection between summer and wintering sites, and provided an estimate of population size and migration mortality (Taylor et al., 2020). Fletcher (1936) first described a tagging process for butterflies: *A small patch on the upper surface of the right forewing is rubbed clear of scales and a small label, written in Indian ink on tracing paper, is attached to it with Canada balsam; the adhesive is allowed to harden and the butterfly then released*. This process was very time-consuming and only achievable when sample sizes were small. Urquhart later described an improved procedure to mark migratory butterflies (Urquhart, 1941, 1960; Urquhart & Urquhart, 1978). Urquhart (1941) adopted the method by punching a small hole through the right forewing near the base of the latter and immediately behind the stout radial vein, which is still widely used around the world to track butterfly migration. For example, Kanazawa et al. (2015) described the migration of Chestnut Tiger butterfly (*Parantica sita niphonica*) from Japan to Hong Kong using a mark-release-recapture process.

Radar studies

Migrating insects can fly at high altitudes, up to 2000 or 3000 m above the ground (Chapman & Drake, 2019; Gatehouse, 1997; Mikkola, 2003); however, most migration is below 1500 m (Drake & Reynolds, 2012). Stefanescu et al. (2013) showed that painted lady and other migrant Lepidoptera can take advantage of favourable winds and fly from the ground to altitudes over 1000 m; however, many butterfly migrants travel close to the ground where their airspeeds are higher than the wind speed, allowing them to make progress in a seasonally appropriate direction even when there is a headwind (Srygley & Dudley, 2007).

Identification of insects flying at high altitudes based on radar echoes started in 1949 (Crawford, 1949), and the detection of a massive locust swarm followed in 1954 (Rainey, 1955); nevertheless, it took more than a decade to deploy radar specifically to observe locusts. At the end of the 1960s, radar was deployed

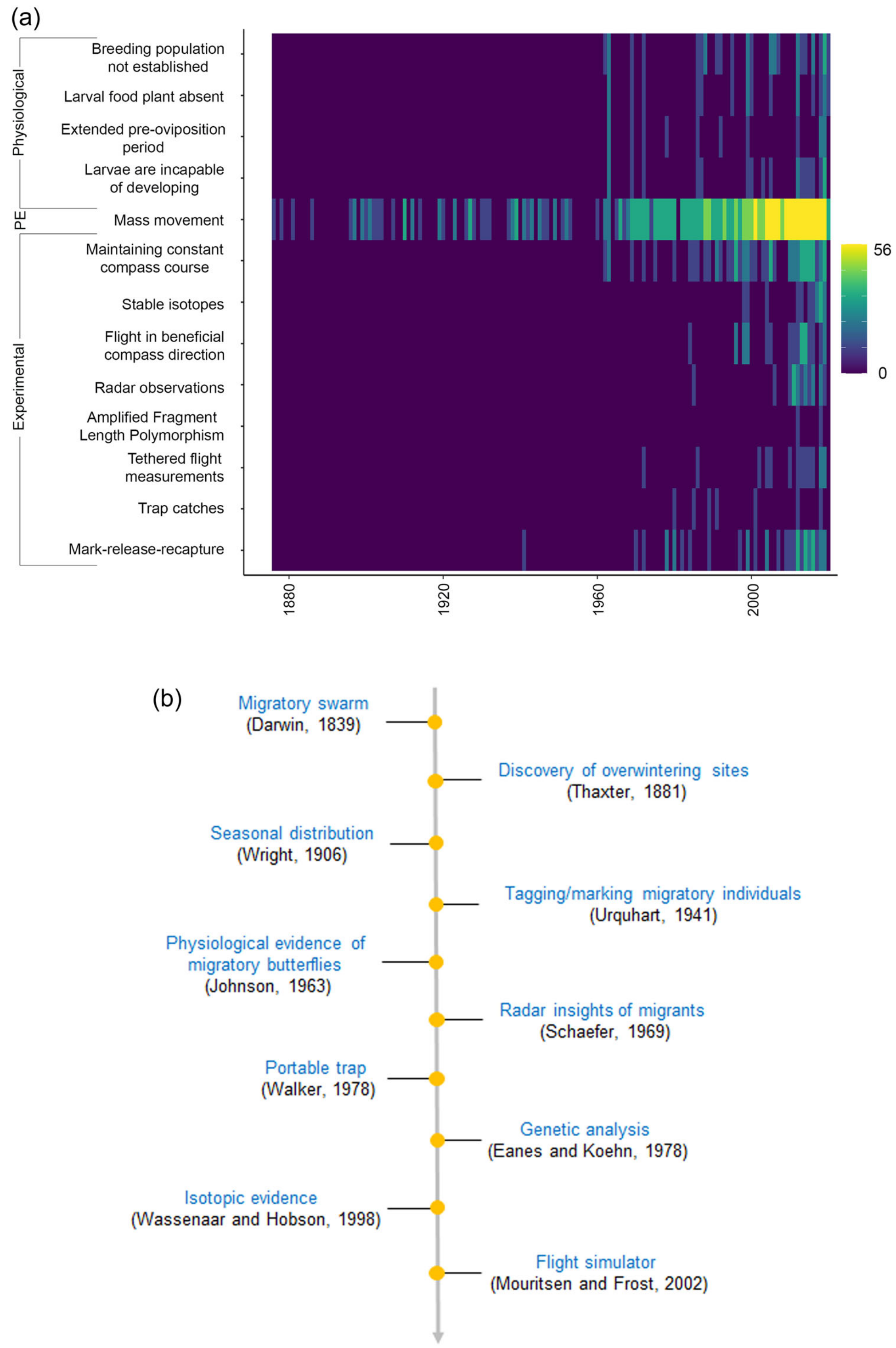

FIGURE 1 (a) Chronological progression of different methodological approaches to studying butterfly migration (PE = population evidence), where the colour bar is representing the number of studies. (b) Chronological development of key methods to diagnose migration in butterflies, where methodological advances are shown in 'blue', and an example reference is given for each.

to observe insect movements in Africa and over the next few decades there was a surge of radar-derived information, mainly on night-flying insects including locusts and moths (Chapman & Drake, 2019; Haskell, 1970; Richter et al., 1973; Schaefer, 1969; Vaughn, 1985). It still took several years to establish migration histories for individual butterfly species (Chapman & Drake, 2019; Stefanescu et al., 2013). With the help of radar and citizen-science data, we now know that high-altitude migration is common for painted lady butterflies in the United Kingdom (Chapman et al., 2010). About seven million painted lady butterflies migrated from southern Europe to the United Kingdom during spring 2009, and 14 million returned southward during fall, when they completed a 15,000-km annual migration requiring six generations (Chapman et al., 2010; Satterfield et al., 2020; Stefanescu et al., 2013). Yet, most radar investigations of insect migration have been directed at species other than butterflies.

Interception traps

During the mid-1970s, Walker successfully established malaise traps as linear barriers in the Florida Peninsula (United States) to observe the movement of migratory butterflies. He described the northward and southward movements of 10 butterfly species and showed that malaise traps can continuously and effectively monitor insect migration within the boundary layer (Walker, 1978). The original traps were made of polyester which could not withstand strong winds and required frequent repair and replacement; a hardwearing-cloth trap overcame these problems. Traps could capture roughly 70% of passing migratory individuals (Walker, 1985a). In the following years, Walker further developed the traps and elucidated the full seasonal flight patterns of these migratory butterflies (Walker, 1985b, 1991, 2001; Walker & Lenczewski, 1989).

Natural markers

Natural markers can be used to ascertain the natal origins of aggregated and moving migrants. For example, Malcolm et al. (1989) used cardenolide fingerprints. Monarch butterfly larvae ingest cardenolides from their hostplant—milkweeds, which is a toxic group of chemicals. Many species of North American milkweeds possess different proportions of these toxins, which remain intact in adult individuals (Freedman, Choquette, et al., 2021; Tan et al., 2019). By extracting these from adult butterflies and visualising them on a thin layer chromatography plate, they determined the 'cardiac glycoside fingerprint'. Adults from different regions ingested different milkweed species, and had unique cardiac glycoside fingerprints. About 90% of monarchs in Mexico had developed on *Asclepias syriaca*—once the most abundant milkweed host in the midwestern US (Malcolm et al., 1989). One limitation of this approach is that some hostplant species contain a similar range of cardiac glycosides and some have none (Brower, 1995; Freedman, Choquette, et al., 2021; Malcolm et al., 1989; Tan et al., 2019).

When insects visit flowers, pollen may become attached to their bodies and it too can be used to track long-distance insect migrations (Hendrix et al., 1987; Mikkola, 1971). Suchan et al. (2019) collected 47 butterfly samples and meta-barcoded the transferred pollen to understand the migration of the painted lady. There was pollen from 157 species of plants from 23 orders, most of which are insect pollinated. Most of these plant species were of African-Arabian origin (73%) and 19% were endemic to that region, strongly suggesting that the butterflies migrate northward into southern Europe from Africa in the spring (Suchan et al., 2019).

Isotopic analyses

The stable isotopes of organic tissues are related to the site where an individual develops, which can be used to infer the most likely natal origin of migratory butterflies (Flockhart et al., 2015; Hobson et al., 2021; Reich et al., 2021; Stefanescu et al., 2016; Talavera et al., 2018; Wassenaar & Hobson, 1998). For example, Wassenaar and Hobson (1998) confirmed the geographic natal origins and established wintering roost sites of monarchs from different regions by sampling and measuring the isotopic elemental composition (stable hydrogen (dD) and carbon (d13C) isotope ratios) of wintering monarchs in Mexico. They compared 597 overwintering monarchs from 13 roosting sites and measured background isotope ratios in the natal sites across their breeding range over a single migration cycle. This revealed that all the monarchs originated from the Midwest United States, although two colonies showed a more northerly origin (Wassenaar & Hobson, 1998). Flockhart et al. (2013, 2015) subsequently used the technique to study the population dynamics and movement of monarchs in greater detail. Recently, Talavera et al. (2018) discovered the migration of *Vanessa cardui*, from Africa to Europe, by analysing isotope values (d2H); Reich et al. (2021) showed how Strontium isotopes ($^{87}Sr/^{86}Sr$) can be used to study migration and dispersal.

Flight chambers

Early designs of tethered flight systems started in the 1950s, but it took many years for the procedures to be refined sufficiently for accurate interpretation (Kennedy & Booth, 1963, 1964; Kennedy & Ludlow, 1974; Kennedy, 1985; Krogh & Weis-Fogh, 1952). Flight chambers eventually revealed several important features of migratory behaviour (Kennedy, 1958, 1985), paving the way for detailed studies on the duration and orientation of migration flights (Mouritsen & Frost, 2002; Mouritsen et al., 2013; Reppert et al., 2004). Tethered flight provides an indication of the flight propensity of the migrants making it possible to study the migratory motivation of insects in the laboratory (Minter et al., 2018; Mouritsen, 2018) in relation to the environmental conditions experienced during development. Flight simulators were a key innovation as they have allowed for experiments investigating preferred headings and response to navigational markers and cues.

3.1.2 | Physiological evidence of migratory individuals

Cecil G. Johnson studied differences in life history traits between migratory and non-migratory butterflies, showing that (i) migratory females start their flight before ovarian development, (ii) migrants are sexually immature in some cases, (iii) migratory individuals usually gain weight as they fuel up for the long journey, and (iv) they have longer forewings than non-migrant individuals (Johnson, 1963, 1966, 1969;

Stefanescu et al., 2021; Wiklund & Friberg, 2022). This work suggested that distinctive physiological and neurophysiological factors are associated with migration, and that ovarian development can be initiated, prolonged, or suppressed depending on the environmental conditions. Recently, Stefanescu et al. (2021) showed that the painted lady fulfils the oogenesis–flight syndrome, whereby the prereproductive period is shorter during the migration period, the mating frequency is highly correlated with the host plant abundance, and mated females can locate potential breeding areas. Additionally, Dudley and Srygley (1994) showed that the airspeeds of butterflies can be predicted from morphological measurements under natural conditions.

3.1.3 | Genetic analysis

Genetic techniques to study migration appeared in the mid-1970s, when Eanes and Koehn (1978) collected monarchs from the United States and Canada and used electrophoretic alleles at six enzyme-loci as genetic markers, and Wright's *F*-statistics to analyse the genetic structure of the population. They found significant allele frequency differences between migratory and nonmigratory individuals (Eanes & Koehn, 1978). In subsequent decades there was rapid improvement in the use of genetic tools to uncover patterns of migratory connectivity (Dingle, 2014; Freedman, de Roode, et al., 2021; Sauman et al., 2005; Xiafang, 2017; Zhan et al., 2014; Zhu et al., 2008). Information about expressed sequence tag resources (Zhu et al., 2008) and the monarch genome (Zhan et al., 2011) has opened up the study of the genetic basis and evolutionary history of migration in monarchs, using a variety of genetic markers including microsatellites (Lyons et al., 2012; Pierce et al., 2014, 2015), and genome-wide nucleotide polymorphism (Zhan et al., 2014). Using amplified fragment length polymorphism (AFLP), Brattström, Åkesson, et al. (2010) attempted to determine the specific migratory routes of red admiral (*Vanessa atalanta*) in Europe. While there were significant differences between study sites, there was no clear pattern in orientation (Brattström et al., 2008; Brattström, Åkesson, et al., 2010; Brattström, Bensch, et al., 2010). In 2011, MonarchBase (http://monarchbase.umassmed.edu) was released to make the genome widely available (Zhan et al., 2011). Sequencing 101 *Danaus* genomes around the world, Zhan et al. (2014) concluded that both *D. plexippus* and southern monarch (*D. erippus*) have a common migratory ancestor. In another study, by analysing whole genome sequences, García-Berro et al. (2022) showed that migratory butterflies have significant higher levels of genome-wide heterozygosity than the nonmigrants.

3.1.4 | Navigation

Migratory butterflies appear to use either a compass alone, or a map and compass (Dingle, 2014). Several species of birds (Chernetsov et al., 2008; Perdeck, 1958; Thorup et al., 2007), the eastern newt (*Notophthalmus viridescens*) (Phillips et al., 1995), the loggerhead sea turtle (*Caretta caretta*) (Putman et al., 2011), and the spiny lobster (*Panulirus argus*) (Boles & Lohmann, 2003) show true navigation; migrating individuals know where they are heading and can compare their current geographic location to the destination (Gould & Gould, 2012; Mouritsen & Frost, 2002). Other migrants seem to use a vector navigation strategy (Mouritsen et al., 2013), where they do not possess a map sense but orient in an inherited direction using just a compass system and a clock or calendar (Gwinner & Wiltschko, 1978; Munro et al., 1993). A map sense indicates the relative position of the destination from a current location, whereas a compass sense enables migrants to travel in a particular direction (Guerra & Reppert, 2015).

It has been suggested that monarchs use both vector navigation (Calvert, 2001) and true navigation (Rogg et al., 1999) to find their overwintering sites. However, whether migrant monarchs possess a true map sense is debated (Mouritsen et al., 2013; Oberhauser et al., 2013). Using over five decades of field data, Mouritsen et al. (2013) suggested that monarch butterflies use a vector-navigation strategy (but see Oberhauser et al., 2013). Among diurnal migrants (e.g., butterflies), a sun compass involving skylight cues plays a key role in orientation. Here, individuals use cues such as the sun's azimuthal position and possibly daylight polarisation patterns to orient, as seen in the painted lady (Merlin et al., 2012; Nesbit et al., 2009; Reppert et al., 2010; Stalleicken et al., 2005). Migrating monarchs use circadian clocks to adjust their directional flight throughout the day (Guilford & Taylor, 2014; Reppert et al., 2010; but see Freedman et al., 2017; Ning et al., 2018). Some migrants use a magnetic compass (inclination angle, polarity, and intensity) to orient (Dreyer et al., 2018; Lohmann, Putman, et al., 2012; Lohmann, 2012); although there is a debate whether southward-migrating monarchs use a magnetic compass (Guerra & Reppert, 2015; Reppert et al., 2010).

3.2 | Trends in migration literature

Even though the importance of studying butterfly migration was recognised very early (Brower, 1995), most research has restricted to a few species and specific regions around the world (Chowdhury, Fuller, et al., 2021).

3.2.1 | Regional pattern

We obtained marked variation in the number of studies per continent; most English-language studies on butterfly migration (total English-language studies = 581) were from temperate or cooler regions, or from the Northern Hemisphere (especially the United States), with far fewer from the sub/tropics, or the Southern Hemisphere (Figure 2). Most North American studies were from the United States and most European studies were from the UK. However, by searching in four Asian languages and Spanish, we found another 344 relevant studies, mostly on species in North America (162 Spanish-language studies), but also in South America (44 in Spanish) and Europe (37 in Spanish), and Asia (98 studies in total: 59 in Japanese, 28 in Simplified Chinese, 11 in Traditional Chinese, and 1 in Spanish, Figure 2). This highlights the importance of including non-English studies in literature reviews. Overall, most studies on butterfly migration were from North America (548 studies, >50%), and only 4% (45 studies) were from Africa.

3.2.2 | Taxonomic pattern

The available studies are clearly biased towards a few species; the monarch (62% of the 926 studies), painted lady (9.6%), and red admiral (5.8%) (Figure 3). There were only six species (monarch, painted lady, red admiral, common emigrant (*Catopsilia pomona*), lesser wanderer (*Danaus chrysippus*) and common crow (*Euploea core*) with more than 30 studies, and 41 species with >10 papers (all on either pierids or nymphalids except for pea blue (*Lampides boeticus*, Lycaenidae), and long-tailed skipper (*Urbanus proteus*, Hesperiidae). Nearly 50% (271 species) of our recorded migratory butterfly species have not been the subject of a thorough single study but are just mentioned once in a paper. On the other hand, the monarch accounted for 62% of the studies (Figure 3). Being a range-expanding species that has spread well beyond its native range, the monarch butterfly figures prominently wherever it is present.

Studies on the monarch dominate not only in North America (nearly 85% of all studies; Figure 2), but even in areas where monarchs do not migrate (e.g., Spain). Elsewhere in the world, studies were biased towards other species. For example, painted lady and red admiral dominated Europe, lesser wanderer and monarch dominated Africa and Australia, and chestnut tiger (*Parantica sita*), and common crow (*Euploea core*) in Asia (see Supporting Information Section: Table S1 for more details).

3.2.3 | Publication trends

The number of English-language peer-reviewed papers on butterfly migration did not change over time (butterfly biology in general and those specifically on butterfly migration; $\chi^2 = 0.14$; $df = 1$; $p = 0.7061$; Generalised Linear Model with a Poisson distribution; Figure 4a).

The proportion of papers on migratory butterflies, compared to all papers on butterflies, ranged from 1% to 3%. While the number of papers on monarchs has increased significantly over the past 30 years ($\chi^2 = 37.223$; $df = 1$; $p < 0.0001$; Generalised Linear Model with a Poisson distribution; Figure 4b), the number of papers on nonmonarch butterfly species has not noticeably risen. In the last few decades, the North American migratory monarch

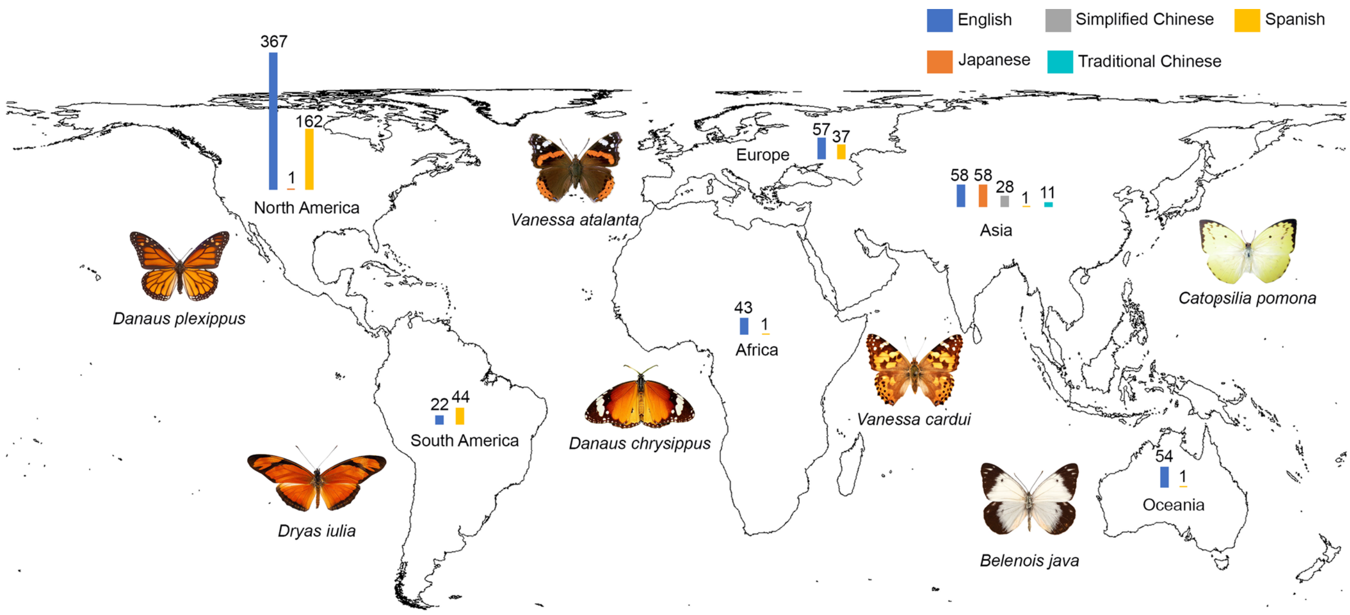

FIGURE 2 The number of butterfly migration studies by language from each continent with some of the most popular regional migratory butterflies (*Danaus plexippus* for North America, *Dryas iulia* for South America, *Vanessa atalanta* for Europe, *Danaus chrysippus* for Africa, *Vanessa cardui* for Europe and Africa, *Belenois java* for Australia, and *Catopsilia Pomona* for Southeast Asia; CC-BY license, see the Supporting Information: Table S2 for photographer details).

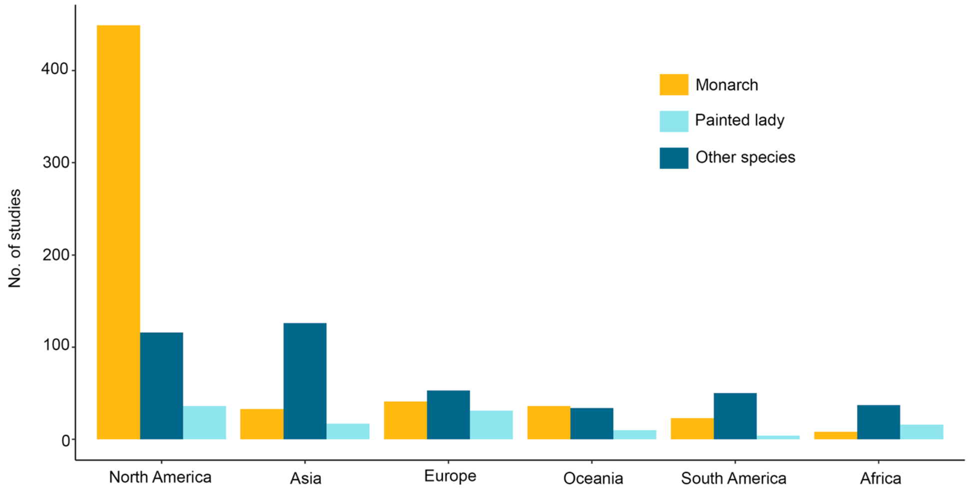

FIGURE 3 The number of butterfly migration studies in each continent for three different butterfly groups (monarch (1 species: orange), painted lady (1 species: skyblue) and all the other butterfly migrants (566 species: dark blue)).

population size has declined by >80%, starting in the 1990s (Semmens et al., 2016; Stenoien et al., 2018; Zylstra et al., 2021); this decline of an iconic species has probably prompted more research.

4 | DISCUSSION AND FUTURE DIRECTIONS

We show that most butterfly migration studies are restricted to certain regions, and that only a few species have been studied in detail (monarch, painted lady and red admiral). There was no increase in the number of publications on butterfly migration over the years, although research on the Monarch has accelerated.

We also showed the potential importance of non-English-language studies to better understand butterfly migration globally. Of course, there are thousands of languages globally, and here, we considered only five non-English languages. Future studies could consider a broader set of languages widely used for scientific studies (e.g., French, German, Italian, Polish, Portuguese, Russian, and other non-European languages). Language restrictions might have impacted our findings. For example, if our search was expanded into German, French, and Portuguese, we might have located more studies from Europe, Africa, and South America (Chowdhury, Gonzalez, et al. 2022). However, given we checked two regional journals (Atalanta and Phegea; regularly publishing studies in German and Dutch), we think that we have already captured many German and Dutch studies. Similarly, although we used rigorous literature search approaches to make the review as comprehensive as possible, it is inevitable that we missed relevant papers with our keyword driven search. There is, however, no reason to believe that this would introduce a systematic bias that would affect our overall conclusion.

Charismatic species, especially if also threatened, often attract a disproportionate amount of research, and research using the latest techniques is often concentrated in advanced-economy countries. This sort of 'research bias' is quite common in biology (Di Marco et al., 2017), but can hamper our understanding of species ecology and conservation (Holman et al., 2015; Jennions et al., 2013; Nuñez et al., 2021; Pyšek et al., 2008). We have identified both taxonomic and geographic biases in published studies on butterfly migration in that most studies: (i) cover North America and Europe, with very few from the tropics or subtropics, and (ii) focus on a handful of species. To reduce bias, researchers could conduct more studies on migration in poorly studied species and regions to identify the true prevalence of migration in butterflies. For example, a recent study has shown that unlike migratory birds, seasonal movements between suitable and unsuitable habitats in migratory butterflies appears most prominent in the tropics (Chowdhury, Zalucki, et al., 2021). Here, we identify a lack of studies in the tropics, suggesting that there is an underrepresentation of tropical butterflies in the migration literature.

A recent review listed several 100 butterfly migrants and the rate of discovery of new migratory species reveals there might be thousands more (Chowdhury, Fuller, et al., 2021). Nevertheless, it is worth noting that there can be both migratory and non-migratory populations and individuals within a species (Slager & Malcolm, 2015; Zanden et al., 2018; Zhan et al., 2014). To understand seasonal movements, it is essential to monitor across a species' full geographic distribution, a task for which active citizen science participation can be highly beneficial (Chowdhury, Aich, et al., 2022; Jarić et al., 2020; Juhász et al., 2020; Mason et al., 2018; Soroye et al., 2018; Chowdhury, Braby, et al. 2021, Chowdhury, Alam, et al. 2021). For example, both amateur and professional

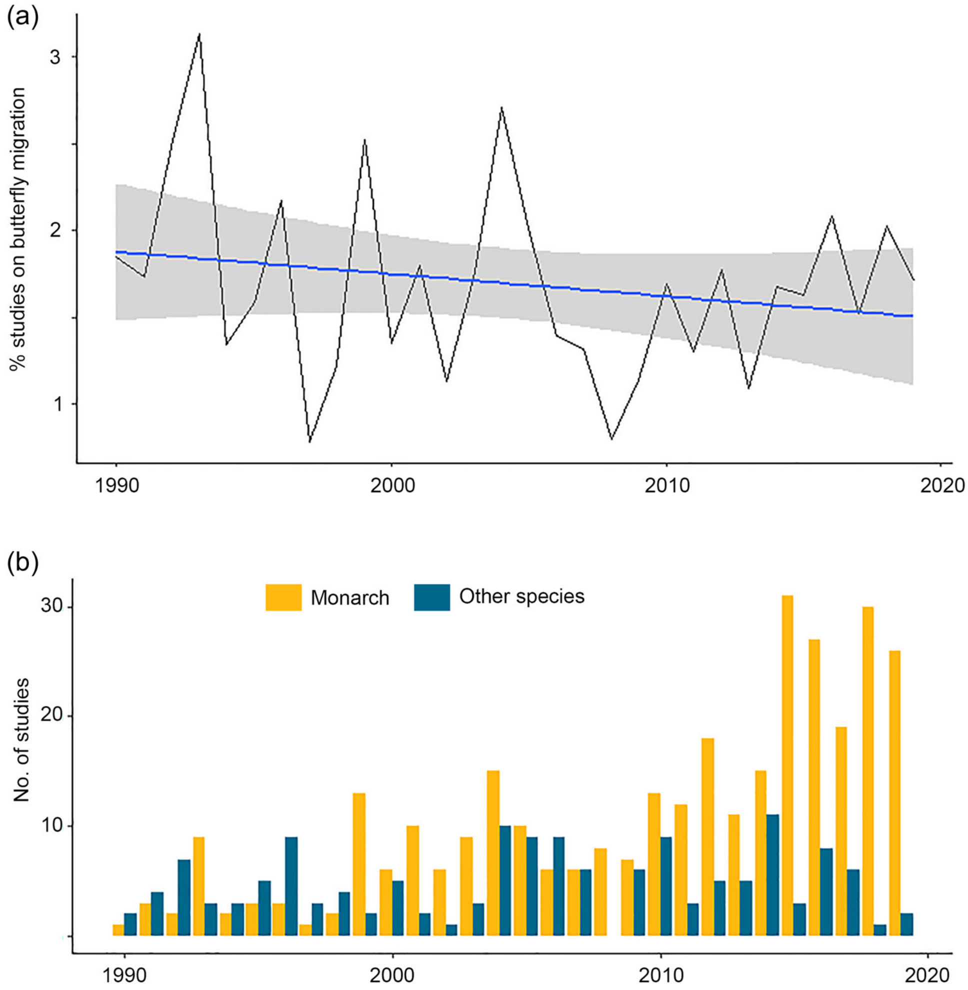

FIGURE 4 Temporal trends in peer-reviewed English-language papers on butterfly migration. (a) Yearly percentages of papers on butterfly migration to all butterfly papers. (b) The number of papers on monarchs and other migratory butterflies.

ornithologists widely use eBird, which has transformed the availability of bird data globally (Amano, Lamming, et al., 2016; Bonney et al., 2009; Sullivan et al., 2009). So how can we engage citizen science in the tropics? Nowadays, iNaturalist, a citizen science project, is increasingly popular both among professional and amateur naturalists (Callaghan et al., 2020; Chowdhury, Aich, et al., 2022; Schuttler et al., 2018). Citizen science tools, such as this, can widen the coverage of space and species in data collection; and collating and analysing the resulting data will help to identify which species are, in fact, migratory. For this reason, maximising funding and shifting research effort towards tropical regions could enable broader discovery of migration in butterflies. In many countries, funding is more readily available for insects of economic significance, such as pests and pollinators. Future studies could examine the disparity in funding for species at elevated extinction risk.

Future research could focus on identifying, tracking, and understanding the migratory trajectories and behaviours of butterfly migrants. Time-honoured techniques such as mark–release–recapture can be used to calculate travel distances, and whether the distance and overall direction of movement is associated with changes in seasonal resources. Isotopic analysis can be used to identify the origin of individuals (Wassenaar & Hobson, 1998; Zanden et al., 2018); flight chamber experiments can be used to record flight duration of butterflies and differentiate migrants and nonmigrants and even differences in orientation (Minter et al., 2018; Mouritsen & Frost, 2002; Reppert & de Roode, 2018; Reppert et al., 2004). Radars can be used in hotspot regions to determine the seasonal flow of movements (Chapman et al., 2010, 2015; Hu et al., 2016; Stefanescu et al., 2021); female butterflies can be collected and dissected to check the status of their ovarian development (Johnson, 1963). Genomic resources such as EST-based microarray analyses, transcriptome libraries and single-nucleotide polymorphism (SNP) marker sets can be used to determine migration routes (Brattström, Åkesson, et al., 2010; Brattström, Bensch, et al., 2010; Liedvogel et al., 2011); and ecological niche and movement modelling tools can uncover spatial patterns of seasonal occurrence and habitat use in migratory butterflies (Grant et al., 2018; Menchetti et al., 2019; Zalucki et al., 2016; Chowdhury, Braby, et al., 2021; Chowdhury, Zalucki, et al., 2021). Further, application of interdisciplinary tool in movement ecology can advance our understanding of butterfly migrants (Jia et al., 2022). In hoverflies, Jia et al. (2022) described the migration of *Episyrphus balteatus* using long-term trapping records, trajectory analysis and intrinsic markers.

During migratory flights, monarch butterflies adjust their flight altitude and vectors by flapping and gliding (Gibo, 1981; Gibo & Pallett, 1979), but we do not know if this occurs in other migratory butterflies. Several studies have shown that some long-distance migratory butterflies use air currents (Chapman et al., 2010; Hu et al., 2016, 2021; Srygley & Dudley, 2007; Srygley, 2001; Stefanescu et al., 2007) but little is known about the cost of migration, metabolism of flight fuels, or how migratory butterflies counter overheating. Moreover, there are some phenotypic differences, especially in traits linked to migration, between eastern and western monarchs, despite genetic studies indicating these populations are closely related (Freedman, de Roode, et al., 2021). Future studies could assess the reasons for these differences between eastern and western monarchs. Similarly, migratory butterflies can be tracked using natural markers such as cardenolides (Brower, 1995; Malcolm et al., 1989). It would be interesting to extend this method to other Danainae butterflies that feed on Apocynaceae.

While undertaking migratory flights, migrants often cross multiple regions, which makes them vulnerable to anthropogenic threats and complicates their conservation (Juhász et al., 2020; Malcolm, 2018; Martin et al., 2007; Reynolds et al., 2017; Runge et al., 2014), Chowdhury, Zalucki, et al. (2021), Chowdhury, Braby, et al. (2021). Due to extensive anthropogenic pressure and human-induced climate change, insects, including butterflies, are declining worldwide (Chowdhury, 2023; Chowdhury, Jennions, et al., 2022; Fox, 2013; Habel et al., 2019; Hallmann et al., 2017; Wagner, 2020; Wagner et al., 2021; WallisDeVries et al., 2011;but see Sparks et al., 2005, 2007). It is notable that more than half of migratory birds across all major flyways have declined in the last 30 years, suggesting that, in general, migratory species are at greater risk than sedentary species (Kirby et al., 2008). The few available time series analyses have shown some migratory butterfly populations to be stable, while others are declining. For example, while the North American migratory monarch population has dramatically declined in the last few decades (Stenoien et al., 2016; Zylstra et al., 2021), populations of painted lady, red admiral and clouded yellow (*Colias croceus*) have remained relatively stable (Fox et al., 2015; Hu et al., 2021). However, it should be noted that time-series data are rare for most migratory butterflies, and unavailable from most parts of the world.

According to Goal-2 of the post-2020 biodiversity framework, area-based conservation measures and ecosystem-based approaches ('nature-based solutions') are crucial to halt ongoing biodiversity decline (Convention on Biological Diversity, 2020). Protected areas and other conserved areas have, and will continue to be, a significant global tool to conserve threatened and endemic biodiversity (Chowdhury, Jennions, et al., 2022; Watson et al., 2014). Only 17% of migratory butterfly species are adequately protected by protected areas globally (Chowdhury, Cardillo et al., 2022). Future studies could identify new protected areas using spatial prioritisation approaches to adequately protect the habitats of migratory butterflies and to meet the post-2020 global biodiversity framework targets (Chowdhury, Jennions, et al., 2022). Future studies could also investigate whether protected areas better help migratory butterfly populations to persist over time. Here, incorporating butterflies in the monitoring plan of protected areas, creating baseline databases, and using them for future assessments will help us to assess the effectiveness of protected areas.

To implement effective migratory species conservation, holistic analyses across the entire distribution are needed, since migrants require a chain of intact habitat (Flockhart et al., 2015; Gao et al., 2020; Runge et al., 2014). Ultimately, knowledge of seasonal movements, locations of stopover sites, protected area coverage, and improved knowledge of the basic biology of migration in butterflies is needed to drive successful conservation planning (Chowdhury, Jennions, et al., 2022). Migratory butterflies perform a broad range of functions in ecosystems including transferring biomass, transporting nutrients, and influencing resource fluxes and food web structure (Bowlin et al., 2010; Dingle, 2014; López-Hoffman et al., 2017; Satterfield et al., 2020). If we are to conserve them effectively, migratory butterflies need far more attention than they currently receive.

AUTHOR CONTRIBUTIONS

Shawan Chowdhury: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; validation; visualization; writing – original draft; writing – review editing. **Myron P. Zalucki**: Funding acquisition; methodology; project administration; resources; supervision; validation; visualization; writing – original draft; writing – review editing. **Tatsuya Amano**: Formal analysis; methodology; validation; visualization; writing – original draft; writing – review editing. **Tomas J. Poch**: Data curation; visualization; writing – review editing. **Mu-Ming Lin**: Data curation; visualization; writing – review editing. **Atsushi Ohwaki**: Data curation; visualization; writing – review editing. **Da-Li Lin**: Data curation; visualization; writing – review editing. **Li Yang**: Data curation; visualization; writing – review editing. **Sei-Woong Choi**: Data curation; visualization; writing – review editing. **Michael D. Jennions**: methodology; resources; validation; visualization; writing – original draft; writing – review editing. **Richard A. Fuller**: Funding acquisition; methodology; project administration; supervision; validation; visualization; writing – original draft; writing – review editing.

ACKNOWLEDGEMENTS

The corresponding author is thankful to the Australian Government, the University of Queensland, and the Centre for Biodiversity and Conservation Science for providing an International Research Training Program Fellowship. SC gratefully acknowledge the support of the German Centre for Integrative Biodiversity Research (iDiv) and the sMon project funded by the German Research Foundation.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Chowdhury, S., Zalucki, M.P., Amano, T., Poch, T.J., Lin, M.-M., Ohwaki, A., et al. (2022) Trends and progress in studying butterfly migration. *Integrative Conservation*, 1, 8–24. https://doi.org/10.1002/inc3.13